Journal of Range Management

TABLE OF CONTENTS: VOL. 55, NO. 2, March 2002

FEATURE ARTICLE

- 106 Perspectives on water flow and the interpretation of FLIR images** by S.L. Larson, L.L. Larson, and P.A. Larson

Economics

- 112 Cull cow management and its implications for cow-calf profitability** by Randall D. Little, Allen R. Williams, R. Curt Lacy, and Charlie S. Forrest
- 117 Elk management strategies and profitability of beef cattle ranches** by Wendy L. F. Torstenson, Michael W. Tess, and James E. Knight

Grazing Management

- 127 Evaluating the ecological relevance of habitat maps for wild herbivores** by Marc E. Stalmans, Ed T.F. Witkowski, and Kevin Balkwill
- 135 Intensive-early stocking for yearling cattle in the Northern Great Plains** by E.E. Grings, R.K. Heitschmidt, R.E. Short, and M.R. Haferkamp

Plant/Animal

- 139 Nutritional value and intake of prickly pear by goats** by Zeno McMillan, Cody B. Scott, Charles A. Taylor, Jr., and J. Ed Huston
- 144 Day and night grazing by cattle in the Sahel** by Augustine A. Ayantunde, Salvador Fernández-Rivera, Pierre H. Hiernaux, Herman Van Keulen, and Henk M.J. Udo

Plant Ecology

- 150 Bud viability in perennial grasses: Water stress and defoliation effects** by Andrea C. Flemmer, Carlos A. Busso, and Osvaldo A. Fernández
- 164 Northern dry mixed prairie responses to summer wildlife and drought** by Catherine Erichsen-Arychuk, Edward W. Bork, and Arthur W. Bailey
- 171 Vegetation responses following wildfire on grazed and ungrazed sagebrush semi-desert** by Neil E. West and Terence P. Yorks

The Trail Boss

Published bimonthly—January, March, May, July, September, November

Copyright 2002 by the Society for Range Management

INDIVIDUAL SUBSCRIPTION is by membership in the Society for Range Management.

LIBRARY or other INSTITUTIONAL SUBSCRIPTIONS on a calendar year basis are \$95.00 for the United States postpaid and \$112.00 for other countries, postpaid. Payment from outside the United States should be remitted in US dollars by international money order or draft on a New York bank.

BUSINESS CORRESPONDENCE, concerning subscriptions, advertising, reprints, back issues, and related matters, should be addressed to the Managing Editor, 445 Union Blvd., Suite 230, Lakewood, Colorado 80228.

EDITORIAL CORRESPONDENCE, concerning manuscripts or other editorial matters, should be addressed to the Editor, Gary Frasier, 7820 Stag Hollow Road, Loveland, Colorado 80538. Page proofs should be returned to the Production Editor, 3059A Hwy 92, Hotchkiss, CO 81419-9548.

INSTRUCTIONS FOR AUTHORS appear on the inside back cover of most issues. *THE JOURNAL OF RANGE MANAGEMENT* (ISSN 0022-409X) is published bimonthly for \$56.00 per year by the Society for Range Management, 445 Union Blvd., Ste 230, Lakewood, Colorado 80228. PERIODICALS POSTAGE paid at Denver, Colorado and additional offices.

POSTMASTER: Return entire journal with address change—Address Service Requested to Society for Range Management, 445 Union Blvd., Suite 230, Lakewood, Colorado 80228.

PRINTED IN USA

Editor-in-Chief

SAM ALBRECHT
445 Union Blvd., Ste 230
Lakewood, Colorado 80228
(303) 986-3309
Fax: (303) 986-3892
e-mail address:
sam_albrecht@ix.netcom.com

Editor/Copy Editor

GARY FRASIER/JO FRASIER
7820 Stag Hollow Road
Loveland, Colorado 80538
e-mail address:
gfrasier@lamar.colostate.edu

Production Editor

PATTY RICH
Society for Range Management
3059A Hwy 92
Hotchkiss, Colorado 81419-9548
e-mail address:
prich@starband.net

Book Review Editor

DAVID L. SCARNECCHIA
Dept of Natural Res. Sci.
Washington State University
Pullman, Washington 99164-6410
e-mail address:
scarneda@mail.wsu.edu

Electronic JRM Editor

M. KEITH OWENS
Texas A&M University
Research Center
1619 Garner Field Road
Ulvade, Texas
e-mail address:
m-owens@tamu.edu

Associate Editors

YUGUANG BAI
Dept. Plant Sciences
University of Saskatchewan
51 Campus Drive
Saskatoon, Saskatchewan
S7N 5A8
CANADA

KLAAS BROERSMA
Agriculture and Agri-Food Canada
3015 Ord Rd.
Kamloops, British Columbia
V2B 8A9 CANADA

JOE E. BRUMMER
Mt. Meadows Res. Ctr.
P.O. Box 598
Gunnison, Colorado 81230

DAVID ELDRIDGE
Dept. Land and Water Conservation
School of Geography
University of New South Wales
Sydney, New South Wales
2052 AUSTRALIA

ROBERT GILLEN
USDA-ARS
Southern Plains Range Res. Sta.
2000 18th Street
Woodward, Oklahoma 73801

Plant Physiology

182 Seasonal dynamics of prairie sandreed rizhome development by Patrick E. Reece, Jennifer S. Nixon, Lowell E. Moser, and Steven S. Waller

Reclamation

188 Seed longevity and seeding strategies affect sagebrush revegetation by D. Terrance Booth

Improvements

194 Herbicide residues and perennial grass on establishment perennial pepperweed sites by James A. Young, Charlie D. Clements, and Robert R. Blank

Plant Ecology

197 Drought and grazing: IV. Blue grama and western wheatgrass by E.J. Eneboe, B.F. Sowell, R.K. Heitschmidt, M.G. Karl, and M.R. Haferkamp

Book Reviews

204 Toxic Plants of North America by George E. Burrows and Ronald J. Tyrl; **Africa's Elephant: A Biography** by Martin Meredith; **Millions of Monarchs, Bunches of Beetles: How Bugs Find Strength in Numbers** by Gilbert Waldbauer.

ELAINE E. GRINGS
USDA-ARS
Fort Keogh-LARRL
Route 1, Box 2021
Miles City, Montana 59301

MARSHALL HAFERKAMP
USDA-ARS
Fort Keogh-LARRL
Route 1, Box 2021
Miles City, Montana 59301

ROBERT A. MASTERS
Dow AgroSciences LLC
3618 South 75th Street
Lincoln, Nebraska 68506

MITCHEL McCLARAN
University of Arizona
301 Biological Science East
Tucson, Arizona 85721-0001

ROBERT PEARCE
5028 Highway 6
Bishop, California 93514

MICHAEL H. RALPHS
USDA-ARS
Poisonous Plant Lab
1150 E 1400 N
Logan, Utah 84341-2881

LARRY REDMON
TAREC
P.O. Drawer E
Overton, Texas 74684

NEIL RIMBEY
University of Idaho
16952 S. 10th Ave.
Caldwell, Idaho 83607

CAROLYN HULL SIEG
S.W. Science Complex
2500 South Pine Knoll
Flagstaff, Arizona 86001

STEVE WARREN
Colorado State University
Center for Environmental
Management of Military Land
Dept. of Forestry Sciences
Fort Collins, Colorado 80523

Drought and grazing: IV. Blue grama and western wheatgrass

E.J. ENEBOE, B.F. SOWELL, R.K. HEITSCHMIDT, M.G. KARL, AND M.R. HAFERKAMP

Authors are former graduate student and Associate Professor, Dept. of Animal and Range Sci. Mont. State Univ., Bozeman, Mont. 59715; Supervisory Rangeland Scientist, former Postdoctoral Rangeland Scientist, and Rangeland Scientist USDA-ARS, Fort Keogh Livestock and Range Research Laboratory, 243 Fort Keogh Rd., Miles City, Mont. 59301.

Abstract

An understanding of the impacts of grazing during and following drought on rangeland ecosystems is critical for developing effective drought management strategies. This study was designed to examine the effects of drought and grazing on blue grama [*Bouteloua gracilis* (H.B.K) Lag. ex Griffiths] and western wheatgrass [*Pascopyrum smithii* Rydb. (Love)] tiller growth dynamics. Research was conducted from 1993 to 1996 at the Fort Keogh Livestock and Range Research Laboratory located near Miles City, Mont. An automated rainout shelter was used during 1994 to impose a severe late spring to early fall (May to October) drought on 6 of twelve, 5- x 10-m non-weighing lysimeters. Twice replicated grazing treatments were: 1) grazed both the year of (1994) and the year after (1995) drought; 2) grazed the year of and rested the year after drought; and 3) no grazing either year. Drought had minimal impact on tiller relative growth rates of plants grazed twice, although it reduced ($P \leq 0.01$) rates of axillary tiller emergence for blue grama (79%) and western wheatgrass (91%). Defoliation periodically increased relative growth rates ($P \leq 0.05$) and tiller emergence ($P \leq 0.01$) of both species. Neither drought nor grazing affected tiller densities or tiller replacement rates of either species nor did they affect productivity of blue grama. Drought, however, reduced ($P \leq 0.01$) productivity of western wheatgrass 50% in 1994 whereas grazing reduced productivity ($P \leq 0.01$) by 46% in 1994 and 69% in 1995. Moderate stocking levels (40–50% utilization) during and after drought did not adversely affect the sustainability of these dominant native grasses.

Key Words: *Bouteloua gracilis*, *Pascopyrum smithii*, production, rainout shelter, rest, water potential

The Northern Great Plains support 7 million animal units (AUs) in the U.S. and Canada (USDA 1993, Willms and Jefferson 1993). Campbell (1936) stated that 2 or 3 years out of 10 would be drought years in the Northern Great Plains. Drought and grazing can affect plant productivity and decrease plant longevity (Ludlow 1986). Large portions of plant communities within the Northern Great Plains are dominated by blue grama (*Bouteloua gracilis*,

Resumen

Un entendimiento de los impactos del apacentamiento durante y después de la sequía en los ecosistemas de pastizal es crítico para desarrollar estrategias efectivas de manejo de la sequía. Este estudio se diseñó para examinar los efectos de la sequía y el apacentamiento en la dinámica de crecimiento de los hijuelos de “Blue grama” [*Bouteloua gracilis* (H.B.K) Lag. ex Griffiths] y “Western wheatgrass” [*Pascopyrum smithii* Rydb. (Love)]. La investigación se condujo de 1993 a 1996 en el Laboratorio de Investigación de Ganado y Pastizales Fort Keogh cerca de Miles City, Mont. Durante 1994 se utilizó un protector de lluvia automatizado para aplicar una sequía severa de fines de primavera e inicios de otoño (Mayo a Octubre) en 6 de los 12 lisímetros de 5 x 10 m. Los tratamientos de apacentamiento se repitieron 2 veces y fueron: 1) apacentado en el año de la sequía (1994) y el año siguiente (1995), 2) apacentado el año de la sequía y descansado el año siguiente y 3) sin apacentamiento en ambos años. La sequía tuvo un impacto mínimo en las tasas relativas de crecimiento de los hijuelos de plantas apacentadas doble, aunque redujo ($P \leq 0.01$) las tasas de emergencia de hijuelos auxiliares del “Blue grama” (79%) y “Western wheatgrass” (91%). La defoliación periódica incrementó las tasas relativas de crecimiento ($P \leq 0.05$) y la emergencia de hijuelos ($P < 0.01$) de ambas especies. Ni la sequía ni el apacentamiento afectaron las densidades de hijuelos o las tasas de remplazo de estos en ninguna de las especies, tampoco afectaron la productividad del “Blue grama”. Sin embargo, la sequía redujo la productividad ($P \leq 0.01$) de “Western wheatgrass”, en 50% en 1994, mientras que el apacentamiento redujo la productividad ($P \leq 0.01$) en 46% en 1994 y 69% en 1995. Niveles moderados de carga (40–50% de utilización) durante y después de la sequía no afectan adversamente la sustentabilidad de estos zacates nativos dominantes.

[H.B.K] Lag. ex Griffiths) and western wheatgrass (*Pascopyrum smithii*, Rydb.). It is apparent that these 2 plant species have evolved with the combined effects of drought and herbivory. Therefore, it is important when managing rangelands to know how individual plants persist in the face of these stressors.

Many researchers have examined the role of tillers in plant survival (Richards et al. 1987, Olson and Richards 1988, Bullock et al. 1994, Zhang and Romo 1995), but quantitative studies on the impacts of grazing during and after drought on tiller population dynamics are lacking. It has been hypothesized that grazing during and following drought can suppress recovery rates of individual plants as well as plant communities (Pieper and Heitschmidt

This research was conducted under a cooperative agreement between USDA-ARS and the Montana Agric. Exp. Sta. Mention of a proprietary product does not constitute a guarantee or warranty of the product by USDA, Montana Agric. Exp. Sta., or the authors and does not imply its approval to the exclusion of other products that may also be suitable. USDA-Agricultural Research Service, Northern Plains Area, is an equal opportunity/affirmative action employer and all agency services are available without discrimination.

Manuscript accepted 26 Mar. 01.

1988, Burkhardt 1996). To test this hypothesis, we examined the effects of grazing during and after a growing season drought on xylem water potentials, tiller relative growth rates (RGR), seasonal axillary tiller emergence, annual tiller replacement, tiller densities, and aboveground net primary production (ANPP) of blue grama and western wheatgrass. Heitschmidt et al. (1999) have published effects of drought on soil water, vegetative productivity and plant species composition.

Materials and Methods

Study Area

This study was part of a large rainout shelter project conducted on the USDA, ARS Fort Keogh Livestock and Range Research Laboratory near Miles City, Mont. (46°19'45"N 105°49'45"W). This area is representative of the semi-arid mixed grass prairie of the Northern Great Plains. Native vegetation on the 22,500-ha research station is a grama-needlegrass-wheatgrass (*Bouteloua-Stipa-Agropyron*) mix (Küchler 1964). Long-term annual precipitation averages 34-cm (NOAA 1996) with about 60–70% received during the mid-April through mid-September growing season (Fig 1). Temperatures may exceed 38°C during summer and decrease to –40°C during winter. The average frost-free period is 150 days.

The experiment was conducted from 1993 to 1996 on native rangeland that had not been grazed 2 years prior to the study. Precipitation was 30% (530 mm) above average (NOAA 1996) the year before the study. The study site was located on a gently sloping (4%), clayey range site in high fair range condition. The soils were very deep, well-drained, fine, montmorillonitic, frigid Aridic Ustochrepts. Vegetation at the site was dominated by blue grama (40–45% by weight) and western wheatgrass (30–35% by weight).

Lysimeters and Treatments

Twelve, 5- X 10-m non-weighing lysimeters were arranged perpendicularly to the slope along a 65-m transect in 2 groups of 6 lysimeters with a 5-m area between groups within a grazing enclosure. An automated rainout shelter was constructed to control the amount of precipitation received on 1 of the 2 sets of 6 lysimeters. The 12- X 35-m metal framed "roof" was mounted on 15-cm diameter plastic wheels atop seven, 5-cm wide rails stationed about 75-cm above the soil surface. Rails extended from the top edge

Fig. 1. Monthly precipitation (cm) from January 1993 through December 1996 and long-term (115 yr) average at Miles City, Mont. including the drought treatment in 1994 (NOAA 1996; Heitschmidt et al. 1999).

(i.e., upslope) to 15-m below the bottom edge of the lysimeters. Rails were located directly over lysimeter borders. The shelter was equipped with a moisture sensitive conductance plate that when wetted, activated a small electric motor and its associated drive system, which moved the shelter across the lysimeters.

Following the 1993 pre-treatment baseline year, twice replicated treatments were: 1) grazed during the year of drought and rested the year after, hereafter referred to as G94; 2) grazed both the year of the simulated drought and the year after, hereafter referred to as the G94-95; and 3) rested in all years, hereafter referred to as the ungrazed treatment (UG). The same 3 treatments were repeated in the non-drought set of lysimeters. Lysimeters were grazed intensively with 6 ewes and their twin lambs for a few hours in early June and early July of both 1994 and 1995 to achieve 40–50% utilization. The simulated drought was imposed (1 growing season) from mid-May to early October 1994.

Precipitation, Soil Water, and Xylem Water Potentials

Precipitation was monitored on site using standard rain gauges (Heitschmidt et al. 1999). Soil water was estimated a minimum of once a month from April through October at depths of 15-, 30-, 60-, 90- and 120-cm using a dielectric soil water probe (Heitschmidt et al. 1999).

Xylem water potentials of blue grama and western wheatgrass plants growing in the ungrazed drought and non-drought treatments were estimated on 7 dates between 18 May and 28 July, 1994 and 6 dates between 15 May and 2 August,

1995. Measurements were made at 0430 and 1230 hours on the youngest fully expanded leaves of individual plants using standard pressure chamber techniques (Scholander et al. 1965). Sample plants were randomly selected along a transect within each lysimeter. Sample size per species/sample date/sample time/lysimeter was 1 in 1994 and 2 in 1995.

Tiller and Production Measurements

Six permanent 14- X 18-cm quadrats per lysimeter were randomly established within mixed blue grama and western wheatgrass communities. Quadrat locations were restricted to areas not previously sampled, and at least 50-cm inside the plot edge. Colored wire rings were used to permanently identify 10 study tillers per quadrat, 5 each of blue grama and western wheatgrass. The same quadrats were used for the duration of the research. If a marked tiller produced axillary tillers at anytime during the growing season, the axillary tillers were marked with a different color to distinguish them from primary tillers. Different tillers were marked in the same manner in 1995.

From an initial population of 360 tillers per species, repeated, season-long measurements ($n = 17$ in 1994; $n = 14$ in 1995) were taken on 270 blue grama and 329 western wheatgrass tillers in 1994 and 320 blue grama and 341 western wheatgrass tillers in 1995. Differences between marked and measured tillers were due to lost markers or excluding data from tillers which were not grazed twice. Tiller measurements began in mid-May and continued weekly through August with additional measurements for quantification of any autumn

growth. Information gathered on an individual tiller during each visit included: plant height, phenology, number of leaves, axillary tillering and tiller senescence.

Measuring tillers nondestructively prevented direct estimates of cumulative biomass through time. Height measurements were converted to biomass by developing height-weight relationships of tillers located on the same clayey range site in the near vicinity of the lysimeters. For each species, tillers were measured, clipped at the soil surface and bundled together with other tillers of the same height (± 1 cm). Five bundles per species representing the range of heights for those tillers found in the lysimeters were collected before each grazing event. Individual bundles containing 5 western wheatgrass and 10 blue grama tillers were placed in plastic bags, transported to the laboratory and immediately cut into segments. Tiller bundles were cut from the base upward in segments of 1-cm for blue grama and 3-cm for western wheatgrass in a manner similar to Tusler (1993), so all height ranges of plants found in the lysimeters were represented. All segments were oven dried at 60°C for 48 hours before weighing.

Tiller relative growth rates ($\text{g g}^{-1} \text{ day}^{-1}$) were calculated according to Radford (1967) as:

$$\text{Tiller relative growth rates} = (\log_e W_{t+1} - \log_e W_t) * I^{-1} \quad (1)$$

where W was tiller weight (g), t was initial time, and I was time increment in days.

Density of western wheatgrass was determined by counting total number of live tillers within each quadrat. Because of the "mat-like" growth form of blue grama, density was determined by counting the number of tillers within a 5.75-cm² circular plot, or 2% of the quadrat area, randomly located within each permanent quadrat. Densities were measured on 24 May 1994, 1995, and 1996.

Standing crop inside 20 randomly located 250-cm² quadrats per lysimeter was harvested monthly by species from 1993 to 1996 (Heitschmidt et al. 1999). Samples were oven dried at 60°C, separated into live and dead components and then weighed. Aboveground net primary production was calculated for blue grama and western wheatgrass by summing all positive increases in standing crop from April to November.

Data Summarization and Analyses

Soil water measurements were analyzed using repeated measures analysis of variance (AOV) with year, depth, treatments

and dates in the model. Years and/or dates and all associated 2- and 3-way interactions were analyzed as within plot repeated measures and tested using full model residuals (Heitschmidt et al. 1999).

Pre-dawn and mid-day water potential data were analyzed separately using repeated measures AOV with drought treatment, plant species, and date as main effects. The error terms for testing the main effects of drought treatments were the replication by treatment interaction. The error terms for testing the main effects of species and the interaction effects of species and drought treatments were replication by treatment by species. The full model residuals were used to test the repeated measures effects of dates and all associated 2- and 3-way interaction effects.

Growth records were summarized using average tiller relative growth rate within 3 time periods. Time periods were: 1) the last 2 weeks of May before the first grazing event; 2) the entire month of June between the first and second grazing event; and 3) July to October of 1994 and July to early September 1995. The number of 1994 post-grazing sampling dates was 8, but this was reduced to 4 in 1995, as both species were essentially dormant throughout both summer periods.

A univariate, repeated measures analysis of variance model was used to analyze tiller relative growth rate data. A 2-way AOV was used to determine the effects of drought and grazing on percent tiller recruitment. Tiller relative growth rates and tiller recruitment are reported for tillers that were grazed twice, since the majority ($\geq 85\%$) of the tillers in the lysimeters were grazed during both grazing events. This was done to reduce confounding effects of combining once grazed and twice grazed tillers.

Tiller densities from May 1994 (i.e., pre-treatment) were included as a covariate in the 2 following years' data. Means were considered to be significantly different when $P \leq 0.05$, unless noted otherwise. Individual lysimeters were considered experimental units for all analyses.

Heitschmidt et al. (1999) reported plant functional group and species compositional differences among treatment plots in 1993. We initially used the pre-treatment year (1993) blue grama and western wheatgrass productivity estimates as covariates in subsequent year analyses. Since the covariates were never significant ($P \geq 0.22$), they were subsequently excluded from the final analyses.

Drought treatments might be considered pseudo-replicated, according to Hurlbert

(1984), since the rainout shelter size and cost precluded classical treatment replication. The use of a single rainout shelter to test the effects of drought is common in the literature (Busso 1988, Busso et al. 1989, 1990, Frank and Ries 1990, NeSmith and Ritchie 1992, Busso and Richards 1993, 1995). Statistical tests used in our study were conservative, since the experimental units were not quadrats, individual plants or individual tillers. In addition, analyses were conducted in a manner similar to the first paper in this series (Heitschmidt et al. 1999).

Results

Precipitation, Soil Water, and Water Stress

In 1993, the pre-treatment year, total annual precipitation was 38% above the long-term average of 34-cm (Fig. 1). Annual precipitation in 1994 was 24.7-cm, 24% below average. Precipitation from 1 May to 31 October 1994 was 16.3 cm compared to the 27.1-cm average. Total annual precipitation for 1995 and 1996 was similar to the long-term average (Heitschmidt et al. 1999).

Heitschmidt et al. (1999) previously reported no differences in soil water dynamics between imposed 1994 drought and natural precipitation and grazing treatment lysimeters. The only significant main effects were year and date.

The drought treatment did not affect either pre-dawn or mid-day leaf water potential of either blue grama ($P = 0.93$) or western wheatgrass ($P = 0.40$; Table 1). Water potentials were affected by plant species (midday; $P \leq 0.01$), date ($P \leq 0.01$) and their interaction ($P \leq 0.01$). Date was the most important factor accounting for 85% of the total sum of squares for predawn and 58% for midday water potentials. Species accounted for less than 5% of the total sum of squares. The date effect followed anticipated seasonal trends of increasing water potentials with decreasing soil water content. The absence of significant drought treatment-by-date ($P \geq 0.18$) and drought treatment-by-date-by-species ($P \geq 0.86$) interactions showed that the magnitude of water stress was similar in both the drought and non-drought treatment plots during 1994 (i.e., the year of the imposed drought) as well as 1995.

Utilization

Ninety-eight percent of marked blue grama tillers (265 of 270) in 1994, and 97% (309 of 320) in 1995 remained in a

Table 1. Predawn and midday leaf water potentials (MPa) for western wheatgrass (Pasm) and blue grama (Bogr) plants growing in drought and nondrought¹ lysimeters at Fort Keogh in 1994 and 1995.

Year	Date	Pre-dawn ²		Mid-day ²	
		Pasm	Bogr	Pasm	Bogr
----- (MPa) -----					
1994	18 May	−0.32d	−0.42d	−2.36cde	−0.62e
	31 May ³	−0.24d	−0.31d	−2.81bcd	−2.12cd
	14 Jun ³	−0.44cd	−0.20d	−3.62ab	−2.69bc
	23 Jun ³	−0.75cd	−1.39c	−3.16abc	−2.11e
	30 Jun	−4.18a	−4.04b	−2.90bcd	−2.29cd
	13 Jul ⁴	−1.04bc	−4.92a	−4.00a	−4.28a
	28 Jul ³	−4.46a	−5.00a	−3.15abc	−4.48a
	1995	15 May	−0.43cd	−0.26d	−1.58e
2 Jun		−0.99bc	−0.59d	−2.22de	−2.08cd
16 Jun		−0.51cd	−0.31d	−2.48cd	−1.75d
30 Jun ³		−0.46cd	−0.50d	−2.02de	−0.70e
17 Jul		−1.42b	−1.42c	−2.84bcd	−2.62bcd
2 Aug		−3.88a	−4.25b	−3.18abc	−3.30b

¹There were no significant ($P \geq 0.10$) differences in drought versus nondrought treatments.

²Means within columns with different letters are significantly different at $P \leq 0.05$.

³Significant ($P \leq 0.05$) mid-day species effects.

⁴Significant ($P \leq 0.05$) predawn species effects.

vegetative phenological stage. On average, utilization was 39% and 47% on blue grama tillers for the first and second grazing events in 1994, and 23% and 45% for the first and second grazing events in 1995. Over 85% of the marked blue grama tillers in the grazed lysimeters were grazed twice in both years.

Ninety-eight percent (323 of 329) in 1994 and 94% (322 of 341) in 1995 of marked western wheatgrass tillers remained in a vegetative phenological stage during the growing seasons. On average, utilization was 49% and 51% for the first and second grazing events in 1994 and 53% and 46% for the first and second grazing events in 1995. Over 90% of marked western wheatgrass tillers were grazed twice in 1994 and 1995.

Tiller Relative Growth Rates

Analyses of relative growth rates of twice-grazed blue grama tillers revealed significant ($P \leq 0.01$) treatment-by-time interactions (Fig. 2). Relative growth rates were reduced ($P = 0.01$) 29% by drought before grazing treatments were imposed (i.e., May) but not different ($P \geq 0.30$) from June through October in 1994 (Fig. 2). Growth rates of defoliated tillers were 107% greater ($P \leq 0.01$) than undefoliated tillers after the first grazing event (i.e., June), but similar ($P = 0.08$) thereafter and not different ($P \geq 0.10$) from zero from July through October (Fig. 2).

The year following the imposed drought (i.e., 1995), the blue grama time-by-drought ($P = 0.02$) and time-by-grazing treatment interactions were significant ($P \leq 0.01$). In May, relative regrowth rates

were 18% greater ($P = 0.01$) for plants exposed to the imposed 1994 drought than for non-drought plants, but rates were similar ($P \geq 0.30$) thereafter (Fig. 2). Relative growth rates in the ungrazed treatment during May 1995 were 19% greater ($P = 0.02$) than in either grazing treatment. However, following the first grazing event of 1995 (i.e., June), relative growth rates were greater ($P = 0.02$) in the G94-95 treatment than the ungrazed control and greater ($P = 0.003$) than the G94 treatment. Relative growth rates from July through August were not different ($P \geq 0.10$) from zero (Fig. 2).

Relative growth rates of marked western wheatgrass tillers grazed twice, were unaffected by drought in 1994 ($P = 0.61$). Relative growth rates were greater ($P \leq 0.01$) in the 2 grazed treatments (G94 and G94-95) compared to the ungrazed treatment (0.007 vs. 0.002 $\text{g}^{-1} \text{day}^{-1}$) in June, and declined from July to October (Fig. 3).

Tiller relative growth rates were not different ($P \geq 0.15$) from zero from July through October (Fig. 3).

Results were similar for western wheatgrass in 1995 in that relative growth rates were unaffected by drought treatment ($P = 0.69$), were greater ($P \leq 0.01$) in the grazed (G94-95) than the 2 ungrazed (G94 and ungrazed) treatments in June, and declined through the season (Fig. 3).

Tiller Recruitment

The percent of primary blue grama tillers which produced an axillary tiller, varied during the 1994 growing season in response to drought and grazing (Table 2). Drought reduced ($P \leq 0.01$) total recruitment 80%, whereas grazing increased ($P \leq 0.01$) recruitment 315% compared to ungrazed treatments. Sixty percent of daughter tillers were produced after the first grazing event. Of those producing axillary tillers, none in the drought treatment produced more than 1 axillary tiller. Eighteen percent in the non-drought treatment produced 2 secondary tillers.

In 1995, the magnitude of recruitment by blue grama was similar ($P = 0.16$) between drought and non-drought treatments (Table 2). Tiller recruitment for combined grazing treatments was 78% greater ($P \leq 0.01$) than without grazing. Ninety-eight percent of the tiller recruitment occurred after the first grazing event. On average, 30% of the blue grama tillers producing axillary tillers produced 2 secondary tillers. It appeared that the seasonal pattern of axillary tillering by blue grama was similar in 1994 and 1995.

Recruitment by western wheatgrass tillers grazed twice also varied in magnitude between the 1994 drought and grazing treatments (Table 2). Drought reduced ($P \leq 0.01$) recruitment 91% (Table 2). Grazed tillers exhibited greater ($P = 0.04$)

Table 2. Least square means (%), SE and P-values proportions of marked primary tillers that produced at least 1 axillary tiller during the growing season for blue grama and western wheatgrass subjected to drought and grazing treatments.

Year	Drought Treatments ¹			P	Grazing Treatments ²			SE	P	D*G ³
	D	ND	SE		G94	G94-95	UG			
Blue Grama ⁴	----- (%) -----				----- (%) -----					
1994	8a	40b	3	≤ 0.01	31a	32a	10b	3	≤ 0.01	0.08
1995	39	49	4	0.16	47a	60a	30b	5	0.01	0.50
Western Wheatgrass ⁴										
1994	7a	79b	3	≤ 0.01	47a	46a	35b	3	0.04	0.07
1995	6	11	3	0.18	5	15	6	3	0.12	0.84

¹D = Drought, ND = Non Drought.

²G94 = Grazed in 1994, G94-95 = Grazed in 1994 and 1995, UG = Ungrazed.

³D*G = Drought by grazing interaction P-value.

⁴Drought or grazing treatment means in the same year (row), with different letters are significantly different at $P \leq 0.05$.

Fig. 2. Mean tiller relative growth rates ($\text{g g}^{-1} \text{day}^{-1}$) for blue grama in response to drought and grazing. Grazing treatments were grazed during and after drought (G94-95), grazed during drought and ungrazed after drought (G94), and ungrazed during and after drought (UG). Different capital letters (A and B) denote significant ($P \leq 0.05$) differences between drought and nondrought within the same monthly period. Small letters (a, b and c) denote significant ($P \leq 0.05$) differences between grazing treatments within the same monthly period.

recruitment compared to ungrazed tillers (Table 2). More than 95% of the recruitment occurred in the fall (September and October) of 1994. No tillers in drought plots recruited more than 1 tiller. In contrast, of the primary western wheatgrass tillers producing axillary tillers in non-drought plants, 11% produced 2 daughter tillers. Eighty percent of the axillary tillers were produced in September through October in 1994.

Tiller recruitment by western wheatgrass during the growing season was similar between drought ($P = 0.18$) and among grazing ($P = 0.12$) treatments in 1995 (Table 2). Only 26% of the western wheatgrass tillers were recruited in the fall (September–October) of 1995. No western wheatgrass tillers produced more than 1 daughter tiller in 1995.

Tiller Density

Estimated pre-treatment tiller densities of blue grama were greater ($P = 0.06$) in

1994 in drought compared to non-drought lysimeters (8,646 vs. 9,854 tillers/ m^2) but not ($P \geq 0.60$) among grazing treatment lysimeters in 1994. Initial tiller densities were included as covariates for the 1995 and 1996 analyses. Tiller densities of blue grama were not ($P = 0.10$) affected by drought in 1995 (8,068 vs. 9,420 tillers m^{-2}), but in 1996, 2 years after the drought was imposed, tiller densities of blue grama stands subjected to drought were 59% greater ($P = 0.02$) than not subject to drought (9,967 vs. 6,263 tillers m^{-2}). Grazing did not ($P = 0.49$) affect densities in 1995 or 1996. No significant ($P \geq 0.20$) drought-by-tiller interactions occurred either year.

Initial (1994) tiller densities of western wheatgrass were different ($P \leq 0.01$) and their covariates were significant ($P \leq 0.04$) in 1995 but not ($P \geq 0.12$) in 1996. Tiller densities were not ($P = 0.71$) affected by drought in 1995 but were reduced 42% ($P = 0.007$) in 1996 (476 vs. 814 tillers m^{-2})

Fig. 3. Mean tiller relative growth rates ($\text{g g}^{-1} \text{day}^{-1}$) for western wheatgrass in response to drought and grazing. Grazing treatments were grazed during and after drought (G94-95), grazed during drought and ungrazed after drought (G94), and ungrazed during and after drought (UG). Different capital letters (A and B) denote significant ($P \leq 0.05$) differences between drought and nondrought within the same monthly period. Small letters (a, b and c) denote significant ($P \leq 0.05$) differences between grazing treatments within the same monthly period.

when compared to non-drought treatments. Tiller densities were not affected ($P = 0.49$) by grazing treatment or drought by grazing treatment ($P \geq 0.52$) interactions in 1995 or 1996.

Aboveground Net Primary Production (ANPP)

Blue grama production averaged 551 kg ha^{-1} across years and grazing treatments (Table 3). Pre-treatment ANPP for blue grama (i.e., 1993) did not differ ($P = 0.11$) between drought treatments, but it was greater ($P = 0.03$) in the 2 grazed treatment plots than the ungrazed (Table 3). Analyses for years 1994 through 1996 showed all drought and grazing treatment effects were non-significant ($P \geq 0.10$). Drought-by-grazing treatment interactions were not significant ($P \geq 0.10$) in any year.

Estimated 1993 ANPP for western wheatgrass did not differ ($P = 0.10$) between drought treatment plots, but was greater ($P = 0.05$) in the G94-95 and

Table 3. Least square means (kg ha⁻¹), SE, and P-values for aboveground net primary production estimates for blue grama and western wheatgrass subjected to drought and grazing treatments.

Year	Drought Treatments ¹		SE	P	Grazing Treatments ²			SE	P	D*G ³
	D	ND			G94	G94-95	UG			
Blue Grama ⁴	----- (kg ha ⁻¹) -----				----- (kg ha ⁻¹) -----					
1993	1,473	1,276	78	0.11	1,421a	1,588a	1,101b	96	0.03	0.14
1994	712	639	90	0.58	680	566	781	110	0.43	0.10
1995	564	476	81	0.47	562	334	663	99	0.13	0.48
1996	516	398	64	0.24	395	357	619	78	0.10	0.90
Western Wheatgrass ⁴										
1993	1,117	1,687	211	0.10	1,138a	1,595b	1,472b	259	0.05	0.49
1994	649a	1,277b	90	≤ 0.01	757a	756a	1,378b	110	0.01	0.98
1995	978	1,376	129	0.07	1,608a	481b	1,442a	158	≤0.01	0.17
1996	961	1,347	166	0.15	1,275	1,029	1,157	204	0.70	0.40

¹D = Drought, ND = Non Drought.

²G94 = Grazed in 1994, G94-95 = Grazed in 1994 and 1995, UG = Ungrazed.

³D*G = Drought by grazing interaction P-value.

⁴Drought or grazing treatment means in the same year (rows), with different letters are significantly different at $P \leq 0.05$.

ungrazed treatment plots than the G94 treatment plots (Table 3). Pre-treatment ANPP were not significant ($P \geq 0.22$) covariates in any initial analyses, therefore, they were not included in the final analysis. Aboveground net primary production was less ($P = 0.01$) in the drought than non-drought treatment in 1994 and greater ($P = 0.01$) in the ungrazed than grazed treatments (G94-95) in 1994. The only difference found thereafter, was that ANPP in G94-95 (which was grazed in 1995) was less ($P \leq 0.01$) in 1995 than in the 2 non-grazed treatments in 1995 (NG and G94). There were no drought by grazing treatment interactions ($P \geq 0.17$) in any year.

Discussion

Based on the results of this study, we conclude that: 1) relative growth rates of tillers which were grazed twice, were largely unaffected by drought and seasonally enhanced by grazing (Fig. 2 and 3); 2) axillary tillering was impeded by drought during the growing season and enhanced by grazing (Table 2); 3) tiller densities were unaffected by drought or grazing; and 4) neither drought nor grazing affected blue grama ANPP whereas drought reduced western wheatgrass ANPP with mixed grazing treatment effects (Table 3).

The major effects of drought were expressed by a slight (19%) reduction in tiller relative growth rates of blue grama in May 1994, a large reduction in tillering for western wheatgrass (91%) and blue grama (80%) during the growing season in 1994, and a large reduction of ANPP for western wheatgrass. Growth and tillering are often reduced by water stress (Brown 1995). Zhang and Romo (1995) reported the number of emerging northern wheatgrass

(*Agropyron dasystachyum* (Hook.) Scribn.) tillers was positively correlated with soil water. Haferkamp et al. (1997 and 1998), Haferkamp and Heitschmidt (1999) and Rummell (1946) reported western wheatgrass tiller density increased with the removal of competition of Japanese brome (*Bromus japonicus* Thunb.).

The responses to the initiation of the drought began to appear early in 1994 as shown by the change in blue grama tiller relative growth rates and the lack of a significant date-by-treatment interaction for western wheatgrass tiller relative growth rates. However, the response to the imposed drought and control lysimeters were similar due to the natural drought-like conditions which existed during 1994. Precipitation was 24% below average, and this drought caused plants to be equally water stressed by May 1994 regardless of drought treatment (Table 1). This conclusion is also supported by the precipitation (Fig. 1), xylem water potentials, and soil water data reported previously by Heitschmidt et al. (1999).

Our results also suggest the effects of a 1-year drought on growth rates did not carry over to the next year. Carry over effects may have been limited by the initial drought as well as above average precipitation that fell in March, April, and May 1995. Busso and Richards (1995) and Busso et al. (1989) did not find the effects of a 1-year drought on numbers of active axillary buds carried over to the next year. Only after 3 consecutive years of drought did Busso et al. (1989) find reduced numbers of metabolically active axillary buds.

Fewer axillary tillers were produced by western wheatgrass in 1995 than in 1994. Increased western wheatgrass tillering is associated with increased fall precipitation the previous year (Haferkamp et al. 1997). However, in this instance, the fall of 1994

was wetter than fall of 1993 (Fig. 1). Thus, the reduction of tillering in 1995 was more likely due to the dry summer of 1994.

Grazing had little long-term effect on blue grama or western wheatgrass. The increase in tiller recruitment with grazing during the growing season agrees with findings of Sims et al. (1973). They reported mowing blue grama plants in late June and early July stimulated additional tillering, mostly from reproductive shoots that had elevated above the mowed height. Mowing earlier in the growing season depressed tillering, whereas mowing in late July and early August stimulated tillering, but insufficient growing season remained for complete development of these late tillers. They also reported increased tillering with mowing for sand bluestem (*Andropogon hallii* Hack.) a rhizomatous warm-season grass.

Our findings that grazing did not reduce ANPP of blue grama, but did decrease ANPP of western wheatgrass can best be explained by the different morphologies of the 2 species. Grass species like blue grama are characterized by short growing shoots and when grazed, these species can maintain much higher proportions of photosynthetic tissue than can species with long shoots like western wheatgrass (Dahl and Hyder 1977). Klipple and Costello (1960) noted that herbage production of western wheatgrass remained the same when utilization of that species increased from about 10% to about 20% but declined sharply when utilization increased to 40%. Launchbaugh (1967) found that forage production of western wheatgrass declined as utilization increased from 44 to 80%. Reed and Peterson (1961), Everson (1966), and Branson (1953) concluded that forage production of western wheatgrass declined with increased utilization.

Many studies have shown the importance of environmental factors on production of mixed-grass rangelands (Coupland 1958, Reed and Peterson 1961, Hyder et al. 1975). Extended drought usually shifts species composition toward short grasses (Smoliak et al. 1972), but species composition shifts toward mid grasses when precipitation is above average (White et al. 1978). Shifts in plant species composition in this study were not observed (Heitschmidt et al. 1999). This lack of change in species composition may have been due to the timing and severity of the imposed drought. We failed to detect an increase in warm-season herbage production as reported by Heitschmidt et al. (1999), but our findings were probably due to slightly different methodologies.

Management Implications

Our results demonstrate a 1-year growing season drought combined with grazing (both during and after drought) did not appear to adversely affect tiller processes. Elimination of livestock grazing during or after a 1-year growing season drought may not be necessary to maintain plant populations on the tiller level for blue grama and western wheatgrass. Moderate stocking levels (40–50% utilization) during and after drought did not adversely affect sustainability of dominant native grasses on these Northern Great Plains rangelands within the conditions of this study.

Literature Cited

- Branson, R.A. 1953.** Two new factors affecting resistance of grasses to grazing. *J. Range Manage.* 6:165–171.
- Brown, R.W. 1995.** The water relations of range plants, p. 291–413. *In:* D.J. Bedunah and R.E. Sosebee (eds.) *Wildland plants: Physiological ecology and developmental morphology*. Soc. Range Manage. Denver, Colo.
- Bullock, J.M., B. Clear Hill and J. Silvertown. 1994.** Tiller dynamics of two grasses—responses to grazing, density and weather. *J. Ecol.* 82:331–340.
- Burkhardt, J.W. 1996.** Herbivory in the Intermountain West. Idaho Forest, Wildl. Range Exp. Sta. Bull. 58, Moscow, Ida.
- Busso, C.A. 1988.** Factors affecting recovery from defoliation during drought in two arid-land tussock grasses. Ph.D. Thesis, Utah State Univ. Logan, Ut.
- Busso, C.A. and J.H. Richards. 1993.** Leaf extension rate in two tussock grasses: Effects of water stress and clipping. *Oecologia* 14:3–15.
- Busso, C.A. and J.H. Richards. 1995.** Drought and clipping effects of tiller demography and growth of two tussock grasses in Utah. *J. Arid. Environ.* 29:239–251.
- Busso, C.A., R.J. Mueller and J.H. Richards. 1989.** Effects of drought and defoliation on bud viability in two caespitose grasses. *Ann. of Bot.* 63:477–485.
- Busso, C.A., J.H. Richards and N.J. Chatterton. 1990.** Nonstructural carbohydrates and spring regrowth of two cool-season grasses: interaction of drought and clipping. *J. Range Manage.* 43:336–343.
- Campbell, R.S. 1936.** Climatic fluctuations, p.135–150. *In:* The Western Range. US Govt. Printing Office. Washington D.C.
- Coupland, R.T. 1958.** The effects of fluctuations in weather upon the grassland of the great plains. *Bot. Rev.* 24:274–312.
- Dahl, B.E. and D.N. Hyder. 1977.** Developmental morphology and management implications, p. 257–290. *In:* R.E. Sosebee (ed.) *Rangeland plant physiology*. Range Science Series No. 4. Soc. Range Manage. Denver, Colo.
- Everson, A.C. 1966.** Effects of frequent clipping at different stubble heights on western wheatgrass (*Agropyron smithii*, Rydb). *Agron. J.* 58:33–35.
- Frank, A.B. and R.E. Ries. 1990.** Effects of soil water, nitrogen, and growing degree-days on morphological development of crested and western wheatgrass. *J. Range Manage.* 43:257–260.
- Haferkamp, M.R. and R.K. Heitschmidt. 1999.** Japanese brome impacts on western wheatgrass in Northern Great Plains rangelands: An update. *Great Plains Research* 9:315–327.
- Haferkamp, M.R., R.K. Heitschmidt, and M.G. Karl. 1997.** Influence of Japanese brome on western wheatgrass yield. *J. Range Manage.* 50:44–50.
- Haferkamp, M.R., R.K. Heitschmidt, and M.G. Karl. 1998.** Clipping and Japanese brome reduce western wheatgrass standing crop. *J. Range Manage.* 51:692–698.
- Heitschmidt, R.K., M.R. Haferkamp, M.G. Karl, and A.L. Hild. 1999.** Drought and grazing: I. Effects on quantity of forage produced. *J. Range Manage.* 52:440–446.
- Hulbert, S.H. 1984.** Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54:187–211.
- Hyder, D.N., R.E. Bement, E.E. Remmenga, and D.F. Hervey. 1975.** Ecological responses of native plants and guidelines for management of shortgrass range. ARS-USDA. Washington, D.C.
- Klipple, G.E. and D.F. Costello. 1960.** Vegetation and cattle responses to different intensities of grazing on shortgrass ranges on the Central Great Plains. U.S. Dep. Agr. Tech. Bull. 1216.
- Küchler, A.W. 1964.** Potential natural vegetation of the conterminous United States. Amer. Geog. Soc. Spec. Pub. 36. Amer. Geog. Soc. N.Y.
- Launchbaugh, J.L. 1967.** Vegetation relationships associated with intensity of summer grazing on a clay upland range site in the Kansas 20- to 24-inch precipitation zone. Kansas Agr. Exp. Sta. Tech. Bull. 154. Manhattan, Kans.
- Ludlow, M.M. 1986.** Simultaneous pressure of water stress and defoliation in rangeland plants, p. 433–436. *In:* P.J. Joss, P.W. Lynch and O.B. Williams (ed.), *Proc. Symp. Rangelands: A resource under siege*, 2nd Int. Rangeland Congress. Cambridge, England.
- National Oceanic and Atmospheric Administration. 1996.** Climatological data, Montana annual summary. Nat. Climatol. Data Center, Asheville, N.C.
- NeSmith, D.S. and J.T. Ritchie. 1992.** Short- and long-term responses of corn to a pre-anthesis soil water deficit. *Agron. J.* 84:107–113.
- Olson, B.E. and J.H. Richards. 1988.** Annual replacement of the tillers of *Agropyron desertorum* following grazing. *Oecologia* 76:1–6.
- Pieper, R.D. and R.K. Heitschmidt. 1988.** Is short-duration grazing the answer? *J. Soil Water Conserv.* 43(2):133–137.
- Radford, P.J. 1967.** Growth analysis formulae - their use and abuse. *Crop Sci.* 7:171–175.
- Reed, M.J. and R.A. Peterson. 1961.** Vegetation, soils, and cattle responses to grazing on northern Great Plains range. USDA For. Serv. Tech. Bull. #1252.
- Richards, J.H., M.M. Caldwell, and B.E. Olson. 1987.** Plant production following grazing: carbohydrates, meristems and tiller survival over winter. *Soc. Range Manage. Symposium*. Boise, Ida.
- Rummel, R.S. 1946.** Some effects of competition from cheatgrass brome on crested wheatgrass and bluestem wheatgrass. *Ecol.* 27:159–167.
- Scholander, P.F., H.T. Hammel, E.D. Bradstreet, and E.A. Hemmingsen. 1965.** Sap pressure in vascular plants. *Sci.* 148:339–346.
- Sims, P.L., R.K. Lang'at, and D.N. Hyder. 1973.** Developmental morphology of blue grama and sand bluestem. *J. Range Manage.* 26:340–344.
- Smoliak, S., J.F. Dormaar, and A. Johnston. 1972.** Long-term grazing effects on Stipa-Bouteloua prairie soils. *J. Range Manage.* 25:246–250.
- Tusler, C.A. 1993.** Livestock defoliation patterns on native range under season-long and spring deferred grazing. M.S. Thesis. South Dakota State University, Brookings, S.D.
- USDA Agricultural Statistics. 1993.** Agricultural statistics. Nat. Agr. Stat. Ser. Washington, D.C.
- White, L.M., J.J. Newbauer III, and J.R. Wight. 1978.** Vegetational differences in native range during 38 years in eastern Montana, p. 260–262. *In:* D.N. Hyder (ed.) *Proc. First Internat. Range Congr. Soc for Range Manage.* Denver, Colo.
- Willms, W.D. and P.G. Jefferson. 1993.** Production characteristics of the mixed prairie: constraints and potential. *Can. J. Anim Sci.* 73:765–778.
- Zhang, J. and J.T. Romo. 1995.** Impacts of defoliation on tiller production and survival in northern wheatgrass. *J. Range Manage.* 48:115–120.

Herbicide residues and perennial grass on establishment perennial pepperweed sites

JAMES A. YOUNG, CHARLIE D. CLEMENTS, AND ROBERT R. BLANK

Authors are Range Scientists and Soil Scientist, USDA, Agricultural Research Service, 920 Valley Road, Reno, Nev. 89512.

Abstract

Perennial pepperweed (*Lepidium latifolium* L.) is a creeping rooted exotic weed that has infested native hay meadows, riparian areas and agronomic fields throughout the western United States. This highly invasive species causes major losses in forage quality and creates numerous management problems. On many sites infested with perennial pepperweed, a near mono-culture exist. Sustainable suppression programs require the establishment of a competitive perennial species. You can not establish seedlings of a perennial competitive species without some initial substantial reduction in perennial pepperweed stands through weed control. Because tillage is not feasible with this creeping rooted species, herbicidal weed control is the primary option. Experience has shown, that the massive and extensive root system of perennial pepperweed can not be completely eliminated with one application of a herbicide. This means that repeated applications of a selective herbicide are required after the perennial seedlings of a competitive species are established. Perennial pepperweed is a broadleaf species that is somewhat susceptible to applications of 2,4-D. Therefore, the choice revegetation species is limited to a perennial grass that is resistant to 2,4-D applications at low rates as a seedlings and moderate rates once established. The saline/alkaline nature of the soils where perennial pepperweed is often found limit the adapted perennial grasses to tall wheatgrass (*Elytriga elongata* [Host] Nevski). The herbicide chlorsulfuron has been shown to be more effective in initially controlling perennial pepperweed than 2,4-D. We determined that applications of chlorsulfuron at rates sufficient to control perennial pepperweed resulted in herbicidal residues that severely reduced or eliminated the establishment of tall wheatgrass seedlings. Application of 2,4-D at flower budding for perennial pepperweed (June), followed by seeding tall wheatgrass in the fall (October), and application of low rates of 2,4-D over the wheatgrass seedlings the next spring (May), gave the best grass seedling establishment and suppression of the perennial weed.

Resumen

El "Pepperweed" (*Lepidium latifolium* L.) perenne es una maleza exótica de enraizamiento rastrero que ha infestado las praderas nativas para producción de heno, las áreas ribereñas y los campos de cultivo del oeste de los Estados Unidos. Esta especie altamente invasiva causa pérdidas mayores en la calidad del forraje y crea numerosos problemas de manejo. En muchos sitios infestados el "Pepperweed" perenne casi forma un monocultivo. Los programas de supresión sustentable requieren del establecimiento de especies perennes competitivas, pero usted no puede establecer plántulas de especies perennes competitivas sin una reducción substancial inicial de "Pepperweed" perenne mediante el control de la maleza. Debido a que la labranza no es factible con estas especies de enraizamiento rastrero, el control con herbicidas es la principal opción. Las experiencias han mostrado que el sistema radical masivo y extenso del "Pepperweed" perenne puede no ser completamente eliminado con una aplicación de herbicida, esto significa que se requieren aplicaciones repetidas de un herbicida selectivo después de que las plántulas de especies perennes competitivas son establecidas. El "Pepperweed" perenne es una especie de hoja ancha que es algo susceptible a las aplicaciones de 2,4-D. Por lo tanto la elección de las especies para revegetación esta limitada a los zacates perennes que son resistentes a las aplicaciones de 2,4-D en bajas dosis cuando el zacate esta en etapa de plántula y a las aplicaciones moderadas una vez que esta establecido. La naturaleza salina/alcalina de los suelos donde a menudo se encuentra el "Pepperweed" perenne limita la selección al zacate perenne "Tall wheatgrass" (*Elytriga elongata* [Host] Nevski), adaptado a estas condiciones. El herbicida chlorsulfuron ha mostrado ser mas efectivo en el control inicial del "Pepperweed" perenne que el 2,4-D. Determinamos que aplicaciones de chlorsulfuron en dosis suficientes para controlar el "Pepperweed" perenne resultan en residuos del herbicida que reducen severamente o eliminan el establecimiento de plántulas de "Tall wheatgrass". Las aplicaciones de 2,4-D en la etapa de aparición de las yemas florales del "Pepperweed" perenne (Junio), seguida por la siembra de "Tall wheatgrass" en otoño (Octubre) y la aplicación en la próxima primavera (Mayo) de dosis bajas de 2,4-D sobre las plántulas de "Tall wheatgrass" dan el mejor establecimiento de las plántulas de zacate y la supresión de la maleza perenne.

Key Words: Chlorsulfuron, tall wheatgrass, saline/alkaline soils

Perennial pepperweed (*Lepidium latifolium* L.), a native to eastern Europe and Asia (Robbins 1940), was accidentally introduced into North America early in the 20th century (Young et al. 1995). A member of the mustard family, this weed has spread to portions of all western states and adjacent Canada. In the Intermountain Area, perennial pepperweed first became established in riparian and wetland areas. It spread to native hay mead-

ows and alfalfa (*Medicago sativa* L.) fields. Native hay meadows located on flood plains are particularly susceptible to perennial pepperweed invasion. The weed is highly adapted, but not restricted to growth on salt affected soils and soils with sodium hazards (Blank and Young 1997).

Perennial pepperweed plants can produce large quantities of viable seeds (Miller et al. 1986). The plants have extensive creeping root systems. Very small fragments of these roots will produce new plants (Young et al. 1997). This makes mechanical control by tillage virtually impossible.

The invasion of native hay meadows by perennial pepperweed is a threat to the range livestock industry of the Intermountain Area because these meadows are a critical portion of the forage base for both hay production and grazing of crop aftermath. Perennial pepperweed can be partially suppressed by grazing, but if grazing is deferred for hay production the plants become quite woody and the resulting hay is of very poor quality. If herbicidal weed control is practiced on these meadows with near mono-cultures of perennial pepperweed, spontaneous regeneration of the meadow is very slow and re-invasion of the weed will occur. This makes seeding of a perennial forage species necessary. The choice of revegetation for these seasonally dry meadows with salt affected soils is limited. Tall wheatgrass (*Elytrigia elongata* [Host] Nevski) is the most widely used species.

The standard herbicide for control of perennial pepperweed has traditionally been 2,4-D [(2,4-dichlorophenoxy) acetic acid] (Young et al. 1998). More recently, herbicides of the sulfonyleurea family, especially chlorsulfuron {2-chloro-N-[(4-methoxy-6-methyl-1, 3, 5-triazin-2-yl) -aminocarbonyl] benzenesulfonamide} have been found to be very effective for the control of perennial pepperweed. Both 2,4-D and chlorsulfuron can be applied at appropriate rates and kill perennial pepperweed in established stands of meadow species and not injure the perennial grasses and grass-like species (Young et al. 1998).

To give the perennial grass plants a chance to biologically suppress perennial pepperweed, repeated herbicide applications are necessary over the seedling stands. This obviously requires the use of a selective herbicide.

The longevity of chlorsulfuron residues and their influence upon tall wheatgrass seedling establishment was unknown for the saline/alkaline soil environments of native hay meadows. Our purpose was to compare seedling establishment of tall wheatgrass on sites where perennial pepperweed was controlled with 2,4-D or chlorsulfuron applications.

Methods

Field trials were located at the main Station Farm of the Nevada Agricultural Experiment Station at Reno, Nev. (39.30 N. Lat., 119.42 W. Long.). The site was a previously irrigated field which in 1993 became so dominant with perennial pepperweed that crop production was no longer feasible. All weed control and seeding trials in this study were conducted without irrigation. The site is on the flood plain of the Truckee River at the confluence of Steamboat Creek. The topographic position of the site is very similar to typical native hay meadows in the Intermountain Area. The principal soil is the Voltaire series, a fine-loamy, mixed, mesic Fluvaquertic Haplaquoll. Soils are moderately to highly influenced by accumulations of salts. The electro-conductivity of the surface soil ranged from 7.4 to 9.8 S m^{-1} during the summer months. The soil profiles have a well developed natric horizon.

Herbicides were applied with 484 liter ha^{-1} of water with a boom mounted on an all-terrain vehicle. Initial herbicide applications were made in mid June when perennial pepperweed was in the flower bud stage. The following October, the cultivar Largo of tall wheatgrass was seeded with a rangeland drill at the rate of 7.2 kg/ha . The initial treatments were, 2,4-D as an amine at 2.2 kg/ha , chlorsulfuron at 71 g/ha , and control. The plots 30 by 100 m in area were arranged in a randomized block design. Initial herbicide application was in June 1996. On separate plots the treatments were repeated in 1996, 1997, and 1998. In April of 1997, one half of

Table 1. Density per m^2 perennial pepperweed plants in May and October 1997, 1998, and 1999 for treatments made in 1996, 1997, 1998.¹

Treatment	Year applied	Year sampled	Perennial pepperweed density	
			May	Oct.
			-- plants/ m^2 --	
Control	1996	1997	14.1b	24.1a
	1997	1998	20.1a	23.6a
	1998	1999	21.4a	24.6a
2,4-D	1996	1997	0.1c	4.0c
	1997	1998	0.1c	4.6c
	1998	1999	0.1c	5.2c
Chlorsulfuron	1996	1997	0.1c	0.1c
	1997	1998	0.1c	0.1c
	1998	1999	0.1c	0.1c

each treatment plot was sprayed with 0.6 kg/ac of 2,4-D over top of the tall wheatgrass seedlings. This was also done for the 1997 and 1998 treatments. The treatments that did not have establishment of tall wheatgrass seedlings were re-seeded each subsequent October. For example the plots originally seeded in 1996 were seeded again in 1997 and again in 1998, if no seedlings established.

The plots were evaluated in May and October annually by randomly locating 4 quadrants 1 m^2 in each treatment. The density of tall wheatgrass plants per meter of row was determined by randomly locating 10 plots 1 m in length along the drill rows in each treatment and counting the plants. Data were subject to analysis of variance and means separated by Duncan's Multiple Range Test.

Table 2. Density per m^2 of perennial pepperweed plants in October 1997, 1998 and 1999 for treatments made in 1996, 1997, and 1998 and re-treated with 0.6 kg/ha of 2,4-D in May 1997, 1998, and 1999.¹

Treatment	Year applied	Year sampled	2,4-D re-applied	Perennial pepperweed density
				October (plants/ m^2)
Control ²	—	—	—	24.1a
Control	1996	1997	1997	8.4a
	1997	1998	1998	20.1a
	1998	1999	1999	19.9a
2,4-D	1996	1997	1997	0.8b
	1997	1998	1998	0.3b
	1998	1999	1999	0.4b
Chlorsulfuron	1996	1997	1997	0.0b
	1997	1998	1998	0.1b
	1998	1999	1999	0.1b

¹Means followed by the same letter are not significantly different at the 0.01 level of probability as determined by Duncan's Multiple Range Test.

²Average of the control plots that were not re-treated with 2,4-D from 1996 through 1998.

Table 3. Density of tall wheatgrass plants per meter of row in May 1997, 1998, and 1999 (seedling year) and plant density on same plots in 1998, 1999, and 2000 (second season after planting) with and without re-application of 0.6 kg/ha of 2,4-D.¹

Treatment and year seeded		Tall wheatgrass density			
		Without second 2-4-D Application		With second 2-4-D Application	
		Seedlings	2 nd year plants	Seedling	2 nd year plants
------(per m of row)-----					
Control	1996	0	0	0	0
	1997	0	0	0	0
	1998	0	0	0	0
2,4-D	1996	0b	0b	7.1a	6.4a
	1997	0.1b	0b	9.1a	7.8a
	1998	0.3b	0b	8.6a	7.4a
Chlorsulfuron	1996	0	0	0	0
	1997	0	0	0	0
	1998	0	0	0	0

¹Within treatments means followed by the same letters are not significantly different at the 0.01 level of probability as determined by Duncan's Multiple Range Test. No letters no differences. Seedling and second year plants compared separately.

Results and Discussion

In May, 11 months after herbicide application, the control of perennial pepperweed plants with either 2,4-D or chlorsulfuron applications appears excellent (Table 1). By October of the year after application, there had been considerable return of perennial pepperweed in the plots treated with 2,4-D.

Application of a light rate of 2,4-D (0.6 kg/ha) over the top of the tall wheatgrass seedlings the spring after they were planted, did not significantly ($P \geq 0.01$) reduce the density of perennial pepperweed in control treatments (Table 2). It did significantly reduce the density of perennial pepperweed in plants in plots that had in the previous year been treated with 2.2 kg/ha of 2,4-D. The 2,4-D treatment over the seedlings had no influence on the few perennial pepperweed plants that existed on the plots previously treated with chlorsulfuron.

The establishment of tall wheatgrass seedlings was very straight forward. If you did not control perennial pepperweed no tall wheatgrass seedlings established (Table 3). If you initially controlled perennial pepperweed with applications of 2,4-D a few seedlings of tall wheatgrass were initially present, but no plants were present the second year after seeding. If you initially controlled perennial pepperweed with 2,4-D and followed with a lower rate of 2,4-D over the seedlings the spring after the seeds were planted, very good stands of tall wheatgrass were obtained (Table 3). The plots treated with chlorsulfuron remained virtually free of perennial pepperweed, but no seedling establishment of tall wheatgrass occurred.

The plots treated with chlorsulfuron were re-seeded annually with tall wheatgrass. The plots where chlorsulfuron was applied in 1996, were seeded in 1996, 1997, 1998, and 1999. Tall wheatgrass seedlings never established on these areas. Until 1999, the areas initially treated with chlorsulfuron remained weed free except for occasional plants of perennial pepperweed that escaped the initial herbicide application. In 1999 Russian thistle (*Salsola turgus* L.), lamb's quarter (*Chenopodium album* L.), and annual kochia (*Kochia scoparia* [L.] Schrader) plants grew on the treated area, but seedlings of tall wheatgrass were not found in the spring 2000.

These large, replicated experimental treatments were repeated for 3 consecutive years with highly consistent results. Diehard defenders of chlorsulfuron point out that we have done no chemical analysis of the soil to prove that residues of the herbicide are responsible for the failure to establish tall wheatgrass seedlings. The consistency of seedling failure in plots treated with chlorsulfuron while side by side plots treated with 2 applications of 2,4-D have excellent stands of the perennial grass is very compelling evidence for persistent residues. The failure of annual weeds to invade areas treated with chlorsulfuron for 3 years is additional evidence for the existence of residues.

The few perennial pepperweed plants that escape initial applications of chlorsulfuron are a cause of concern. They increased in area by extending creeping roots and putting up additional stems even though perennial grass seedlings could not be established on the plots. The plants are not necessarily resistant to chlorsulfuron.

They may be accidents of faulty herbicide distribution in the initial application and their depth of rooting allows them to spread below soil horizons with herbicide residues. The existence, persistence, and spread of these plants creates an additional hazard with the use of chlorsulfuron to control perennial pepperweed.

The apparent persistence of chlorsulfuron residues that limit perennial grass establishment is probably heightened by the high pH of the salt affected soils on the study site. Most native hay meadows where perennial pepperweed is invading have similar soils.

Literature Cited

- Blank, R. R. and J. A. Young. 1997. *Lepidium latifolium*: Influences on soil properties, rate of spread, and competitive stature. pp. 69–80 In: J. H. Brock, W. Wade, P. Pysek, and D. Green (eds.) Plant Invasion: Studies From North America and Europe. Backhuys Publ., Leiden, The Netherlands.
- Miller, G. K., J. A. Young, and R. A. Evans. 1986. Germination of seeds of perennial pepperweed. Weed Sci. 34:252–255.
- Robbins, W. W. 1940. Alien plants growing without cultivation in California. Bull. 637. Calif. Agr. Exp. Sta., Berkeley, Calif.
- Young, J. A., D. E. Palmquist, and R. R. Blank. 1998. The ecology and control of perennial pepperweed (*Lepidium latifolium* L.) Weed Techn. 12:402–405.
- Young, J. A., D. E. Palmquist, and S. O. Wotring. 1997. The invasive nature of *Lepidium latifolium*: A review. pp. 59–68 In: J. H. Brock, W. Wade, P. Pysek, and D. Green (eds.) Plant Invasion: Studies From North America and Europe. Backhuys Publ., Leiden, The Netherlands.
- Young, J. A., C. E. Turner, and L. F. James. 1995. Perennial pepperweed. Rangelands 17:121–123.

Seed longevity and seeding strategies affect sagebrush revegetation

D. TERRANCE BOOTH

Author is Rangeland Scientist, USDA-ARS, High Plains Grassl. Res. Sta., 8408 Hildreth Road, Cheyenne, Wyo. 82009.

Abstract

Three hypotheses were tested relating to Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* (Beetle and Young) revegetation on coal-mined land in Wyoming: (1) that fourwing saltbush (*Atriplex canescens* (Pursh) Nutt.) seeded > 2.2 kg pure live seed (pls)/ha would exclude sagebrush, (2) the contrasting view that the saltbush, as a "pioneer plant", facilitated sagebrush stand development [by promoting beneficial soil microbiological activity], and (3) that sagebrush stand development would be greater on fresh-stripped, than on stored, topsoil. The hypotheses were tested by comparing stand development on field plots: 1) seeded to sagebrush in February 1992, and March 1993; 2) fallowed in 1992, and sagebrush seeded in March 1993; 3) seeded to 'Wytana' fourwing saltbush in November, 1991, with sagebrush over-seeded in March, 1993, and; 4) no seeding. The experimental design was a randomized complete block with split plots of stored and fresh-stripped topsoil and with 3 replications. New sagebrush were detected annually through 4 post-seeding spring counts. Seed efficiency was affected by seeding strategy, but efficiency, density, and height were not affected by topsoil source. Proximity to saltbush did not affect sagebrush heights. The results imply that a 'Wytana' density ≤ 5 seedlings/m² is unlikely to deter or promote development of the sagebrush stand, but it will significantly increase total-shrub seed efficiency and density. Seeding strategies, particularly pre-sowing fallow and mixed-species seedings, will likely have a greater influence on sagebrush revegetation than will topsoil source when topsoils are handled as they were in this study.

Key Words: Wyoming big sagebrush, fourwing saltbush, reclamation, fallow, early seral species, pioneer plants, ecological restoration, soil erosion

Sagebrush (*Artemisia tridentata* Nutt.) and other xerophytic shrubs are a conspicuous component of western North American

Resumen

Se probaron tres hipótesis relacionadas a la revegetación de minas de carbón en Wyoming con "Wyoming big sagebrush" (*Artemisia tridentata* Nutt. ssp. *wyomingensis* (Beetle and Young): (1) que el "Fourwing saltbush" (*Atriplex canescens* (Pursh) Nutt.) sembrado a una densidad > 2.2 kg semilla pura viable/ha excluiría al "Sagebrush", (2) El punto de vista contrastante de que el "Saltbush", como una "planta pionera", facilitaría el desarrollo de la población de "Sagebrush" (al promover la actividad microbiológica benéfica del suelo) y (3) que el desarrollo de la población "Sagebrush" sería mayor en bandas de suelo superficial recién colocado (fresco) que en suelo almacenado. Las hipótesis se probaron comparando el desarrollo de poblaciones en parcelas de campo con los siguientes tratamientos: 1) "Sagebrush" sembrado en febrero de 1992 y Marzo de 1993; 2) barbechado en 1992 y "Sagebrush" sembrado en Marzo de 1993; 3) 'Wytana' fourwing saltbush sembrado en Noviembre de 1991 y sobresembrado con "Sagebrush" en Marzo de 1993 y 4) parcelas testigo sin sembrar. El diseño experimental fue un bloques completos al azar en parcelas divididas en el que la parcela grande fue el tipo de suelo y se tuvieron 3 repeticiones. A través de 4 años después de la siembra, en los conteos anuales de primavera, se detectaron nuevas plantas de "Sagebrush". La eficiencia de la semilla fue afectada por la estrategia de siembra, pero la eficiencia, densidad y altura no fueron afectadas por la fuente de suelo. La proximidad de "Saltbush" no afectó la altura del "Sagebrush". Los resultados implican que una densidad de 'Wytana' ≤ 5 plántulas/m² es improbable que impida o promueva el desarrollo de la población de "Sagebrush", pero incrementará significativamente la eficiencia total de la semilla del arbusto y la densidad. Las estrategias de siembra, particularmente el barbecho pre-siembra y las siembras de especies mezcladas, probablemente tendrá una mayor influencia en la revegetación de "Sagebrush" que la fuente de suelo, cuando las fuentes de suelo superficial son manejadas es manejado como en este estudio.

rangelands and provide key benefits to the function and utility of the ecosystems they occupy (McKell and Goodin 1973). For that reason they are encouraged, and in Wyoming are legally mandated (Federal Register 1996), for reclamation of coal-mined rangelands.

Several approaches have been tested for improving sagebrush establishment. These include sowing sagebrush and other shrubs without competing grasses, various surface seeding techniques, topsoil management (Monsen and Meyer 1990, Skilbred 1990, Schuman et al. 1998), sowing in combination with manipulated snow catchment, mulching, and sowing shrubs first and herbaceous plants later (Stevens et al. 1981, Brock 1982, Schuman et al. 1998).

This work was supported in part by the Abandoned Coal Mine Lands Research Program at the University of Wyoming. Support was administered by the Wyoming Dept. of Environmental Quality from funds returned to Wyoming from the Office of Surface Mining of the U.S. Dept. of Interior. I thank Scott Belden, Environmental Coordinator, North Antelope Coal Mine for his cooperation and assistance; Drs. E.J. Deputt and G.E. Schuman for their part in preparing the grant proposal; Dr. G.V. Richardson who consulted on statistical design, analyses, and interpretation; L.W. Griffith, P.K. Freeman, J.R. Cockrell, C.L. Mahelona, E.M. Taylor, and M.C. Mortenson who provided technical assistance; and Drs. E.J. Deputt, E.D. McArthur, and R.D. Piper for their critical review of an earlier version of this report. Mention of trade names is for information only and does not imply an endorsement.

Manuscript accepted 7 May 01.

Two hypotheses dominated Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* (Beetle and Young) revegetation discussions when this study was begun. The “exclusion” hypothesis stated that where fourwing saltbush (*Atriplex canescens* (Pursh) Nutt.) was seeded at 2.2 kg pure live seed (pls)/ha or greater rates, monotypic stands of that shrub would develop and exclude other shrubs, particularly sagebrush. The alternative or “pioneer plant” hypothesis held that poor soil physical characteristics and low levels of mycorrhizal inoculum in mined-land soils was the reason for poor stands of climax plants such as sagebrush (Booth 1985). Fourwing saltbush was recommended as an early seral species that could “...hasten the natural successional patterns” on New Mexico mined land by Wagner et al. (1978), and Booth (1985) postulated the shrub could function in that role in Wyoming. Meyer (1990) also suggested “pioneer” shrubs prepare reclaimed sites for later seral species. Therefore, I tested the “exclusion” and “pioneer” hypotheses on fresh-stripped and stored topsoil by monitoring sagebrush stands through 4 post-seeding growing seasons.

Materials and Methods

Site Description and Preparation

The research was conducted at the North Antelope Coal Mine, about 100 km south of Gillette, in Wyoming's Powder River Basin (43° 31' 41" N, 105° 17' 04" W). Precipitation in this continental climate ranges from 250 to 330 mm annually with 70% being received April–August (Table

1). Fresh topsoil was composed of a complex of loamy and clayey calcareous, mesic, shallow, Ustic Torrorthents (Schuman et al. 1998). The study was begun in August 1990, on 1/2 ha of leveled, regraded, and deep-ripped coal-mine spoil. Topsoil, which was either fresh-stripped or from a 5-year-old stockpile (designated as “stored”), was replaced to an average depth of 30 cm, ripped, and disked (topsoil stockpiles were 10- to 15-m-high mounds seeded to native cool-season grasses) (Schuman et al. 1998).

In late April 1991, ‘Step toe’ barley (*Hordeum vulgare* L.) was seeded at 50 kg pls/ha to produce a stubble mulch over the entire study site. In mid-July the barley was mowed to remove seed heads.

Seeding Strategy

The sagebrush seeding-strategy plots were installed as follows (treatment symbols are indicated in parentheses): 1) sagebrush seeded in 1992, and in 1993 (ARTRx2), 2) fallow in 1992, sagebrush seeded in 1993 (Fallow-ARTR), 3) fourwing saltbush seeded in fall 1991, and sagebrush seeded in 1993 (ATCA-ARTR) and, 4) no seeding (Control).

The fourwing saltbush was ‘Wytana’ (*Atriplex canescens* Nutt. ssp. *aptera* (A. Nels.)), obtained from the Bridger Plant Materials Center, Bridger, Mont. The seed was harvested in 1986 and had 92.4% purity and 14% germination with a TZ test of 7% (tested 5 Oct. 1990). Total viability was counted as 14%. ‘Wytana’ has 107,900 seeds/kg (J. Sheetz, personal communication) and was drilled at 26 kg pls/ha. The rate was equal to 2.6 g pls/m² (281 live seeds/m²) and was about 12 times greater

than the 2.2 kg pls/ha suggested by some to be an upper limit above which the resulting saltbush stand would competitively exclude other shrubs (Booth 1985). However, ‘Wytana’ is a smaller shrub than most commercially available fourwing saltbush. [It is also well adapted to the extreme temperatures common to eastern Montana and Wyoming (Soil Conservation Service 1988).]

Sagebrush seed was collected locally (Powder River Basin) in December 1991. It was cleaned using a debarker (Booth et al. 1997) and a clipper cleaner as is the standard commercial practice. The purity was 52% and the germination was 74% (tag values). Sagebrush was broadcast late February 1992, at 2.4 kg pls/ha and mid-March 1993, at 2.0 kg pls/ha. Wyoming big sagebrush has 4.0 to 5.4 million seeds per kg (Meyer, In press). At 4 million seeds/kg, seeding rates would have dispersed 960 and 800 seeds/m² in 1992, and 1993, respectively. No perennial grasses were seeded on any of the plots.

Data Collection

Sampling

Shrub stand development was monitored in 1992 with 9, systematically located 1-m² quadrats in each treatment plot (Mueller-Dombois and Ellenberg 1974, p.74). Fifteen, 1-m² permanent quadrats were used in 1993 and thereafter. Shrubs were counted each spring (late April to early June). Counts were made by placing colored markers by each shrub as they were identified. The markers were counted, the plot photographed using 35mm color-print film, and the markers recollected. The camera was equipped with a

Table 1. Monthly precipitation and mean monthly temperature, North Antelope Coal Company, Gillette, Wyo., 1992–1994. The 1978–1995 precipitation average is 32.3 cm.

Month	1992		1993		1994		1995		1996	
	Precip	Temp	Precip	Temp	Precip	Temp	Precip	Temp	Precip	Temp
	(cm)	(°C)	(cm)	(°C)	(cm)	(°C)	(cm)	(°C)	(cm)	(°C)
Jan	0	-0.6	0	-7.2	0.20	-3.3	0.05	-2.2	0.03	-7.8
Feb	0.68	2.2	0.38	-7.7	0.15	-6.1	0.66	-1.6	0.23	-2.8
Mar	3.15	4.4	1.47	2.2	0.41	3.3	0.97	0.6	0.56	-2.8
Apr	0.76	7.7	6.48	5.5	2.79	6.6	2.01	3.3	1.571	6.1
May	2.26	13.2	5.94	12.7	2.87	14.9	8.94	8.3	12.171	8.9
Jun	6.43	16.5	14.15	14.3	8.36	18.2	7.21	15.0	4.421	17.8
Jul	7.75	17.6	9.70	17.1	4.93	19.8	1.68	20.0	0.711	21.1
Aug	2.95	18.2	10.13	18.2	0.81	20.9	0.03	22.8	1.42	20.6
Sep	1.75	15.4	2.29	12.1	1.22	16.0	0.23	13.9	2.24	13.3
Oct	0.41	8.8	2.36	6.1	5.49	7.2	1.96	6.1	4.111	8.9
Nov	0.89	-0.6	0.36	6.1	5.49	7.2	0.10	4.4	0.25	-2.2
Dec	<u>1.19</u>	-6.6	<u>0.10</u>	-1.7	<u>0.05</u>	-1.7	<u>0</u>	-3.3	<u>0.29</u>	-4.4
Total	28.22		53.36		27.86		23.84		28.00	

¹Data recorded at Rochelle Mine due to sensor malfunction at North Antelope site.

28mm lens and was mounted 1.5 m above the center of the plot.

The color prints were used to track seedling populations during the study period. Prints were scanned using a Hewlett-Packard ScanJet 4C color scanner, then "MapInfo Professional" software (MapInfo Corporation, Troy, N.Y.) was used to map and monitor each seedling in all 360 quadrats for the 4 years that photographs were made.

Seed Efficiency Analysis

Seed efficiency is the number of live plants/unit of seed sown. I compared shrub seed efficiency as total shrubs (1996 count)/1,000 seeds and as number of sagebrush (1996 count)/1,000 seeds. Thus, seed efficiency reflects both seedling establishment and seedling survival. For these calculations I estimated sagebrush seeds at 4.0 million/kg (Meyer In press) and used 107,900 seeds/kg for 'Wytana'.

Shrub Density and Height Analysis

Shrub density (total shrubs/m²) was compared for 1996 without regard to seeding rates. Also for fall 1996, sagebrush height was measured for all plants in 1, randomly-selected quadrat per seeding-strategy plot. Sagebrush in the ATCA-ARTR treatment were segregated according to those plants that were within, or outside, an arbitrary 7.6-cm radius of a saltbush plant.

Experimental Design and Statistical Analysis

The experimental design was a randomized complete block with split plots and with 3 replications. Main plots were fresh and stored topsoil with seeding strategies randomly assigned within topsoils. Except for cohort analysis, the several statistical analyses used the "Mixed" procedure (SAS 1988, 1996, Littell et al. 1996). The "differences" option was used to compare least-square means.

Cohort counts within strategies across years were compared with confidence limits for the proportion, cohort count over the total of all cohorts, using the normal approximation (Steel and Torrie 1980, pages 478–479).

Results and Discussion

Seed Longevity and Cohorts

New sagebrush seedlings were detected from photographic data during all 4 annual counts made after March 1993. The pho-

Table 2. Count of live sagebrush in May, 1996, by age-class and seeding strategy, and test of cohort differences. Counts for 1993 include seedlings established in 1992 and 1993. Counts made fall of 1992 found 0.1 and 0.4 seedlings/m² in ARTRx2 fresh, and stockpiled topsoil. There were no sagebrush seedlings in any of the other plots in spring or fall of 1992.

STRATEGY	COHORT (Year Detected)			Total All Cohorts
	1996	1995	1993	
	(total 1996 sagebrush by count ²)			
Fallow-ARTR ¹	42 c	55 c	297 a	538
ARTRx2	42 d	74 c	286 a	644
ATCA-ARTR	14 b	46 b	64 b	308
Control	0	1	0	1

¹Fallow-ARTR= plots fallowed in 1992 and seeded to sagebrush in 1993; ARTRx2= sagebrush was seeded in 1992 and 1993; ATCA-ARTR= 'Wytana' seeded in 1992 and sagebrush over-seeded in 1993; and Control= not seeded.

²Total for 90 quadrats. Cohort values within rows followed by the same letter are not significantly different at $P \leq 0.05$ as tested by confidence limits for cohort/total proportions using the normal approximation (Steel and Torrie 1980). The Control was not tested due to lack of variance among years; confidence intervals for seeding strategies did not include 1 or 0. This implies that all other strategies were significantly greater than the Control and is the only valid comparison among strategies.

tographs also show that each cohort population—including the cohort resulting from the 1996 germination—was significantly greater than the control for all strategies (Table 2). Only 1 sagebrush was found among all unseeded plots in the study, evidence that; (1) the annual appearance of new seedlings in seeded plots did not result from natural seed dispersion and, (2) fresh-stripped topsoil did not act as a seed source.

Young and Evans (1989) reported basin big sagebrush (*Artemisia tridentata* Nutt. ssp. *tridentata*) did not maintain seed viability for more than a few months. However, seed dormancy in Wyoming big sagebrush may contribute to greater seed longevity (McDonough and Harniss 1974, Booth et al. 1997). This is the first study to measure the effect of Wyoming big sagebrush seed dormancy on seedling emergence from the soil, and to document the appearance of new seedlings during 4 annual post-seeding counts.

The 1994 cohort was the largest (Table 2). This was likely due to favorable 1993 weather (Table 1). Many seedlings likely established during the cool, wet, 1993 spring but remained too small to detect in 1993. Or, there may have been considerable 1993 post-count seedling establishment. In either case, the pulse in seedling establishment is consistent with other

reports of thick stands of sagebrush establishing with favorable weather conditions (Lommasson 1948, Went 1955, Booth et al. 1999).

The Need to Seed

The lack of shrubs on unseeded control plots (Table 2) is evidence of the need to seed shrubs, even on fresh-stripped topsoil. Howard and Samuel (1979) found < 0.1 sagebrush, and < 0.4 total-shrub seedlings/m² 1 year after fresh-stripped topsoil was spread at Kemmerer, Wyoming. Approximately the same result was obtained at Oak Creek, Colo. (Howard and Samuel 1979). These are unacceptably low densities (Federal Register 1996) for mines in shrub-dominated landscapes.

Benefits of High Sagebrush Seeding Rates

The ARTRx2 (sagebrush seeded in 1992, and in 1993) total seeding rate was 4.4 kg/ha or 1,760 seeds/m² and it produced the most sagebrush by the all-cohort count (Table 2). For comparison, Fallow-ARTR (fallow in 1992, sagebrush seeded in 1993) was seeded at 800 seeds/m² (2.0 kg/ha). Booth et al. (1999) reported a linear relationship between shrub densities of old (> 10 years) stands and shrub seeding

Table 3. Means for the sagebrush-only, seed efficiency analysis ($P = 0.15$ for differences among seeding strategies). Seeding-strategy symbols are as described in Table 2.

Seeding Strategy	Number sagebrush (mean/1,000 seeds)	Mean separations among seeding strategies
Fallow-ARTR	7.5	Fallow-ARTR vs. ARTRx2 $P = 0.08$
ATCA-ARTR	4.3	ARTRx2 vs. ATCA-ARTR $P = 0.82$
ARTRx2	3.9	ATCA-ARTR vs. Fallow-ARTR $P = 0.11$

Fig. 1. Seed efficiency as shrubs (1996 count)/1,000 seeds by seeding strategy. Means followed by the same letter are not different at $P < 0.001$ for ATCA-ARTR versus all other values, and at $P = 0.10$ for Fallow-ARTR versus ARTRx2. The seed efficiency of sagebrush within the ATCA-ARTR treatment is given for reference. Shrub seeding strategies and symbols are: ARTRx2 = sagebrush was seeded in 1992 and 1993; Fallow-ARTR = fallowed in 1992 and seeded to sagebrush in 1993; ATCA-ARTR = 'Wytana' saltbush seeded in 1992 and sagebrush over seeded in 1993, ATCA = 'Wytana' fourwing saltbush, ARTR = sagebrush. Data were calculated using 107,930 'Wytana' seeds/kg (J. Sheetz, personal communication) and 4.0 million Wyoming big sagebrush seeds/kg (Meyer, In press).

rates up to 1,000 seeds/m² for shrub-seed mixtures containing Wyoming big sagebrush. They recommended the 1,000 seeds/m² rate (2.5 kg/ha) for mixtures with Wyoming big sagebrush. These data support that recommendation.

Seed Efficiency as affected by Seeding Strategy and Topsoil Management

The ATCA-ARTR (fourwing saltbush seeded in fall 1991, sagebrush seeded in 1993) strategy had the greatest seed efficiency (total shrubs/1,000 seeds) and was the most consistently successful strategy (Fig. 1). The success of mixed-shrub seedings was also reported by Booth et al. (1999). Fallow-ARTR was the second most efficient strategy and ranked first when only sagebrush was considered (Fig. 1 and Table 3).

Lack of a difference in sagebrush seed efficiency between ARTRx2 and ATCA-ARTR (Table 3), suggests "Wytana" had no measurable effect (positive or negative) on sagebrush establishment and survival. Although 1993 precipitation was 165% of average, the remaining years of the study had below average precipitation (Table 1).

Thus, lack of a saltbush effect is not due to lack of competition for moisture in the year following seedling establishment.

Topsoil had no influence on sagebrush, or total shrub seed efficiency ($P = 0.82$ for sagebrush and $P = 0.76$ for total shrubs). The topsoil x seeding strategy interaction was also not significant ($P = 0.23$ for sagebrush and 0.32 for total shrubs).

Shrub Density Not Affected by Seeding Strategy or Topsoil Management

Shrub density (shrubs/m²) was not affected by seeding strategies ($P = 0.62$) or topsoil management ($P = 0.97$). The interaction was $P = 0.12$. This interaction is not

considered important because (1) interactions are more likely to show significance since they combine main effects, and (2) there is no consistent pattern among means (Table 4). Saltbush density averaged 5.0 shrubs/m² in the ATCA-ARTR treatments.

Table 4. Total shrub density (shrubs/m²) by topsoil and seeding strategies (topsoil x seeding strategy $P = 0.12$). Differences among means are not significant. Seeding strategy symbols are as described in Table 2.

Topsoil	Seeding Strategy	Density (Shrubs/m ²)
Stored	ARTRx2	10.2
	F-ARTR	4.9
	ATCA-ARTR	7.7
Fresh	ARTRx2	4.6
	F-ARTR	8.3
	ATCA-ARTR	9.5

Sagebrush Heights Not Affected by Seeding Strategy, Topsoil Management, or Proximity to Saltbush

Heights of sagebrush plants did not vary by seeding strategy ($P = 0.91$), topsoil ($P = 0.57$), the interaction ($P = 0.87$), or proximity to 'Wytana' fourwing saltbush ($P = 0.56$) (Table 5).

Soil Erosion

The annual photographs of 360 quadrants systematically located throughout the study area are a reliable record of soil surface conditions during the study. The photographs show barley straw remained on the plots through 1995, though by that time many perennial grasses and forbs were present. Erosion rills and soil pedestals do not appear in the photographs, nor were they noted when field data were collected.

Summary of Topsoil Results

There were no differences between fresh stripped and stored topsoil for any test variable ($P = 0.57$ for sagebrush height

Table 5. Sagebrush mean height (mm) by seeding strategy, topsoil source, and distance from "Wytana" fourwing saltbush. Means are not different (P values ≥ 0.56). Seeding-strategy symbols are as described in Table 2.

Seeding Strategy	Sagebrush height (mm)	Topsoil	Sagebrush height (mm)	'Wytana' distance	Sagebrush height
ARTRx2	48	Stored	54	≤ 7.6 cm	43
Fallow-ARTR	51	Fresh	48	> 7.6 cm	55
ATCA-ARTR	53				

was the lowest observed significance level of any test of topsoil effects). This was unexpected since the fresh-stripped topsoil contained greater numbers of vesicular mycorrhizae spores (Schuman et al. 1998). Also, Stahl et al. (1998) have shown in greenhouse studies that mycorrhizae-infected sagebrush seedlings survive greater drought stress than non-mycorrhizal seedlings. The reasons topsoil had no effect may be partly due to soil surface variation among the plots and replications. During 1993–1994 (see precipitation data in Table 1) parts of the study area subsided as much as 30 cm. (estimated), resulting in flow-patterns across plots and replications and decreasing site uniformity. Lack of a topsoil effect may also have been due to the management of the stored-topsoil (Schuman et al. 1998).

Whatever the reasons, detecting an effect from topsoil under field conditions was difficult even with uniform plots. In the adjacent study (Schuman et al. 1998), soil surfaces remained uniform but sagebrush densities on fresh-stripped topsoil were significantly greater ($P < 0.10$) than those on stored topsoil only where grass was not seeded (Table 2 and text, page 226, in Schuman et al. 1998).

The high sagebrush seed efficiency and shrub densities $\geq 1/\text{m}^2$ occurred on both types of soils, suggesting that micro-site moisture differences had a greater influence on sagebrush seedling establishment than did topsoil source; and, that stored topsoil, managed as in this study, will support dense stands of sagebrush (Table 4).

Fallowing and Shrub Stand Establishment

The Fallow-ARTR strategy produced significantly ($P = 0.10$) more surviving shrubs/1,000 seeds (1996 count) than were produced by the ARTRx2 strategy. Although the effect of this seeding strategy for the sagebrush-only analysis was marginally significant ($P = 0.15$), there are reasons to believe the strategy was as effective for sagebrush alone as for the 2 shrubs together.

Shrubs have extensive root systems that utilize moisture deep in the soil profile (West and Tueller 1972, Anderson et al. 1972) and fallowing is an effective means of replenishing that soil moisture. This is especially true for topsoiled areas protected by stubble mulch (Schuman et al. 1980, Schuman and Powers 1981). It is logical to conclude that a fallowing strategy would increase the seed efficiency of all shrubs

and I recommend it be tested in other situations for promoting shrub revegetation. Fallowing can also be effective without a stubble mulch. Chet Skilbred, Sr. Environmental Scientist for Glenrock Coal Company, Glenrock, Wyoming, offers the following for successful sagebrush revegetation (Nov. 1998 letter to author).

“Glenrock Coal Company's (GCC) field procedure is to deep rip (about 1 m) the regraded spoils and allow these spoils to accumulate moisture prior to application of the topsoil. Following application of about 76 cm of the topsoil, GCC again deep rips. This field practice seems to accelerate (moisture) recharge and provide a better seedbed.”

Meeting The Shrub Density Standard

The shrub densities that resulted from the seeding treatments are more than adequate to meet wildlife needs and environmental law (Table 4, Federal Register 1996). While I acknowledge the influence of 1993's favorable weather in producing high shrub densities, I also believe revegetation procedures that produced up to 10 times greater-than-required shrub densities (Table 4) with favorable weather, will be useful when weather patterns are less favorable.

There are several findings of this study that have application for meeting the Wyoming shrub density standard. One, there is the probable increase in seed efficiency from fallowing. Two, use of stubble-mulch-protected fallow with high Wyoming big sagebrush seeding rates (2.5 kg/ha) in a mix with other shrubs such as ‘Wytana’ is likely to result in synergistic increases in shrub densities. Three, as demonstrated by this study, high seeding rates for Wyoming big sagebrush are important for seeding-year establishment and to create a soil seed bank that may produce significant populations of new seedlings annually for 4 post-seeding growing seasons (Table 2). Four, as demonstrated by this study, seeding sagebrush with ‘Wytana’, where the ‘Wytana’ density is ≤ 5 seedlings/ m^2 , is unlikely to hinder sagebrush stand development. Where ‘Wytana’ was seeded with sagebrush the mixed-shrub stand was 43% sagebrush and the difference in total-shrub density equaled 10,000 more 1996-shrubs/ha than resulted from the double-seeding strategy, ARTRx2.

Conclusions

The “exclusion” and “pioneer-plant” hypotheses, as applied to fourwing saltbush on coal-mined land, are both rejected for lack of evidence. I also found no evidence that sagebrush stand development was greater on fresh-stripped topsoil than on topsoil stored for 5 years. I conclude that where soils are handled as they were in this study, the variability associated with micro-site moisture differences will have a greater effect on sagebrush establishment and survival than will topsoil source.

The soil-seed bank of Wyoming big sagebrush remained viable and capable of producing seedlings through 4 post-seeding growing seasons and I believe that situation will occur with most Wyoming big sagebrush seedlings of good quality seed. Lastly, I believe fallowing to be an effective tool for shrub revegetation.

Literature Cited

- Anderson, D.J., R.A. Perry, and J.H. Leigh. 1972. Some perspectives on shrub / environment interactions, p. 172–181. *In*: C.M. McKell et al.(eds), Proc. wildland shrubs - their biology and utilization, July 1971, Logan, Ut., Intermount. Forest and Range Exp. Sta., Gen. Tech. Rep. INT-1, Forest Serv., Ogden, Ut.
- Booth, D.T. 1985. The role of fourwing saltbush in mined land reclamation: a viewpoint. *J. Range Manage.* 38:562–565.
- Booth, D.T., Y. Bai, and E.E. Roos. 1997. Preparing sagebrush seed for market: effects of debearder processing. *J. Range Manage.* 50:51–54.
- Booth, D.T., J.K. Gores, G.E. Schuman, and R.A. Olson. 1999. Shrub densities on pre-1985 reclaimed mine lands in Wyoming. *J. Restoration Ecol.* 7:1–9.
- Brock, J.H. 1982. Interseeding and interplanting techniques for southwest reclamation, p.192–195. *In*: E.F. Aldon and W.R. Oaks (eds), Proc. reclamation of mined lands in the Southwest, Oct. 1982, Albuquerque, N.M., New Mexico Chapter Soil Conserv. Soc. Amer., Albuquerque, N.M.
- Federal Register. 1996. Office of Surface Mining and Enforcement. 30 CFR Part 950. Wyoming Regulatory Program - final rule; approval of amendment. 61 (152):40735.
- Howard, G.S. and M.J. Samuel. 1979. The value of fresh-stripped topsoil as a source of useful plants for surface mine revegetation. *J. Range Manage.* 32:76–77.
- Littell, R.C., G.A. Milliken, W.W. Stroup, and R.D. Wolfinger. 1996. SAS system for mixed models. SAS Inst. Inc., Cary, N.C.
- Lommasson, T. 1948. Succession in sagebrush. *J. Range Manage.* 1:19–21 (reprinted in *Rangelands* 15 (1993):109–110).

- McDonough, W.T. and R.O. Harniss. 1974.** Effects of temperature on germination in three subspecies of big sagebrush. *J. Range Manage.* 27:204–205.
- McKell, C.M. and J.R. Goodin. 1973.** United States arid shrublands in perspective, p. 12–18. *In: Proc. 3rd Workshop of U.S. / Australia Rangelands Panel*, Tucson, Arizona. Soc. for Range Manage. Denver, Colo.
- Meyer, S.E. 1990.** Shrubland restoration—an ecologist's perspective. Handout: Workshop on plant species and wildlife habitat establishment successes and failures. Billings, Mont. USDA Forest Service, Intermountain Research Station, Shrub Sci. Lab., Provo, Ut.
- Meyer, S.E.** In press. *Artemisia*. *In: F. Bonner and S. Krugman (eds). Woody plant seed manual*, 3rd edition. USDA-Forest Service. (electronic pre-print available at: <http://www.wpsm.net/Genera.htm#e>)
- Monsen, S.B. and S.E. Meyer. 1990.** Seeding equipment effects on establishment of big sagebrush on mine disturbances, p. 192–199. *In: Proc. 5th Billings symposium on disturbed land rehabilitation*, Mar. 1990, Billings, Mont., (Vol. I), Reclam. Res. Unit. Pub. No. 9003, Montana State Univ., Bozeman, Mont.
- Mueller-Dombois, D. and H. Ellenberg. 1974.** Aims and methods of vegetation ecology. John Wiley and Sons, N.Y.
- SAS. 1988.** SAS/STAT user's guide, release 6.03 Edition. SAS Inst. Inc., Cary, N.C.
- SAS. 1996.** SAS/STAT software: changes and enhancements through release 6.11. SAS Inst. Inc., Cary, N.C.
- Schuman, G.E. and J.F. Power. 1981.** Topsoil management on mined lands. *J. Soil and Water Conserv.* 36:77–78.
- Schuman, G.E., D.T. Booth, and J.R. Cockrell. 1998.** Cultural methods for establishing stands of Wyoming big sagebrush on mined lands. *J. Range Manage.* 51:223–230.
- Schuman, G.E., E.M. Taylor, Jr., F. Rauzi, and G.S. Howard. 1980.** Standing stubble versus crimped straw mulch for establishing grass cover on mined lands. *J. Soil and Water Conserv.* 35:25–27.
- Skilbred, C.L. 1990.** Direct seeding of sagebrush species on regraded mine lands in east central Wyoming. Handout: Workshop on plant species and wildlife habitat establishment successes and failures, Billings, Mont. Glenrock Coal Co., Glenrock, Wyo.
- Soil Conservation Service (SCS). 1988.** Plant materials handbook. Distributed by US Dept. of the Interior, Office of Surface Mining, Reclamation and Enforcement.
- Stahl, P.D., G.E. Schuman, S.M. Frost, and S.E. Williams. 1998.** Arbuscular mycorrhizae and water stress tolerance of Wyoming big sagebrush seedlings. *Soil Sci. Soc. Amer. J.* 62:1309–1313.
- Stevens, R., W.L. Moden, and D.W. McKenzie. 1981.** Interseeding and transplanting shrubs and forbs into grass communities. *Rangelands* 2:55–58.
- Steel, R.G.D. and J.H. Torrie. 1980.** Principles and procedures of statistics. McGraw-Hill Book Company, N.Y.
- Wagner, W.L., W.C. Martin, and E.F. Aldon. 1978.** Natural succession on strip-mined lands in northwestern New Mexico. *Reclamation Rev.* 1:67–73.
- Went, R.W. 1955.** The ecology of desert plants. *Scientific Amer.* 192:68–75.
- West, N.E. and P.T. Tueller. 1972.** Special approaches to studies of competition and succession in shrub communities, p. 165–171. *In: C.M. McKell et al. (eds), Proc. wildland shrubs—their biology and utilization*, July 1971, Logan, Ut., Intermount. Forest and Range Exp. Sta., Gen. Tech. Rep. INT-1, Forest Serv., Ogden, Ut.
- Young, J.A. and R. Evans. 1989.** Dispersal and germination of big sagebrush (*Artemisia tridentata*) seeds. *Weed Sci.* 37:201–206.

Seasonal dynamics of prairie sandreed rhizome development

PATRICK E. REECE, JENNIFER S. NIXON, LOWELL E. MOSER, AND STEVEN S. WALLER

Authors are Professor, University of Nebraska, Panhandle Research and Extension Center, 4502 Avenue Scottsbluff, Nebr. 69361; Extension Educator, Sioux County Extension, 325 Main, Harrison, Nebr. 69346; Professor, Dept. of Agronomy, 352 Keim Hall, University of Nebraska, Lincoln, Nebr. 68583; Associate Dean, 103 Agricultural Hall, University of Nebraska, Lincoln, Nebr. 68583.

Abstract

Multiple generations of rhizome-connected tillers stabilize soils and produce measurable amounts of herbage on sandy rangeland throughout the world. However, little is known about the dynamics of rhizome development in these clonal plant species. Seasonal relationships between foliar characteristics and rhizomes of prairie sandreed [*Calamovilfa longifolia* (Hook) Scribn.] were examined on sands range sites at 30-day intervals from May through September 1989 and 1990 at the University of Nebraska, Panhandle Experimental Range near Scottsbluff. Quadrats were excavated each year from two, 5 x 5 Latin Square macroplots in each of 2 grazing histories, long-term rest or current-year deferment. Under dry conditions in 1989, a 65% reduction in the length of new rhizomes during July preceded a 64% reduction in live tillers in August. After which, rhizome length and live tiller density were unchanged and mean tiller weight increased during September. When average precipitation occurred in 1990, a 25% reduction in live tillers and concurrent increases in new rhizome length and mean tiller weight occurred during July. Rhizome bud densities increased throughout the growing season at different but predictable rates ($R^2 \geq 0.95$) for grazing histories, regardless of precipitation. Length of new rhizomes was highly correlated ($R^2 = 0.91$) with live herbage throughout the growing season. Measurable increases in total rhizome length did not occur until live herbage of prairie sandreed exceeded a threshold of about 50 g m⁻². Maximum increase in length of new rhizomes per unit of live herbage was about 10 cm g⁻¹ near 100 g m⁻². Given its dependence on vegetative reproduction and relatively high palatability to beef cattle, periodic or repeated years of full growing season deferment may be the only reliable method of obtaining measurable increases in prairie sandreed populations.

Key Words: *Calamovilfa longifolia*, warm-season grass, clonal growth, reproduction threshold, tiller dynamics

Resumen

Generaciones múltiples de hijuelos conectados por rizomas estabilizan los suelos y producen cantidades medibles de forraje en los pastizales arenosos del mundo. Sin embargo, poco se conoce respecto a las dinámicas de desarrollo de los rizomas en estas especies vegetales clonales. Se examinaron las relaciones estacionales entre las características foliares y los rizomas del zacate "Prairie sandreed" [*Calamovilfa longifolia* (Hook) Scribn.]; el estudio se llevó a cabo en la Estación Experimental de Pastizales Panhandle de la Universidad de Nebraska, cerca de Scottsbluff, y se realizó en sitios de pastizal arenosos en intervalos de 30 días de Mayo a Septiembre de 1989 a 1990. Cada año se excavaron cuadrantes en dos macro parcelas de un Cuadro Latino 5 x 5 situadas en dos áreas con diferente historial de manejo del apacentamiento, descanso a largo plazo y diferimiento del año actual. En 1989, bajo condiciones de sequía, una reducción del 65% de la longitud de los nuevos rizomas registrada en Julio precedió a una reducción del 64% de los hijuelos vivos registrada en Agosto. Después de la cual, la longitud de los rizomas y la densidad de los hijuelos vivos permanecieron sin cambio y la media de peso de los hijuelos se incrementó durante Septiembre. En 1990, año con precipitación promedio, en Julio se observó un 25% de reducción en los hijuelos vivos e incrementos concurrentes de la longitud de los rizomas nuevos y la media de peso de los hijuelos. Las densidades de yemas de hijuelos se incrementaron a través de la estación de crecimiento a diferentes tasas (pero predecibles) ($R^2 > 0.95$) para las historias de apacentamiento, sin importar la precipitación. A lo largo de la estación de crecimiento la longitud de los nuevos rizomas estuvo altamente correlacionada ($R^2 = 0.91$) con el forraje vivo. No ocurren incrementos medibles en la longitud total de los rizomas hasta que el forraje vivo del "Prairie sandreed" excedió un umbral de aproximadamente 50 g m⁻². El máximo incremento de la longitud de los rizomas nuevos por unidad de forraje vivo fue aproximadamente de 10 cm g⁻¹ casi 100 g m⁻². Dada su dependencia en la reproducción vegetativa y su gustocidad relativamente alta para el ganado para carne, el diferimiento periódico o repetido de la estación de crecimiento completa puede ser el único método confiable para obtener incrementos medibles en poblaciones de "Prairie Sandreed".

Published as Paper 12924 Journal Series, Nebraska Agricultural Research Division. The authors wish to thank Gordon Moeller, Jay and Gretchen Lees, Myron Riggs, Mick Friemuth, Jack Alexander, Lori Williams, Maureen Skavdahl, Mollie Reece, Bill Goodwin, Hazel Fritschen, Laurie Baker, Echo Fisher, Cheryl Bolen, and Paige Wolken for the many hours they invested in excavating and processing samples. We would also like to express our appreciation to Sharon Holman for the preparation of the manuscript and to Ann Koehler for preparation of the graphics.

Manuscript accepted 20 Jul. 01.

The relative value of rhizomes in reproduction, resource acquisition, and interactions among rhizome-connected shoots has been reported for graminoid (Hartnett 1989, Jónsdóttir and Callaghan 1990, Jónsdóttir 1991, de Kroon et al. 1992, Wikberg et al. 1994, Makita 1996) and forb (Hartnett 1990, Hara and

Wakahara 1994, Schmid et al. 1995) species. However, most of this information is limited to end-of-season measurements. Field studies of grass rhizome dynamics during the growing season are rare (Brejda et al. 1989) and quantification of seasonal relationships between rhizome and shoot characteristics during the growing season has not been reported.

Networks of rhizome-connected tillers are highly effective in stabilizing sandy soils in the Nebraska Sandhills, the largest stabilized sand dune formation in the western hemisphere encompassing about 4.9 million ha. Prairie sandreed [*Calamovilfa longifolia* (Hook) Scribn.] is a co-dominant, warm-season, rhizomatous grass in mid- to late seral plant communities on all upland sites in the Sandhills and on many sandy range sites in the northern Great Plains of USA and Canada (GPFA 1986). Prairie sandreed tillers develop almost exclusively from buds at the distal end of rhizomes which are unbranched and relatively long and deep compared to other plant species in the Sandhills (Brejda et al. 1989, Nixon 1993, Hendrickson et al. 1998).

Our primary objective was to quantify seasonal relationships between prairie sandreed shoot and rhizome characteristics in natural plant communities. Excavation macroplots were also blocked by grazing history and protected from defoliation to evaluate seasonal dynamics of rhizome development after more than 14 years of rest compared to a single year of full growing season deferment. Based on preliminary field evaluations, we hypothesized that length of new rhizomes within a given soil volume increases monotonically as live herbage of prairie sandreed increases within the sample area during the growing season. We further hypothesized that the rate of change in rhizome length per unit change in herbage is independent of grazing history.

Materials and Methods

The study was conducted during 1989 and 1990 at the University of Nebraska, Panhandle Experimental Range (PER, 42° 08' N, 103° 43' W), 19 km northwest of Scottsbluff, Nebraska. Soils are Valent fine sands (Mixed Mesic Ustic Torripsamment). About 73% of annual precipitation occurs during the growing season from May to September. Long-term average annual precipitation was 340 mm with 270 mm in 1989 and 350 mm in 1990. Rangelands in mid- to late seral

stages at this location are dominated by prairie sandreed. Other abundant species include needleandthread (*Stipa comata* Trin. & Rupr.), blue grama [*Bouteloua gracilis* (HBK) Lag. ex Griffiths], and sand dropseed [*Sporobolus cryptandrus* (Torr.) A. Gray]. Sand bluestem (*Andropogon halli* Hack.) is abundant in late seral stages (GPFA 1986).

Four macroplots with uniform distribution of prairie sandreed tillers were selected in a 5.0-ha enclosure constructed in 1974 and in the pasture where the enclosure was located. The pasture had been moderately stocked at 1.0 AUM ha⁻¹ and continuously grazed from May through September since 1978. Two macroplots within each grazing history were randomly selected for excavation in each year. Fences were constructed to exclude cattle from 2 previously grazed macroplots in the pasture in April each year. A 5 x 5 grid of 0.5-m² quadrats (0.71 x 0.71 m) with 0.71-m wide alleys was marked on selected macroplots in April 1989 and 1990. Excavation dates were assigned to quadrats within rows and columns according to randomization procedures for Latin Squares. Five quadrats were excavated to a depth of 30 cm from 2 macroplots in the long-term-rested area and 2 macroplots in the current-year-deferred areas at 30-day intervals from 30 May to 30 September in 1989 and 1990. Prairie sandreed plants were separated from soil and other plant material over wire screens at the excavation site, bagged, and transported on dry ice to freezers.

Plant material was separated into live shoots, crowns, rhizome buds, new rhizomes, and old rhizomes. Initially rhizomes grow horizontally from the point of origin followed by vertical growth which culminates in the development of a shoot if the rhizome is not aborted. Rhizomes originate from buds nears the base of vertical crowns. Rhizome buds were differentiated and visually discernable shoots less than 2-cm long. Buds elongating beyond 2 cm were classified as new rhizomes. New rhizomes had numerous, light tan, intact exterior scales. Rhizomes in this category formed connections between crowns of current-year and/or prior-year shoots or they originated from a shoot and had not emerged. Old rhizomes were dark tan to black with no scales or low densities of fractured scales. Length of rhizomes was measured by hand. Intact networks of old rhizomes often connected 6 to 8 crowns. Plant components were oven dried at 50°C to a constant weight. Mean tiller weights were calculated from total weight of live

herbage and density of live tillers within each excavated area.

The average laboratory time required to separate prairie sandreed from a single 0.5-m² quadrat into plant components in 1989 was 3.5 hours. During August and September 1989, the quarter of the quadrat with the density of live prairie sandreed tillers most similar to the average for the entire 0.5 m² quadrat was excavated separately. Variances and means for quarter and full quadrat data sets were similar based on F and t-tests at $P \leq 0.05$. In 1990, the area of excavated experimental units was reduced to 35 x 35 cm, the quarter with a tiller density most similar to the original 0.5 m² quadrat.

Data were analyzed as a Latin Square using old rhizome length as a linear covariate with the General Linear Models Procedure (SAS 1986). Experimental units were individual quadrats within Latin Square macroplots, blocked by grazing history. Season and season by year interaction effects with grazing history were tested. However, comparisons of means for grazing histories were not valid without replication which was precluded by labor constraints. The Least-Squares Means Procedure within SAS was used for mean separation among excavation dates (Searle et al. 1980). Treatment effects were reported as significant at $P \leq 0.10$. Values used to compute regression equations (SAS 1986) for seasonal changes in density of differentiated rhizome buds below crowns on long-term-rested and current-year-deferred macroplots were the means of 20 excavated quadrats. Values used to compute regression equations for the relationships between the length and weight of new prairie sandreed rhizomes and between live prairie sandreed herbage and the length of new rhizomes were the means of 10 excavated quadrats.

Results and Discussion

Dormant season precipitation from 1 October to 30 April was 42% of long-term average before the 1989 growing season compared to 129% before the 1990 growing season (Fig. 1). Peak standing herbage is highly correlated with the quantity of moisture in Valent soils in mid-April (Dahl 1963). Additionally, total herbage production per unit of spring soil moisture is about 58 and 167% greater than for soil moisture received during early and late summer, respectively (Dahl 1963). While precipitation during June was only 5% of the long-term average in 1989 and 23% in

Fig. 1. Cumulative annual precipitation from 1 Oct. to 30 Sept. for the 1989 and 1990 growing seasons and the 30-year average (•—•) at the University of Nebraska, Panhandle Experimental Range near Scottsbluff, Nebr.

1990, cumulative precipitation beginning in October 1989 was similar to the 30-year average during most of the 1990 growing season because of above average precipitation during the preceding dormant season. Cumulative precipitation beginning in October 1988 was about 10 cm below the 30-year average from 1 June to 31 August 1989, the primary growing season for prairie sandreed (Fig. 1).

Tillers

Regardless of precipitation regime or grazing history, measurable declines in the density of live prairie sandreed tillers occurred during each growing season (Table 1). Densities of live tillers declined by about 64% on all macroplots during August 1989 and about 25% during July 1990 (Table 1). Similar changes in live tiller density for grazing histories in both

years indicated that mortality rates were density independent. Prairie sandreed tiller recruitment in western and central Nebraska is poorly correlated with concurrent 15 or 30 day precipitation totals (Hendrickson et al. 2000). However, in this and other studies of prairie sandreed, tiller recruitment and end-of-season tiller numbers increased as cumulative precipitation increased from the preceding October to the end of the current growing season (Cullan et al. 1999, Hendrickson et al. 2000). Epic events of tiller mortality are relatively common for rhizomatous graminoids in subarctic and temperate environments (Callaghan 1976, Kroon et al. 1992); however, they have not been observed in prairie sandreed populations 240 km east of the Panhandle Experimental Range (PER) at the University of Nebraska-Lincoln Gudmundsen Sandhills Laboratory (Cullan et al. 1999) where long-

term precipitation is 560 mm compared to 340 mm at the PER.

Mean tiller weights increased about 117% on current-year-deferred macroplots and about 175% on long-term-rested macroplots each year during the month in which measurable declines of live tiller densities occurred (Table 1). Tiller densities were unchanged and mean tiller weight continued to increase the remainder of the growing season in both years. Stable late-summer tiller densities are consistent with other studies which indicate about 80% of prairie sandreed tillers emerge by mid-June after which emergence generally remains low the remainder of the growing season (Hendrickson et al. 2000). End-of-season tiller densities increased 91% from 1989 to 1990 on current-year-deferred macroplots compared to 142% on long-term-rested macroplots (Table 1). Higher end-of-season densities and mean weights of live tillers on long-term-rested compared to current-year-deferred macroplots in 1990 are indicative of relatively high levels of plant vigor commonly observed in prairie sandreed in high seral plant communities in this area.

Rhizomes

Monthly rates of change in the density of differentiated buds that could produce rhizomes were similar for grazing histories except during July and August when bud density on long-term-rested macroplots increased by about 1.6 buds $m^{-2} day^{-1}$ compared to 0.3 buds $m^{-2} day^{-1}$ on current-year-deferred macroplots (Fig. 2). This pattern was consistent over years regardless of precipitation regime. Corresponding delays in differentiation of rhizome buds (Nixon 1993) and herbage production (Table 1) during May on long-term-rested compared to current-year-deferred macroplots indicated litter accumulation on rested sites may have reduced soil temperatures (Willms et al. 1993). Mean densities of buds for grazing histories in May 1990 were similar to densities in September 1989 indicating most of the rhizome buds in September survived into the subsequent year. End-of-season bud densities for grazing histories were similar in 1989, but 52% higher on long-term-rested than current-year-deferred macroplots in September 1990 when near average precipitation occurred (Nixon 1993).

The relationship between total weight and length of new rhizomes was highly predictable ($R^2 = 0.90$) regardless of the month or year of sampling (Fig. 3). Mean biomass ranged from 6.4 g m^{-1} with 52 cm

Table 1. Mean density and weight of live prairie sandreed tillers for grazing histories from May through September 1989 and 1990 at the University of Nebraska, Panhandle Experimental Range near Scottsbluff, Nebr.

Date	1989		1990	
	Current-year-deferred	Long-term-rested	Current-year-deferred	Long-term-rested
Tiller Density ¹ (no. m^{-2})				
May 30	169a	262a	139ab	240a
Jun 30	179a	200b	166a	258a
Jul 30	190a	248a	133b	181b
Aug 30	70b	87c	107b	186b
Sep 30	58b	69c	127b	200b
Mean Tiller Weight ² (mg)				
May 30	311cd	137d	162b	30d
Jun 30	399bc	300bc	291b	189c
Jul 30	237d	173cd	614a	527b
Aug 30	525b	467ab	492a	435b
Sep 30	681a	515a	505a	812a

¹Numbers within columns with the same letter are not significantly different, $P > 0.10$.

²The month by grazing history by year interaction for mean tiller weight was significant at $p = 0.021$.

Fig. 2. Seasonal patterns in the density of differentiated buds on vertical rhizomes below crowns of prairie sandreed that could produce new rhizomes (x = days after 30 May) from May through September on long-term-rested ($\circ$) and current-year-deferred ($\bullet$) macroplots at the University of Nebraska, Panhandle Experimental Range.

Fig. 3. The relationship between total weight and total length of new prairie sandreed rhizomes from May through Sept. 1989 ($\circ$) and 1990 ($\bullet$) at the University of Nebraska, Panhandle Experimental Range.

m^{-2} to $3.1 g m^{-2}$ with $1073 cm m^{-2}$ (Fig. 3). About 94% of the reduction in mean biomass per unit length occurred within the first 20% of the observed range in total length. Mean biomass was about $3.3 g m^{-2}$ when length of new rhizomes reached $200 cm m^{-2}$. After soil moisture deficits induced reductions in total length of new rhizomes during July 1989 (Fig. 4), mean biomass per unit length was 82% greater on current-year-deferred macroplots and 49% greater on long-term-rested macroplots (Fig. 3) indicating low-weight rhizomes may have senesced more frequently than heavy rhizomes. Additionally, remaining intact rhizomes may have received proportionately greater amounts of carbohydrates from shoots (Welch 1968) or carbohydrates may have been translocated from senescing rhizomes into intact rhizomes (Jónsdóttir and Callaghan 1990). Carbohydrate concentrations in prairie sandreed rhizomes generally increase rapidly during late summer (Welch 1968). However, little change occurred in mean biomass per unit length when rapid rhizome growth occurred during August and September 1990 (Fig. 3 and 4).

Length of old rhizomes within excavated sample volumes was a significant linear covariate in the analysis of tiller density, herbage, and density of buds that could produce rhizomes. Water and/or nutrients may be translocated from old non-assimilating tillers to connected tillers with live shoots (Jónsdóttir and Callaghan 1988). In contrast, length and weight of new rhizomes were not affected by length of old rhizomes. This contrasts with highly sig-

nificant linear relationships between preceding and current-year rhizome biomass for herbaceous species in temperate environments (de Kroon et al. 1992). However, based on the number of interconnected crowns and assuming 1 crown per year, old rhizomes may have been as much as 7 years old in our study. While crowns may produce more than 1 rhizome in a single year, only 1 crown has developed at the distal end of rhizomes per year in our preliminary field studies of plants grown in containers. Additionally, a percentage of preceding-year rhizomes may have been included in the new rhizome category if color and scale condition criteria were met. Growth of new prairie san-

dreed rhizomes after buds differentiated appeared to be primarily dependent upon resources from assimilating tillers.

The limiting effects of soil moisture deficits on length of new rhizomes in 1989 were uniformly profound regardless of grazing history (Fig. 4). Tiller weights increased from July to September (Table 1) with no change in length of new rhizomes and no difference in rhizome length between grazing histories (Fig. 4) in September. However, when average precipitation occurred in 1990, length of new rhizomes at the end of the growing season was 3.4 times greater for long-term-rested than current-year-deferred macroplots (Fig. 4). Density and mean weight of live

Fig. 4. Mean total length of new prairie sandreed rhizomes at 30-day intervals during the growing season on long-term-rested and current-year-deferred macroplots at the University of Nebraska, Panhandle Experimental Range.

Fig. 5. The relationship between total length of new rhizomes and total live herbage of prairie sandreed from May through Sept. 1989 (○) and 1990 (●) at the University of Nebraska, Panhandle Experimental Range.

tillers in late September were both about 60% higher on rested than on deferred macroplots in 1990 (Table 1) resulting in a mean of 10.7 in of new rhizomes per 1.0 m².

Lack of correlation between length of new prairie sandreed rhizomes and tiller density was similar to *Carex bigelowii* (Wikberg et al. 1994) which also exhibits epic events of tiller mortality. In contrast, live herbage of prairie sandreed accounted for 91% of the variation in new rhizome length regardless of grazing history or the year or month of sampling (Fig. 5). The relationship between total length of new rhizomes and mean tiller weight was similar to, but less predictable ($R^2 = 0.76$) compared to total live herbage (Nixon 1993). Therefore, we accept our hypothesis that the relationship between rhizome length and live herbage is not affected by grazing history. The lack of grazing history effects is consistent with studies of *Carex bigelowii* on subarctic rangeland (Jónsdóttir 1991). Strong relationships between total live herbage and length of new rhizomes have also been reported for forbs *Aster lanceolatus* and *Solidago canadensis* (Schmid et al. 1995) and *Paris tetraphylla* (Hara and Wakahara 1994).

During both years, measurable increases in total length of new rhizomes did not occur until herbage exceeded a threshold of about 50 g m⁻² (Fig. 5) which may correspond to the 4 to 5 leaf stage after which Brejda et al. (1989) reported initiation of new rhizome growth. Beyond this threshold, increases in rhizome length per unit of herbage were highest, about 10 cm g⁻¹, near 100 g m⁻² (Fig. 5). Increases in rhizome length per unit of live herbage were about 40% lower when live herbage was near 50 and 150 g m⁻¹ (Fig. 3 and 5).

Therefore we reject our hypothesis that length of new prairie sandreed rhizomes increases at a constant rate as the mass of live herbage increases.

Precipitation regime by grazing history interaction effects on herbage production were pronounced; however, the relationship between live herbage and length of new prairie sandreed rhizomes was independent of precipitation, grazing history, or excavation date indicating a wide population of inference for the results of this study. Measurable increases in rhizome length in a given year may increase the potential for herbage production if the percentage of tillers originating from relatively long rhizomes increases (White 1977 Brejda et al. 1989) and/or access to limited soil nutrients increases. Interaction between grazing history and precipitation in this study indicates availability of soil moisture will control the extent to which potential herbage production is expressed in semiarid environments.

Prairie sandreed is a mid- and late seral species capable of producing relatively large amounts of herbage critical for ecosystem functions and livestock production. Reproduction of this species is almost exclusively vegetative from crowns formed at the distal end of rhizomes (Brejda et al. 1989, Cullan et al. 1999). Clonal growth into surrounding areas without prairie sandreed and its ability to survive burial on disturbed sites are important processes in secondary succession (Weaver 1965, Maun and Perumal 1999). Consequently, the occurrence of a live-herbage threshold for rapid growth of rhizomes should be considered when developing grazing management strategies designed to increase the composition of

this species. Heavy defoliation during the growing season before threshold levels of herbage have been produced would preclude measurable increases in the composition of prairie sandreed in most years, regardless of grazing systems. The likelihood of producing enough herbage for rapid rhizome development after heavy defoliation in summer-grazed pastures, declines as the growing season progresses and/or precipitation declines (Reece et al. 1999).

Deferring grazing until seedheads have emerged in August would improve the potential for increasing the composition of prairie sandreed (Reece et al. 1996). Tillers that develop from the longest prairie sandreed rhizomes are generally the largest and most likely to produce seedheads (White 1977). Nutritive value and palatability of reproductive tillers to beef cattle decline when seedheads emerge (Reece et al. 1999). These relatively large and generally ungrazed tillers may be critically important for grazing resistance in prairie sandreed by translocating nutrients to connected vegetative tillers (Jónsdóttir and Callaghan 1990, Cullan et al. 1999) that continue to be highly palatable through the summer grazing season (Northup 1993). Given the relatively high preference by cattle for prairie sandreed (Northup 1993, Cullan et al. 1999), periodic or repeated full growing season deferment may be the only reliable method of obtaining measurable increases in prairie sandreed populations. On sites where cool-season graminoids produce 20 to 50% of the herbage, heavy grazing of cool-season species in April, before prairie sandreed tillers emerge, may enhance this species response to full growing-season deferment (Reece et al. 1999).

Literature Cited

- Brejda, J.J., L.E. Moser, and S.S. Waller. 1989. Rhizome and tiller development of three Nebraska Sandhills warm-season grasses. p. 211-215. In: T.B. Bragg and J. Stubbendieck (eds.) Proc. Eleventh North Amer. Prairie Conf Lincoln, Nebr.
- Callaghan, T.V. 1976. Growth and population dynamics of *Carex bigelowii* in an alpine environment: strategies of growth and population dynamics of tundra plants 3. Oikos 27:402-413.
- Cullan, A.P., P.E. Reece, and W.H. Schacht. 1999. Early summer grazing effects on defoliation and tiller demography of prairie sandreed. J. Range Manage. 52:447-453.
- Dahl, B.E. 1963. Soil moisture as a predictive index to forage yield for the sandhills range type. J. Range Manage. 16:128-132.

- de Kroon, H., T. Hara, and R. Kwant. 1992. Size hierarchies of shoots and clones in clonal herb monocultures: do clonal and non-clonal plants compete differently? *Oikos* 63:410–419.
- Great Plains Flora Association. 1986. Flora of the Great Plains. T.M. Barkley (ed.). University Press Kansas. Lawrence, Kan.
- Hara, T. and M. Wakahara. 1994. Variation in individual growth and the population structure of a woodland perennial herb, *Paris tetraphylla*. *J. Ecol.* 82:3–12.
- Hartnett, D.C. 1989. Density- and growth stage-dependent responses to defoliation in two rhizomatous grasses. *Oecologia* 80:414–420.
- Hartnett, D.C. 1990. Size-dependent allocation to sexual and vegetative reproduction in four clonal composites. *Oecologia* 84:254–259.
- Hendrickson, J.R., L.E. Moser, K.J. Moore, and S.S. Waller. 1998. Morphological development of 2 warm-season grasses in the Nebraska Sandhills. *J. Range Manage.* 51:456–462.
- Hendrickson, J.R., L.E. Moser, and P.E. Reece. 2000. Tiller recruitment patterns and biennial tiller production in prairie sandreed. *J. Range Manage.* 53:537–543.
- Jónsdóttir, I.S. 1991. Effects of grazing on tiller size and population dynamics in a clonal sedge *Carex bigelowii*. *Oikos* 62:177–188.
- Jónsdóttir, I.S. and T.V. Callaghan. 1988. Interrelationships between different generations of interconnected tillers of *Carex bigelowii*. *Oikos* 52:120–128.
- Jónsdóttir, I.S. and T.V. Callaghan. 1990. Intracolonial translocation of ammonium and nitrate nitrogen in *Carex bigelowii* Torr. ex Schwein. using ^{15}N and nitrate reductase assays. *New Phytol.* 114:419–428.
- Makita, A. 1996. Density regulation during the regeneration of two monocarpic bamboos: self-thinning or intracolonial regulation? *J. Vegetation Sci.* 7:281–288.
- Maun, M.A. and J. Perumal. 1999. Zonation of vegetation on lacustrine coastal dunes: effects of burial by sand. *Ecol. Letters* 2:14–18.
- Nixon, J.L. 1993. Dynamics of prairie sandreed rhizome development. M.S. Thesis. Univ. Nebraska. Lincoln, Nebr.
- Northup, B.K. 1993. Utilization of native forages of the Nebraska Sandhills by yearling cattle. Ph.D. Diss. Univ. Nebraska. Lincoln, Nebr.
- Reece, P.E., T.L. Holman, and K.J. Moore. 1999. Late-summer forage on prairie sandreed dominated rangeland after spring defoliation. *J. Range Manage.* 52:228–234.
- Reece, P.E., J.E. Brummer, R.K. Engel, B.K. Northup, and J.T. Nichols. 1996. Grazing date and frequency effects on prairie sandreed and sand bluestem. *J. Range Manage.* 49:112–116.
- SAS. 1986. SAS/STAT users guide. Release 6.03. SAS Inst., Inc., Cary, N.C.
- Schmid, B., F.A. Bazzaz, and J. Weiner. 1995. Size dependency of sexual reproduction and clonal growth in two perennial plants. *Can. J. Bot.* 73:1831–1837.
- Searle, S.R., F.M. Speed, and G.A. Milliken. 1980. Populations marginal means in the linear model: an alternative to least squares means. *Amer. Statistician* 34:216–221.
- Weaver, J.E. 1965. Native vegetation of Nebraska. Univ. Nebraska Press. Lincoln, Nebr.
- Welch, T. G. 1968. Carbohydrate reserves of sand reedgrass under different grazing intensities. *J. Range Manage.* 21:216–220.
- White, L.M. 1977. Perenniality and development of shoots of 12 forage species in Montana. *J. Range Manage.* 30:107–110.
- Wikberg, S., B.M. Svensson, and B.A. Carlsson. 1994. Fitness, population growth rate and flowering in *Carex bigelowii*, a clonal sedge. *Oikos* 70:57–64.
- Willms, W.D., S.M. McGinn, and J.F. Dormaar. 1993. Influence of litter on herbage production in the mixed prairie. *J. Range Manage.* 46:320–324.

Vegetation responses following wildfire on grazed and ungrazed sagebrush semi-desert

NEIL E. WEST AND TERENCE P. YORKS

Authors are Professor and Research Associate, respectively, Department of Rangeland Resources, Utah State University, Logan, Utah 84322-5230.

Abstract

A 20-year set of cover data on sagebrush semi-desert plant communities responding to wildfire and livestock grazing near Mills in central Utah provided an opportunity to compare the assumptions and adaptability of classical and state-and-transition models for describing secondary succession. Cover data were organized and analyzed by plant species, growth forms, and other ground cover classes. Graphical analysis, ordination (employing semi-strong hybrid multi-dimensional scaling), regression, and analysis-of-variance were used to determine whether the patterns observed were best described as community change (tightly linked species) or individualistic change (each species acting independently). Distinct differences in total plant cover, growth form, and species composition were found between burned (both grazed and ungrazed) and the unburned and grazed treatments. Conventional graphical and statistical analyses of burned and ungrazed plots showed greater and earlier expansion of perennial grasses and then relatively less cover-weighted compositional change in recent years compared to the other treatments. Vegetation on none of the treatments appears to have stabilized toward either the pre-burn sagebrush semi-desert, a new state or the potential natural community for the site involved. Pathways of change reflected in the ordinations have been complex in all treatments. The only obvious trends in responses of individual species were to fire and the inverse relationship of cheatgrass to total perennial vegetational cover. All this evidence points to few tight linkages between species or growth form groups and thus favors viewing these patterns individually. While the state-and-transition model allows greater flexibility than the classical model in the depiction of plant community/individual species changes consequent to any management action, it doesn't apply readily everywhere, as exemplified by this case study.

Key Words: community dynamics, Clementsian model, state-and-transition model, ordination, trend, condition

Research was funded by the Utah Agricultural Experiment Station of which this journal is Paper No. 7289. This research would have not been possible without permission from previous landowners as well as the current land owner, Ben Gambino. Also, a long list of students and the West family helped in annually collecting the data. All data and ancillary records are deposited in the Archive Section of the Merrill Library at Utah State University. Special thanks go to Susan Durham and Jim Haefner for advice on analysis methods.

Manuscript accepted 13 Apr. 01.

Resumen

Un juego de datos de 20 años sobre cambios de la cobertura vegetal de comunidades semidesérticas de "Sagebrush" en respuesta a fuegos naturales y apacentamiento de ganado de áreas cerca de Mills, en la parte central de Utah, dieron una oportunidad para comparar los supuestos y la adaptabilidad de los modelos clásicos y los de estado y transición para describir la sucesión secundaria. Los datos de cobertura fueron organizados y analizados por especies de plantas, formas de crecimiento y otras clases de cobertura de suelo. El análisis gráfico, la ordenación (empleando un híbrido semi-fuerte de escalamiento multidimensional), el análisis de varianza y regresión se utilizaron para determinar si los patrones observados fueron los mejores para describir como cambia la comunidad (especies fuertemente ligadas) y los cambios individualísticos (cada especie actuando individualmente). Se encontraron distintas diferencias entre los tratamientos de quema (ambos, apacentados y sin apacentar) y los sin quema y apacentados, diferencias respecto a la cobertura vegetal total, la forma de crecimiento y la composición de especies. Los análisis gráficos y estadísticos convencionales de las parcelas quemadas y sin apacentar mostraron una expansión mayor y mas temprana de los zacates perennes y por lo tanto un cambio relativamente menor de composición ponderada por cobertura en los años recientes comparado con otros tratamientos. En ninguno de los tratamientos la vegetación parece haberse estabilizado hacia las condiciones previas a la quema del "Sagebrush" semidesértico, un nuevo estado o la comunidad natural potencial del sitio involucrado. Las rutas de cambio reflejadas en los ordenamientos han sido complejas en todos los tratamientos. Las unicas tendencias obvias en las respuestas de las especies individuales fueron al fuego y la relación inversa del "Cheatgrass" con la cobertura vegetal total perenne. Toda esta evidencia apunta a unos pocos vínculos fuertes entre grupos de especies o formas de crecimiento y de este modo favorece el ver estos patrones en forma individual. Mientras el modelo de estado y transición permite una mayor flexibilidad que el modelo clásico en la representación de los cambios de especies individuales o comunidades en consecuencia de cualquier acción de manejo, este no aplica fácilmente en todas partes, como se ejemplifica en este caso.

Basic ecologists, beginning about 1958, have rejected the linear, gradual, deterministic and reversible model of succession to climax (called the "classic" model here) associated with F.E. Clements (Burrows 1990). Rangeland ecologists slowly accepted this situation and have been searching for a replacement theory (Lauenroth and Laycock 1989) and a more modern means to

monitor rangeland trend and judge condition (West and Smith 1997). Some (e.g. Laycock 1991, 1995) think that the state-and-transition model (Westoby et al. 1989a) will be that replacement. Joyce (1993), however, cautions the profession not to abandon older ways of applying successional theory to the monitoring of trend and assessment of condition until we have adequate means of operating within a new theoretical framework. Scarnecchia (1995) persuasively argues that theory and methods should not be intimately linked if the profession is to mature. Both theory and methods will continue to evolve independently anyway.

The classic successional model is based on a mechanical metaphor (Botkin 1990), the static concept of stability (lack of change unless disturbed), and an ability to return to the previously defined single state of constancy (climax) after disturbance (Joyce 1993). The classic model assumes tight linkages between species and positive feedback of plants in changing microclimate and soils (facilitation) and advocates steady, unidirectional change toward climax. The state-and-transition model (Westoby et al. 1989a, 1989b) implies that plant community composition makes dramatic changes only during times of unusual environmental influences. Furthermore, the species composition of differing plant communities in particular states, on a particular ecological site, fluctuate within defined limits (Treshow and Allan 1985), which can also be expressed as several domains of attraction, or boundedness (Lewontin 1969, Friedel 1991, Crowley 1992), depending on the degree of responses to disturbance.

Most modern observers consider the longer-term, directional differences between species presence and abundances within stands of vegetation occupying the same ecological sites and enduring similar treatments to indicate individualistic change (uncoordinated temporal changes by individual plant species in a particular community). While the state-and-transition model is capable of depicting either individualistic or co-ordinated compositional change, an examination of data in light of the manager's needs should indicate the favored perspective in particular circumstances.

How is a rangeland technician/manager to go about monitoring with this swirl of scientific and technological change about him or her? Rather than just considering these needs abstractly, we find it useful to work with case studies and analyze data in alternative ways. The following reviews

how a 20-year interannual set of data on plant community and soil surface exposure in a sagebrush semi-desert area changed after wildfire. Some of the plots were subsequently grazed, but other plots were protected from livestock grazing. We will compare the responses in these differing treatments with competing theoretical and analytical frameworks.

Our objective was to opportunistically examine changes in vegetation cover and bare soil in a Utah instance and compare the assumptions and adaptability of classical and newer models of secondary succession. In particular, we wished to compare data organized by plant species, growth forms and other ground cover classes, analyzed by statistical, graphical and ordination techniques. The literature led us to expect that alternate stable states would be created by wildfire, particularly when followed by livestock grazing. Detection of the several putative stable states was expected to be most easily discerned by ordination. We also expected that there would be evidence of tight rather than loose or no connections between species and growth forms as they replaced each other over time.

Materials and Methods

The study site is located on privately-owned land 7.9 km west of the village of Mills, Juab Co. in central Utah (39° 29' N, 112° 7' W) on a dissected fan remnant or

ballena (Peterson 1981) on the northeastern flank of the Canyon Mountains. Slopes are 1 to 2% east-facing, with elevations ranging between 1,617 and 1,622 meters (5,305 to 5,320 ft). Mean annual precipitation is about 300 mm and is, on average, concentrated from October to April. The mean annual air temperature is about 8° C (Trickler and Hall 1984).

Soils in the study area were mapped as Borvant cobbly loam, 2–8% slopes (Trickler and Hall 1984). Profiles are mostly shallow, with less than 50 cm of calcareous, gravelly to very gravelly loam above a petrocalcic horizon, which overlies stratified layers of gravelly loam and calcium carbonate-cemented material (Boettinger et al. 1997). These soils are classified as loamy-skeletal, carbonatic, mesic shallow Petrocalcic Paleoxerolls. The designated ecological site is Upland Shallow Loam (Juniper-Pinyon) with a potential natural community composed of 40% perennial grasses, 10% perennial forbs and 50% shrubs (by relative contribution to peak new growth phytomass) (Trickler and Hall 1984).

Vegetation at the study site immediately pre-burn and during the first 3 years of recovery following the wildfire of 26 July 1981 have been previously reported (West and Hassan 1985). This earlier paper also has further details about the fire. Since these responses to the pulse treatment of the fire were likely transitory (Tilman 1988), subsequent vegetational change was of continuing interest. Table 1 lists

Table 1. The 3 plant species contributing the greatest average cover in each of 5 lifeform classes at our study site.

Lifeform	Rank 1	Rank 2	Rank 3
Perennial grasses	bluebunch wheatgrass <i>Pseudoroegneria spicata</i> (Pursh) A. Löve ssp. <i>spicata</i>	Indian ricegrass <i>Achnatherum hymenoides</i> (Roemer & J.A. Schultes) Barkworth	Sandberg bluegrass <i>Poa secunda</i> J. Presl
Annual grasses	cheatgrass <i>Bromus tectorum</i> L.		
Shrubs	Wyoming big sagebrush <i>Artemisia tridentata</i> Nutt. ssp. <i>wyomingensis</i> Beetle & Young	Nevada jointfir (or Mormon tea) <i>Ephedra nevadensis</i> S. Wats.)	yellow rabbitbrush <i>Chrysothamnus viscidiflorus</i> (Hook.) Nutt.
Annual forbs	Russian thistle <i>Salsola kali</i> L.	northern tansymustard <i>Descurainia sophioides</i> (Fisch. ex Hook.) O.E. Schulz	prickly lettuce <i>Lactuca serriola</i> L.
Half-shrubs	broom snakeweed <i>Gutierrezia sarothrae</i> (Pursh) Britt. & Rusby	granite prickly phlox <i>Leptodactylon pungens</i> (Torr.) Torr. ex Nutt.	phlox <i>Phlox longifolia</i> Nutt.
Perennial forbs	mountain pepperweed <i>Lepidium montanum</i> Nutt.	sandwort <i>Arenaria fendleri</i> Gray	fleabane <i>Erigeron argentatus</i> Gray

Plant name source: USDA, NRCS 1999. The PLANTS database (<http://plants.usda.gov/plants>).

Fig. 1. Summarization of disturbance history for the various treatments.

the 3 most important plant species (in terms of average cover) in each of the life-form categories used.

The history of the treatments is summarized in Figure 1. Pre-fire vegetational and ground surface data were collected in 1981 within 4 original macro-plots used for another study (Hassan and West 1986). Establishment of a new well following the fire made a previously unwatered and lightly grazed portion of the 4,700 ha pasture, of which the study site is in the northwestern corner, accessible to cattle grazing. In order to opportunistically observe the changes in vegetation after fire, with and without the concomitant press-type (Tilman 1988) effect of livestock grazing, the 4 original macro-plots were separately fenced and 2 storage gauges for crop-year (1 September to 30 June) precipitation were established within 2 of the 4 exclosures within the burned and ungrazed treatment (Fig. 1).

Additional macro-plots were established outside of the exclosures on the same ecological site to conduct an ad hoc "experiment" on vegetation dynamics in burned and unburned patches under grazed conditions (Fig. 1). Large enough unburned patches on the same ecological site were, unfortunately, unavailable to also fence and thus balance the design. Monitoring to support adaptive resource management will, however, require compromises between the scientists' need for experimental rigor with managers' needs for timely decision making (Szaro 1999, Thomas and Birchfield 2000).

All available treatments were replicated (Fig. 1), although numbers of replicates varied with the opportunities available. The study area had probably been lightly grazed in winter by sheep several decades before the wildfire event. The owners during the early part of our study period, however, leased the land only for cattle

use. Neither the owner or leasee were willing to provide specifics of the grazing arrangement. We, therefore, can provide only qualitative impressions that there were usually "moderate" levels of grazing on the areas outside the fenced exclosures. Livestock grazing prior to collection of data would have a negative impact on the amount of plant cover remaining in the unfenced plots. Also there were some years late in the time series when cattle had not used the areas around the exclosures at all. These less frequent circumstances will be pointed out in the discussion of results. The pre-burn rangeland at this site was considered to be in "high good" (late seral) condition in 1981 by conventional methods (West and Hassan 1985).

The 4 exclosures (burned and ungrazed) and the unfenced, burned and grazed plots measured 20 m by 50 m. Four exclosures (each 20 m by 50 m in size) were fenced during the fall of 1981 on comparable segments of the largely burned ballena. These constituted the 4 replicates of the burned and ungrazed treatment. Four other areas of 20 m by 50 m size in adjacent locations on similar terrain were also marked out at that time. These involved the burned and grazed treatment. Both of these treatments constituted subsamples of the larger available burned areas. The rarer unburned and grazed patches had to be sampled by three, 20 m by 20 m macro-plots and occupy most of the "islands" left within the mostly burned ballena. Five years following initiation of the study, some of the area outside the fenced exclosures was chained by the owner to topple scattered, fire-killed juniper snags. This activity seriously altered 1 of the unburned and grazed replicates and further sampling was not done there.

A second wildfire occurred on a subset of the original plots before the 1987 data collection. However, because of a drought (Fig. 2) and consequent lack of continuous fine fuel, the effects of that fire were very patchy. From yearly photographs taken at permanent points and field journal notes, it appeared that Exclosures #2 and #3 were partially impacted, Exclosure #1 escaped entirely, and Exclosure #4 was completely reburned. Effects of the second fire on the vegetation were no longer either visually or statistically discernable the year following its occurrence in early July 1987. None of the grazed plots were impacted by the 1987 fire. In 1996, shortly after data collection, 1 of the unburned and grazed plots was burned, and so lost for further comparisons.

Fig. 2. Total crop-year (Sept. 1-June 30) precipitation (mm) at the study area, 1981–2000. Average of two storage gauges, except 1981–3 and 1988 when gauges were vandalized and an estimate was made by correlation with the Scipio station located 26 km to the SSE at 1,615 m elevation, $r^2 = 0.67$.

Both cover and end-of-growing season aboveground plant standing crop data were collected in 1982 (West and Hassart 1985). The latter was time-consuming, and if repeated annually, would have severely altered the vegetation on these relatively small macro-plots. Thus, only the cover in the topmost layer in the sward was estimated after 1982 in all plots. Canopy cover data are also more easily related to remotely-sensed imagery than phytomass. Canopy cover data were rapidly and non-destructively collected, using a gimbaled point technique (Winkworth and Goodall 1962), near the end of each growing season (third week of July). One hundred stations, from random starting points for 4 stepped off transects, were visited per macro-plot, and readings interpreted as percentage canopy cover of the current year's plant growth. Bare soil, gravel, rock, microphytes (moss + lichen), standing dead and litter were also enumerated where no live plants occurred directly above a point (sampling station). These sample numbers were considered adequate to detect changes in total community cover and cover classes greater than 3%, through duplicate sampling 1 day apart in 1993 (Hosten 1995). Treshow and Allan (1985) employed similar numbers of subsamples for comparable vegetation.

In addition to graphing cover over time for total live and dead cover, growth form groups and species composition in each plot, ordination diagrams were used to discern temporal trends in total canopy cover-weighted plant community species composition within each replicate of each

treatment. Semi-Strong Hybrid (SSH) Multi-Dimensional Scaling (Faith et al. 1987) was the chosen indirect ordination tool using the PATN (Belbin 1992) software package. The continuous form of the Kulczynski Similarity Index (Belbin 1992) was used as input. Judging the similarities/dissimilarities of ordinations is difficult just by visual inspection. In order to judge "tightness" and similarity/dissimilarity of the successional trajectories between treatments, we calculated mean distances between sequential points in

time, total lengths of the time trajectories, numbers of crossovers, and directions of the yearly segments from the centroid. The SSH multi-dimensional scaling was chosen because it produces a measure of adequacy of fit to the scattergram termed "stress" (Faith et al. 1987). "Stress" is analogous to distances of points from the regression line in a least squares sense (Dillon and Goldstein 1984, p. 129). The values of "stress" potentially range from 0 to 1.0, but points with "stress" values above 0.2 are considered unreliable (Dillon and Goldstein 1984) and thus not discussed here. Discrete clusters of points in different quadrants of ordination space would be taken as evidence of alternate stable states. Closely clustered points [separated by distances shorter than those expected by a combination of sampling error and those due to climatic fluctuation (Rabotnov 1974)] would be taken as evidence of no ecologically significant change in species or lifeform composition.

Data bearing on the classical static notion of stability could be gathered only on the burned and ungrazed treatment because the chronic impact of livestock grazing occurred outside these 4 exclosures. The degree of return to pre-fire plant community composition was ascertained from both graphs of cover by lifeforms and from ordination diagrams by visually comparing the placement of ordination points against a background representing ordination of all plots during all years including 1981. Comparison of vegetation change between all of the treat-

Fig. 3. Total and growth form canopy cover due to live plants within the burned and ungrazed exclosures, 1981–2000.

Fig. 4. Total and growth form canopy cover due to live plants within the burned and grazed macro-plots, 1982–2000

ments could be legitimately done with 1982 and older data because ordination space is flexible and relational, changing as data are added or subtracted (Dillon and Goldstein 1984). The placement of data points representing plots outside the exclosures, where cattle usually grazed, were compared to those inside the exclosures to determine possible additive effects of grazing and the interactions between burning and grazing.

While the graphical and ordination approaches helped us to visualize the important changes in vegetation within these plots over time, we also needed a means of deciding whether the differences observed had statistical significance. Accordingly, commercial statistical software packages were used; JMP® was the basis for regression, and SYSTAT® for testing ANOVA models. To address the possibility of lack of independence between years (serial correlation), we used a general linear mixed model for longitudinal data incorporating each macroplot as a block (accommodating variability among them) and explicitly accounting for the covariance among repeated measures within a macroplot (Verbeke 1997). A 5% probability for false separation among least square means was the chosen level of statistical significance.

Results and Discussion

Mean Total Cover

Mean total cover due to living plants within the four burned and ungrazed exclosures averaged 57%, but varied between 37% and 79% over the 20 years

of available data (Fig. 3). Live plant cover appeared to increase during wet periods and decline during droughts (Figs. 2 and 3). The correlation of total live cover to total precipitation received during the preceding crop year was, however, only 0.42 ($p = 0.07$), indicating lagged soil moisture effects and other influences on plant cover were also probably operative.

Mean total live plant cover within the 3 burned and grazed plots (Fig. 4) followed the same trends as the burned and ungrazed macro-plots, except that the average cover was 46%, and minima (22%) and maxima (73%), each of which were less than on the burned and ungrazed treatment even though no cattle grazing took place on these unfenced macro-plots

in 1997, 1999, and 2000.

Mean total live cover in the unburned and grazed plots (Fig. 5) followed similar trends with the average cover (47%) and maxima similar (68%, in 2 different years), whereas the minimum was greater (37%) than the other grazed treatment.

Shrub Cover

Prior to the fire of 1981, shrubs, which were mostly Wyoming big sagebrush (West and Hassan 1985), constituted 32% of live plant cover on the 4 burned and ungrazed macro-plots (Fig. 3). The unburned and grazed remnants had 22 to 26% relative shrub cover for the first 3 years following the 1981 fire (Fig. 5). That proportion increased only slightly over the next 17 years (Fig. 5). The shrub cover increase on the burned areas was mainly due to Mormon tea. This shrub has shown several periods of growth (sometimes exceeding its pre-burn cover about two-fold) and diminishment that were not always synchronous in the 3 treatments (Fig. 6). *Artemisia* has been slow to reestablish at our burned locations. The return of sagebrush at this sagebrush semi-desert (West 1983) site is much slower following fires than in sagebrush steppe (Bunting 1984, Britton and Clark 1984, West 2000). As Treshow and Allen (1985) found for another sagebrush semi-desert site in Utah, shrub cover varied little during the period of study on the unburned but grazed plots (Fig. 5). The dominant Wyoming big sagebrush is a deep rooted evergreen known not to vary as much as herbaceous species in response to drought (Passey et al. 1982).

Fig. 5. Total and growth form canopy cover due to live plants within the unburned and grazed macro-plots, 1982–2000.

Fig. 6. Mean total canopy cover due to Mormon tea observed in the three treatments from 1982–2000.

Perennial Grass Cover

Perennial grasses constituted about 32% cover (55% of the relative live cover) in 1981 before the first fire (Fig. 3). After an initial large reduction due to the fire, relative cover of the perennial grasses in the burned and ungrazed treatment increased steadily until 1994 when the second drought during the study period began (Fig. 2). Absolute cover of perennial grasses also increased until 1994 in this treatment (Fig. 3). Since 1994 perennial grass cover has fluctuated and other perennial life forms (half-shrubs, forbs) have increased, both in relative and absolute senses.

Perennial grass cover on the burned and grazed plots increased during the first 5 years following the 1981 fire and then fluctuated greatly (Fig. 4), apparently mainly due to variations in both precipitation (Fig. 2) and grazing. No apparent cattle grazing occurred here in 1997, 1999, and 2000. Moderate levels of utilization were qualitatively observed until 1996 when the heaviest degree of cattle grazing was noted.

Perennial grass cover in the unburned and grazed macro-plots has varied the least of any growth form over time (Fig. 5), never exceeding 30% absolute cover or 50% of relative live cover. This is apparently a result of the continuing control of the micro-environment in these patches by sagebrush (Pierson and Wight 1991, Treshow and Allan 1985).

Annual Grass Cover

Annual grasses were the major cover component on all burned macro-plots from 1982 to 1984 (Figs. 3 and 4). Their

absolute and relative contributions to live cover decreased nearly to 0 from 1989 to 1993 (Hosten and West 1994) on all treatments during the greatest drought occurring during the study period (Fig. 2). Annual grasses, however, increased in

both absolute and relative senses on all treatments in the generally wetter period since 1993 (Fig. 2), until 2000, when precipitation was again below the long term mean (Figs. 2, 3, 4, and 5).

Ordinations

Although copies of full tabular data showing cover composition by individual species (besides Mormon tea, Fig. 6) under the 3 treatments over 20 years are available from the authors, their demand for printed space precludes their publication here. Accordingly, we have chosen to graphically show the overall changes in plant community composition through ordination of data from the 3 treatments (Fig. 7). Ordination is a dimension-reducing, pattern-seeking, relational technique. That is, the dimensions of covers of all individual species or growth form categories are reduced to 2 dimensions (axes) so the results of the multivariate analyses can be viewed on paper.

To test the sensitivity of ordination to differences in data input, we compared the SSH ordinations of the burned, ungrazed treatment with and without the 1981 pre-burn data. This created trajectories which started and stopped in differing quadrants

Fig. 7. Ordination of mean cover-weighted plant species composition in the three treatments from 1982–2000. The gray area represents the overall area within which points were found through ordinations of individual macro-plots.

Table 2. Characteristics of ordination pathways. Mean values for each of three treatments. Lengths are relative units, positive degrees of change are clockwise, negative are counter clockwise, quadrant I=0-90°, II=91-179°, III=180-269°, IV=270-359°

Treatment	Mean segment length	Total path length	Number of crossovers	Net degrees of change	Frequency of Points in Quadrants			
					I	II	III	IV
Burned, Ungrazed	2.8	27	4	-287	2	7	4	6
Burned, Grazed	3.0	28	3	523	4	6	5	4
Unburned, Grazed	3.5	33	3	556	3	6	4	6

(Figs. 7a and b). The pre-burn vegetation was sagebrush dominated (West and Hassan 1985) and had a longer list of plant species present than in any other subsequent year. We, thus, confirmed the importance of only using data collected between 1982 and 2000 when comparing ordinations of data from the 3 treatments.

The comparison of 1982-2000 successional trajectories in ordination space was made with the aid of 5 enumerations (Table 2). The burned, ungrazed treatment showed the shortest total length of trajectory path and shortest average length of steps between years. Counter-clock-wise tracking canceled out most of the clockwise movement and created 4 crossovers, the most observed in any treatment. Most of the movement in the burned, ungrazed trajectory was in Quadrants II and IV (Table 7b).

The burned and grazed treatment showed an intermediate total length of pathway and mean for segment lengths between years (Table 2, Fig. 7c). The high positive net degrees of change fortifies the visual impression of a tendency for this trajectory to spiral clockwise. No particular quadrants were favored. The unburned, grazed treatment showed the longest total trajectory length and thus, also the greatest mean segment length (Table 2). This treatment also showed the strongest evidence of a clockwise twist to the time trajectory. Quadrants II and IV were favored in this treatment. The number of crossovers in the trajectories for the different treatments were very similar.

From inspections of ordinations, we found it difficult to conclude that the vegetation was stable in any of the treatments. The only consistent result was the pronounced protrusion into the second quadrant on the 2 grazed treatments during 1996, the year with the greatest degree of forage utilization by cattle. Thus, ordination did not portray secondary successional patterns in easy to interpret ways. While the literature generally favors ordination

as a way of compressing data on compositional change, this study demonstrated that where total species lists are short and temporal changes are drastic, differences in a few species with episodic occurrence (e.g. Mormon tea, cheatgrass) can result in very different pathways of secondary succession being expressed.

Regression Analyses

Another, simpler way to make comparisons of vegetational changes over time between treatments is to graph scatter plots, visually compare, and regress the time courses of life form cover by treatment. While we did this for all life form groups, the most notable patterns were observed for total perennials (Fig. 8) and perennial grasses (Fig. 9). This was true regardless of whether all the data in a treatment were combined (Figs. 8 and 9) or analyzed replication by replication (not shown). Both the linear regressions and statistical analysis of their slopes (Underwood 1997) showed there has been a significantly ($p < .05$) faster increase of perennials in the burned and ungrazed than the other 2 treatments. No significant change in perennial cover was detected in either type of grazed treatment. The drought of 1986-92 (Fig. 2) had no consistent effect on these patterns. Perennial grasses were the major contributors to the total perennial cover in the burned treatments, thus, when they were considered alone (Fig. 9), it was no surprise that the burned and ungrazed treatment showed perennial grass cover increased at the most rapid rate and sustained the greatest average cover of these plants at the end of the study.

Another interesting feature of the regression analyses was that while there was no evidence from linear fits that either total perennial (Fig. 8) or perennial grass (Fig. 9) cover had yet reached the maximum in the burned and ungrazed treatment, many nonlinear fits were tried but a

4th order nonlinear fit of the combined data did increase the R^2 about 50% and indicated a leveling off since about 1993. This asymptotic response is to be expected in ungrazed vegetation of this region (Passey et al. 1982, Sneva and Britton 1983). We also analyzed these data with each replicate as a data point. These results showed a similar pattern, with an increased variance, but are too visually cluttered to reproduce effectively here.

The drought period of 1986-92 (Fig. 2) did not reduce the cover of perennial grasses, but did reduce the cover of annual grasses, regardless of treatment (Fig. 3, 4, and 5). Annual grasses, however, have rebounded comparatively more since the drought on the burned plots, both grazed and ungrazed (Figs. 3 and 4). This conclusion is further supported by plotting the relationship of perennial grass cover to annual grass cover by treatment over all years, irrespective of the time course (Fig. 10). In the ungrazed macro-plots, there was a clear tradeoff of more perennial grass as annual grasses declined and vice versa, a situation not found in either the burned and grazed or unburned and grazed macro-plots ($p < .05$) (Fig 10).

Analysis of Variance (ANOVA)

Another common way to compare the effects of treatments is through ANOVA (Underwood 1997). Total perennial cover, (Fig.11a), was similar in the exclosures (burned and ungrazed) and the unburned and grazed treatment, but lower ($p < .01$) in the burned and grazed treatment. Annual grass cover (Fig.12b) was significantly ($p < 0.05$) lower in the unburned and grazed treatment. The largest separation among life form groups was for perennial grasses (Fig. 11c), where the repeated measures ANOVA confirmed that the burned and ungrazed treatment had significantly higher cover ($p < .001$). This result supports the earlier discussion of the temporal pattern of increases in the perennial grass component (Fig. 3 and 9).

Conclusions

This long-term study has found several results that are counter to the expectations derived from earlier, and mostly shorter-term investigations reported in the literature (West and Young 2000). First of all, once cheatgrass came to dominate in the first few years following the 1981 wild-fire, we expected this widespread invader grass to stay abundant thereafter. Instead, the perennial grasses recovered vegeta-

Fig. 8. Regressions of mean total perennial canopy cover observed in the three treatments from 1982–2000, plus 1981 mean pre-fire cover for the burned and ungrazed exclosures. Poly = fourth order polynomial fit.

Fig. 9. Regressions of mean total perennial grass canopy cover observed for each of the three treatments from 1982–2000, plus 1981 mean pre-fire cover for the burned and ungrazed exclosures. Poly = fourth order polynomial fit.

Fig. 10. Cover of perennial grasses in relation to cover of annual grasses by treatment over all years.

tively and came to dominate plant cover ever since, especially in the ungrazed macro-plots. Furthermore, cheatgrass and other annuals almost became locally

absent from 1989–1992, during the longest and most profound drought experienced during the study. This means that the threshold (Stringham et al., in press) to

a new annual-dominated state, as has occurred often elsewhere (West and Young 2000), has not been crossed at the site studied here.

The reinvasion of sagebrush and juniper following the wildfire was unexpectedly slow. Although several surges of Mormon tea recovery and subsequent dieback were detected, that species also recovered vegetatively. Wyoming big sagebrush and Utah juniper must return through seed dispersal. Even though unburned patches with mature sagebrush and juniper have persisted nearby (less than 50 m away), sagebrush seedlings are few, and juniper seedlings undetected, so far, in the burned macro-plots. This would support the conclusion that bunchgrasses were probably more dominant in the past (Trickler and Hall 1984) before the fire regime was altered (West 2000). The potential natural community for this site, however, is expected (Trickler and Hall 1984) to have about 50% cover by woody species.

Looking at the results of our analyses in total, not just by species or growth form groups, suggests that permanent changes in state have not yet occurred here, regardless of treatment. We are, however, using the definitions of Stringham et al. (in press), where changes in state are what happens when thresholds of permanent change in the abiotic environment occur, usually following accelerated soil erosion. Except for the obvious negative interactions between annuals, particularly cheatgrass, and all perennials, primarily the bunchgrasses, we see only loose linkages between species and life form groups in vegetational recovery following fire and subsequent sporadic cattle grazing of the unfenced plots.

We expected ordination to be the most revealing method for interpreting species-oriented vegetation change. We found, however, that the type of ordination we used is very sensitive to changes in the input data, low species numbers and the dramatic shifts in this vegetation over time. Graphic analysis was more easily interpretable than ordination. Regression and ANOVA also had some utility in distinguishing between treatments with known statistical significance. All the different methods of analysis used showed unique and partial views of results that complement one another.

The owner of the privately-held land upon which we conducted this study expects to continue to derive some income from livestock grazing. Thus, to him, the vegetation in the exclosures is not the reference condition or what he expects to see

Literature Cited

Fig. 11. Least square means and standard error bars for (a) total perennial cover, (b) perennial grass and, (c) annual grass cover in the three treatments. Differing lower case letters over the bars indicate statistical significant differences at $p < 0.05$. Different treatments designated by same code as used in Figure 1.

across all portions of the pasture where the Upland Shallow Loam (Juniper-Pinyon) Ecological Site occurs. On the nearby federally owned (BLM) land with the same ecological site, livestock production is not necessarily the sole or primary objective. Soil protection and wildlife interests rank higher there. In those circumstances, the vegetation within the exclosures have higher value as references for judging condition (Szaro 1999).

It should be noted that our study area is not typical of most sagebrush semidesert (West 1983) sites in the eastern Great Basin. The ballena on which the data were taken is a remnant of an alluvial fan that has undergone considerable dissection (Peterson 1981). In other words, the land upon which the plots occur is very old. This is shown by the continuous accumulation of the petrocalcic layer (Boettinger et al. 1997) with only a shallow surface horizon above. Thus, because of this great age of the soil, most of the nutrients have probably either long ago left the site or are occluded on the calcium carbonate (phosphorus in particular).

In 1981, we found sagebrush dominated vegetation with remnants of herbaceous perennials. The wildfire destroyed the sagebrush and widely scattered juniper over most of the ballena. While cheatgrass dominated in the first few years following the fire, the perennial grasses recovered vegetatively and have come to dominate since, especially in the ungrazed exclosures. We speculate that such an unexpected result (the transitive role of cheatgrass) can only be expected on sites with low stores of and capacities to fix nitrogen and other critical elements to plant growth.

In summary, we have found the collection and analysis of interannual vegetational data aggregated and analyzed in various ways in this opportunistic "experiment" to be illuminating of the issues involved in modernization of our approaches to applying ecology to determine rangeland condition and trend. While our specific results apply only to 1 ecological site, we feel we have demonstrated with minimal effort (4 person days per year of field work), the usefulness of long-term data sets in guiding acceptance or rejection of some of the general suggestions in the literature as to how to organize data for and interpret the results of monitoring to guide management decisions. We recommend that others look for similar opportunities elsewhere.

- Belbin, L. 1992.** PATN: Pattern analysis package users guide. Commonw. Scientific and Indust. Res. Organ., Div. of Wildlife and Rangelands Res., Canberra, ACT, Australia.
- Boettinger, J.L., J.A. Doolittle, N.E. West, E.W. Bork and E.W. Schupp. 1997.** Nondestructive assessment of rangeland soil depth to petrocalcic horizon using electromagnetic induction. *Arid Soil Res. and Rehabilitation* 11:375–390.
- Botkin, D.B. 1990.** *Discordant harmonies*. Oxford University Press, New York, N.Y.
- Bunting, S.C. 1984.** Fires in sagebrush-grass ecosystems: successional changes, p. 7–11. *In: K. Sanders and J. Durham (eds.) Rangeland fire effects: a symposium*. U.S. Dept. Interior Bureau of Land Manage., Boise, Ida.
- Britton, C.M. and R.G. Clark 1984.** Effects of fire on sagebrush and bitterbrush, p. 22–26. *In: K. Sanders and J. Durham (eds.) Rangeland fire effects: a symposium*. U.S. Dept. Interior, Bureau of Land Manage., Boise, Ida.
- Burrows, C.J. 1990.** *Processes of vegetation change*. Unwin Hyman, London.
- Crowley, P.H. 1992.** Density dependence, boundedness, and attraction: Detecting stability in stochastic systems. *Oecologia* 90:246–254.
- Dillon, W.R. and M. Goldstein. 1984.** *Multivariate analysis: methods and applications*. John Wiley and Sons, New York N.Y.
- Faith, D.P., P.R. Minchin, and L. Belbin. 1987.** Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* 69:57–68.
- Friedel, M.H. 1991.** Range condition assessment and the concept of thresholds: a viewpoint. *J. Range Manage.* 44:422–426.
- Hassan, M.A. and N.E. West. 1986.** Dynamics of soil seed pools in burned and unburned sagebrush semi-deserts. *Ecol.* 76:269–272.
- Hosten, P.E. 1995.** Assessing the relative utility of models of vegetation dynamics for the management of sagebrush steppe rangelands. Ph.D. Diss., Utah State Univ., Logan, Ut.
- Hosten, P.E. and N.E. West. 1994.** Cheatgrass dynamics following wildfire on a sagebrush semidesert site in central Utah, p. 56–62. *In: S.B. Monsen, and S.G. Kitchen (compilers), Proc. Symposium Ecology And Management Annual Rangelands*, U.S. Dept. Agr. Forest Service, Intermountain Res. Sta., Gen. Tech. Rep. INT-GTR-313, Ogden, Ut.
- Joyce, L.A. 1993.** The life cycle of the range condition concept. *J. Range Manage.* 46:132–138.
- Lauenroth, W.K. and W.A. Laycock (eds.) 1989.** *Secondary succession and the evaluation of rangeland condition*. Westview Press, Boulder, Colo.
- Laycock, W.A. 1991.** Stable states and thresholds of range condition on North American rangelands—A viewpoint. *J. Range Manage.* 44:427–433

- Laycock, W.A. 1995.** New perspectives on ecological condition of rangelands: can state and transition or other models better define conditions and diversity, p. 140–164. *In:* L. Montes and G.E. Olivia (eds.) *Proceedings International Workshop on Plant Genetic Resources Desertification and Sustainability*. Centro Regional Patagonia Sur, INTA-EEA, Rio Gallegos, Santa Cruz, Argentina.
- Lewontin, R.C. 1969.** The meaning of stability, p. 13–22. *In:* G.M. Woodwell and H.H. Smith (eds.), *Diversity and stability in ecological systems*. Brookhaven Sym. Biology 22. Brookhaven National Laboratory, Upton, N.Y.
- Passey, H.B., V.K. Hugie, E.W. Williams, and D.E. Ball. 1982.** Relationships between soil, plant community, and climate on rangelands of the Intermountain West. U.S. Dept. Agr. Soil Cons. Serv., Tech. Bull. 1669.
- Pierson, F.B. and J.R. Wight. 1991.** Variability of near surface temperature on sagebrush rangeland. *J. Range Manage.* 44:491–497.
- Peterson, F.F. 1981.** Landforms of the Basin and Range Province defined for soil survey. Nevada Agr. Exp. Sta. Tech. Bull. 28, Univ. Nevada, Reno, Nev.
- Rabotnov, T.A. 1974.** Differences between fluctuations and succession, p. 21–21. *In:* R. Knapp (ed.) *Vegetation Dynamics. Handbook of Vegetation Science*. Vol 8. W. Junk Publ., The Hague, Netherlands.
- Scarnecchia, D.L. 1995.** Viewpoint: The rangeland condition concept and range sciences search for identity: A system viewpoint. *J. Range Manage.* 48:181–186.
- Sneva, F. and C.M. Britton. 1983.** Adjusting and forecasting herbage yields in the Intermountain Big Sagebrush Region of the Steppe Province. Oregon Agr. Exp. Sta. Bull. 659. Oregon State Univ., Corvallis, Ore.
- Stringham, T.K., W.C. Krueger, P.J. Meiman and P. Shaver, in press.** States, transitions, and thresholds: Further refinement for rangeland applications. Addendum to National Range and Pasture Handb. Natural Resources Cons. Service, Grazing Lands Tech. Institute, Fort Worth, TX.
- Szaro, R. 1999.** Monitoring and evaluation, 223–230. *In:* N.C. Johnson, A.J. Malk, R.C. Szaro, and W.T. Sexton (eds.), *Ecological stewardship*, Vol. I, Elsevier, Amsterdam.
- Tilman, D. 1988.** Plant strategies and the dynamics and structure of plant communities. Princeton Univ. Press, Princeton, N.J.
- Thomas, J.W. and J. Birchfield. 2000.** Science, politics and land management. *Rangelands* 22 :45–51.
- Treshow, M. and J. Allan. 1985.** Uncertainties associated with the assessment of vegetation. *Environ. Manage.* 9:471–478.
- Trickler, D.L. and D.T. Hall. 1984.** Soil survey of Fairfield-Nephi area Utah. U.S. Dept. Agr. Soil Conservation Service, Salt Lake City, Ut.
- Underwood, A.J. 1997.** Experiments in ecology. Cambridge Univ. Press, Cambridge, U.K.
- Verbeke, G. 1997.** Linear mixed models for longitudinal data, 63–155. *In:* G. Verbeke and G. Molenberghs (eds.), *Linear Mixed Models in Practice: A SAS-oriented approach*. Lecture Notes in Statistics. No. 126, Springer-Verlag, New York.
- West, N.E. 1983.** Great Basin-Colorado Plateau Sagebrush Semi-desert, p. 331–349. *In:* N.E. West (ed.) *Temperate deserts and semi-deserts*. Elsevier Sci. Publ., Amsterdam, Netherlands.
- West, N.E. 2000.** Synecology and disturbance regimes of sagebrush steppe ecosystems, p. 15–26. *In:* P.G. Entwistle et al., compilers, *Proceedings: Sagebrush Steppe Ecosystems Symposium*, Bureau of Land Management Publication No. BLM/ID/PT-001001+150 Boise, ID.
- West, N.E. and M.A. Hassan. 1985.** Recovery of sagebrush-grass vegetation following wildfire. *J. Range Manage.* 38:131–134.
- West, N.E. and E.L. Smith. 1997.** Improving the monitoring of rangelands. *Rangelands* 19:9–14.
- West, N.E. and J.A. Young. 2000.** Intermountain valleys and lower mountain slopes, p. 255–284. *In:* M.A. Barbour and W.D. Billings (eds.), *North American Terrestrial Vegetation*, 2nd ed. Cambridge Univ. Press, New York.
- Westoby, M., B. Walker and I. Noy-Meir. 1989a.** Opportunistic management for rangelands not at equilibrium. *J. Range Manage.* 42:266–274.
- Westoby, M., B. Walker and I. Noy-Meir. 1989b.** Range management on the basis of a model which does not seek to establish equilibrium. *J. Arid Environ.* 17:235–239.
- Winkworth, R.E. and D.W. Goodall. 1962.** A crosswire sighting tube for point quadrat analyses. *Ecol.* 43:342–343.

Northern dry mixed prairie responses to summer wildlife and drought

CATHERINE ERICHSEN-ARYCHUK, EDWARD W. BORK, AND ARTHUR W. BAILEY

Authors are former Range Management Specialist, Alberta Agriculture, Food and Rural Development, Hanna, Alberta, Canada, T0J 1P0; and Assistant Professor and Professor emeritus, Department of Agricultural, Food & Nutritional Science, University of Alberta, Edmonton, Alberta, Canada, T6G 2P5.

Abstract

In August 1994, wildfire burned 6,500 ha of native Dry Mixed Prairie in southeastern Alberta. The following year, a study was initiated to monitor the recovery of major plant communities. Burning was followed by 3 successive years of drought, reducing total vegetative cover by 10%. Exposed soil increased to a high of 23%, three years after the fire. Litter and grass production were reduced through 1997, with the greatest decline in 1995 when grass production on burned and unburned areas averaged 890 and 1,468 kg ha⁻¹, respectively. Of the major forage species, *Stipa* spp. and *Koeleria macrantha* (Ledeb. J.A. Schultes f.) were affected for a single year and *Agropyron* spp. 2 years by burning. Both *Agropyron* and *Stipa* abundance displayed interactions with topographic position in response to fire. In 1995, *Agropyron* increased on uplands with burning from 90 to 143 kg ha⁻¹, but decreased on lowlands from 383 to 238 kg ha⁻¹, a pattern repeated in 1996. In contrast, *Stipa* declined at both positions, but only for a single year. Where livestock grazing occurred after the fire, forage removal was greater on burned areas. Drought conditions, in combination with summer wildfire, reduced Dry Mixed Prairie range productivity and ground cover for several years and intensified livestock grazing, highlighting the need for changes in rangeland management under these conditions.

Key Words: composition, forage, litter, preference, production, topography

In August 1994, a late summer wildfire burned through approximately 6,500 ha of native northern Dry Mixed Prairie in southeastern Alberta. Although a number of studies have looked at fire effects in the more mesic northern Mixed Prairie and Fescue Grasslands of the Aspen Parkland in western Canada (e.g. Coupland 1973, Bailey and Anderson 1978, Anderson and Bailey 1980, Redmann et al. 1993, Gerling et al. 1995), relatively little is known of the response of Dry Mixed Prairie vegetation to fire in the Canadian Great Plains. In the single documented study of fire within this region (Clarke et al. 1947), fire was examined during the spring and fall under prescribed conditions rather than as wildfire during the late summer dry period. Wildfires, because they tend to occur during the driest part of the year, are likely to cause greater damage within rangeland ecosystems (Wright 1974b).

Authors wish to thank Lorne Cole, Range Management Specialist for Special Areas District, Hanna, Alberta, for his assistance with data collection, and 2 anonymous reviewers for their comments on earlier versions of the manuscript.

Manuscript accepted 8 Jul. 01.

Resumen

En Agosto de 1994, un fuego natural quemó 6,500 ha de Pradera Seca Mixta del sudeste de Alberta. En el año siguiente se inicio un estudio para monitorear la recuperación de las principales comunidades vegetales. La quema fue seguida de tres años consecutivos de sequía reduciendo la cubierta vegetal total en un 10%, y tres años después del fuego, el suelo expuesto se incrementó a un máximo de 23%. El mantillo y la producción de zacates se redujo desde el incendio hasta 1997, registrándose la mayor disminución en 1995, cuando la producción de zacate de áreas quemadas y no quemadas promedio 890 and 1468 kg.ha⁻¹, respectivamente. De las principales especies forrajeras, *Stipa* spp. y *Koeleria macrantha* fueron afectadas por la quema solo un año y *Agropyron* spp. por dos años. La abundancia de *Agropyron* y *Stipa* mostraron interacciones con la posición topográfica en respuesta al fuego. En 1995, en las tierras altas, el *Agropyron* aumento con el fuego de 90 a 143 kg.ha⁻¹, pero disminuyo en las tierras bajas de 383 a 238 kg.ha⁻¹, este patrón se repitió en 1996. En contraste, el *Stipa* disminuyó en ambas posiciones, pero solo un año. Cuando el ganado apacento después del fuego la remoción de forraje fue mayor en las áreas quemadas. Las condiciones de sequía, en combinación con los fuegos no prescritos de verano redujeron la productividad de la Pradera Seca Mixta y la cobertura del suelo por varios años, e intensifican el apacentamiento del ganado, resaltando la necesidad de cambios en el manejo de los pastizales bajo estas condiciones.

Rangeland plant communities of the northern Mixed Prairie are generally thought to be well-adapted to wildfire, as this type of disturbance was an important part of these ecosystems prior to European settlement (Bailey 1978). Wright and Bailey (1982) estimate a natural historical fire frequency of 5 to 10 years in the Northern Great Plains. Lightning and aboriginal people were the probable cause of many fires (Nelson and England 1971).

Bailey and Anderson (1978) found that single prescribed burns in spring or fall had little effect on total herbage production in northern Fescue Prairie. In more water-limited environments, rangeland productivity is typically reduced by fire (Redmann 1978, Engle and Bultsma 1984). Fire removes litter, increasing soil temperatures and moisture loss (De Jong and MacDonald 1975, Facelli and Pickett 1991).

Burning can affect the species composition of northern Great Plains rangelands. Burning Fescue Prairie, particularly in fall, reduced *Festuca hallii* (Vasey) Piper¹ (Anderson and Bailey 1980, Gerling et al. 1995). Coupland (1973) found *Agropyron*

¹Nomenclature follows Moss (1992).

smithii Rydb. and *Koeleria macrantha* (Ledeb.) J.A. Schultes f. declined the year after burning, while *Carex* spp. and *Stipa viridula* Trin. increased. Clarke et al. (1947) found *Stipa-Bouteloua gracilis* (HBK.) Lag. communities to be more tolerant of fire than *Agropyron* communities in southern Alberta.

Grazing management also influences the recovery of burned rangelands because burning may increase subsequent livestock utilization (Daubenmire 1968, Wright 1974b, Willms et al. 1980). Burned and grazed Mixed Prairie pastures recover more slowly than areas protected from grazing (Clarke et al. 1947). Both Hopkins et al. (1948) and Launchbaugh (1964) found similar results in Shortgrass Prairie.

Although several studies have examined fire impacts on Alberta grasslands, most involve prescribed burning during spring or fall, and have been limited to regions with favorable precipitation. As a result, this study was initiated to examine the effects of the 1994 August wildfire on northern Dry Mixed Prairie ground cover, herbage production and species composition over 3 subsequent years. A second component of the study examined utilization by cattle for 2 years after the fire on adjacent burned and unburned rangeland to assess livestock foraging preferences.

Methods

Study Area

The study area is located in the Special Areas administrative district south of Buffalo, Alberta, Canada (50°44' N, 110°38' W), within the Dry Mixed Grass Ecoregion (Strong and Leggat 1992). Average summer temperatures for the region are 16.2°C, and annual precipitation averages 272 mm, with significant moisture deficits during July and August (Strong and Leggat 1992). The landscape of the area is moderately undulating, with soils typically medium-textured, well to moderately well-drained Brown Chernozems (Haploxerolls).

The 1994 wildfire burned over 6,500 ha of Dry Mixed Prairie rangeland, which included an entire grazing lease and approximately 5% of a local community pasture before being brought under control. Range condition throughout the study area was good to excellent prior to the fire (assessed as per Wroe et al. 1988). Within the community pasture, cattle were free to graze selectively on burned and unburned areas during the course of the study beginning in 1995, at a stocking rate of 0.64 AUM·ha⁻¹.

Vegetation within the study area consisted of predominantly cool-season (C3) plants. Available water and soil nutrients severely limit forage production in the region (Strong and Leggat 1992), with plant growth typically complete by mid-summer. Dominant plant species include *Stipa comata* Trin. & Rupr., *Stipa curtisetata* (A.S. Hitchc.) Barkworth, *Bouteloua gracilis*, *Agropyron dasystachyum* (Hook.) Scribn. and *smithii*, as well as *Koeleria macrantha*, with their representation in plant communities heavily dependent on site conditions (Willms and Jefferson 1993). Table 1 shows the relative abundance of major plant species within burned and unburned areas of both upland and lowland topographic positions. Unburned data indicate that the upland and lowland areas are indicative of the *Stipa-Bouteloua-Agropyron* (S-B-A) and *Stipa-Agropyron* (S-A) faciations, respectively (Coupland 1961). *Artemisia frigida* Willd. was a common half-shrub throughout the area, with *Symphoricarpos occidentalis* Hook. present on lowlands as well (Table 1).

Vegetation Sampling and Assessment

Sample sites were situated within dominant range sites (upland and lowland topography) in May 1995 on the grazing lease. Transects were randomly situated in pairs along the fire-line, on both burned and adjacent unburned areas. Six transects were positioned on lowland sites and 8 on upland sites. Each transect was 20 meters long, randomly positioned and permanently marked.

A variation of the weight-estimate technique was used to estimate forage yield. On each transect, six previously unsampled 0.25 m² quadrats at stratified intervals were assessed in 1995, 1996, and 1997, with lowlands sampled a fourth time in 1998. Yearly vegetation assessments were done at peak standing phytomass (late July to early August), providing a reliable estimate of total forage production (Redmann et al. 1993).

The grazing lease was rested from livestock grazing in 1995 and 1996 to facilitate range recovery. Although pronghorn antelope could not be excluded from the area, forage utilization by this species was estimated to be negligible on the burned area in both years. In 1997 and 1998, 1 m² cages were used to prevent livestock grazing on all sample quadrats. Cattle use of the area around the transects remained light to moderate, with use never exceeding an estimated 30%.

Data collection on each quadrat was conducted as described in Wroe et al. (1988). For each quadrat, the percent groundcover of total (live and dead) vegetation, bare soil and *Selaginella densa* Rydb. was estimated using cover classes (Daubenmire 1959). All plant species present were identified and the percentage contribution of each to total yield, based on dry matter weight, visually estimated. Estimates were later checked by clipping and weighing herbage of each species present within other representative quadrats.

After the cover assessment was complete, all litter and vegetation present in the 0.25 m² quadrat was harvested. All

Table 1. Average species composition (% weight estimate) of the dominant plant species (minimum 1%) at Buffalo, Alberta, within the burned and unburned areas at each topographic position. Data are pooled over all years (1995–1997).

Species:	Upland (S-B-A)		Lowland (S-A)	
	Burned	Unburned	Burned	Unburned
	(% weight)			
Grasses:				
<i>Agropyron smithii</i> & <i>dasystachyum</i>	11.3	7.6	13.7	15.2
<i>Bouteloua gracilis</i>	6.2	8.4	2.1	3.2
<i>Carex</i> spp.	8.5	6.3	14.0	13.4
<i>Koeleria macrantha</i>	19.8	12.8	13.2	5.6
<i>Poa sandbergii</i>	7.3	2.4	3.3	1.7
<i>Stipa comata</i> & <i>spartea</i> var. <i>curtiseta</i>	37.7	39.8	50.9	52.9
Forbs:				
<i>Anemone patens</i>	0.4	0.2	0.7	1.3
<i>Artemisia frigida</i>	1.3	17.4	0.8	3.4
<i>Comandra pallida</i>	1.0	1.0	0.2	0.4
<i>Sphaeralcea coccinea</i>	2.2	1.6	1.2	0.9
<i>Vicia americana</i>	0	0	0	2.1
<i>Zygadenus gramineus</i>	0	0	0.6	1.4
Shrubs:				
<i>Artemisia cana</i>	0.9	0.3	1.0	0
<i>Rosa arkansana</i>	0	0	1.1	0.3
<i>Symphoricarpos occidentalis</i>	0	0	6.4	6.8

standing phytomass was clipped at ground level and sorted into dead material, as well as live graminoid, forb and shrub species. Shrubs were combined with forbs due to their limited abundance. Fallen litter was carefully raked from the soil surface and added to standing dead material, with the sum of these components collectively referred to as litter. Lichens, *Selaginella densa* and *Phlox hoodii* Richards. were not harvested. Each component was bagged separately by quadrat, dried to constant mass, and weighed, followed by conversion to kg ha⁻¹ to provide standing crop values. The production of each species per quadrat was determined by multiplying the average proportions estimated for each species by composited dry matter (kg ha⁻¹) harvested by growth form.

On the adjoining Buffalo-Atlee Community Pasture, 4 additional upland sites were randomly selected to assess cattle utilization on burned and unburned Dry Mixed Prairie in 1995 and 1996. Eight cages, each 1 m², were used to obtain ungrazed herbage production, with 4 cages on each of the burned and unburned areas. At each cage, 0.25 m² paired quadrats from both inside and outside the cage were assessed using the procedure described previously. Cages were not moved to avoid confounding yield data with localized site heterogeneity; instead, clipped quadrats within cages were rotated to avoid re-sampling in subsequent years. Actual herbage and litter utilization was calculated for each cage as the difference between ungrazed and grazed quadrats.

Analysis

Statistical analysis was done using Proc GLM in SAS (SAS 1990). All data were evaluated in each of the 3 postfire monitoring years with a 2 x 2 factorial model for the effects of burning, topographic position (lowland vs upland) and their interaction (e.g., Burn x Position). Only the Burn and Burn x Position results are presented here as fire was the factor of interest in this study, with any significant interactions used to aid interpretation of the main effect. Dependent variables included the estimated standing crop of major forage species, actual grass, forb, and litter weights, as well as the ground cover of total vegetation, bare soil and *Selaginella*. All comparisons across the fire boundary occurred within randomly selected but internally uniform range sites. In addition, sample sites were all located where the fire-line was man-made (i.e., grader-bladed), negating the risk of site confoundment across the fire boundary.

Table 2. Seasonal and total precipitation data for the nearest weather station at Brooks, Alberta, from 1993 to 1999, inclusive.

Year:	Season ¹				Total	Deviation ²
	Winter	Spring	Summer	Fall		
	(mm precipitation)					— (%) —
1993	26.5	141.2	126.2	48.5	342.4	0.4
1994	62.9	136.6	52.6 ³	36.6	288.7	-15.4
1995	12.6	97.9	126.2	51.6	288.3	-15.4
1996	12	74.2	124.6	78.6	289.4	-15.1
1997	56.8	94.8	63.0	20.4	235.0	-31.1
1998	77.8	143.4	63.2	28.1	312.5	-8.3
1999	22.8	192.9	159.8	19.7	395.2	15.9
7 Year Mean	36.6	138.1	99.0	41.3	315.1	-7.6
St. Dev.	23.3	47.3	36.8	17.5	48.3	
30 Year Mean	47.0	131.7	113.2	49.0	340.9	

¹Winter, spring, summer, and fall, represent the inclusive periods Jan. - March, April - June, July - Sept., and Oct. - Dec., respectively.

²Represents deviation from 30 year mean.

³Coincides with time of wildfire.

Cattle utilization data were evaluated only for differences between burn treatments, as all sampling sites were situated on upland topography. For all data sets, each year was analyzed separately in an attempt to assess the specific duration of fire effects. Variables were considered significantly different when $p < 0.05$.

Results and Discussion

Growing Conditions

Precipitation in 1994 at Brooks, the nearest weather station approximately 85 km southwest of the study area, was 289 mm, 15% below the 30 year mean of 341 mm (Table 2). During the summer of 1994, only 53 mm of precipitation fell at Brooks: this value is 54% below the long-term mean and likely provided ideal conditions for the August wildfire. Notably, precipitation for the 15 months leading up to the fire were at or above normal, and may have ensured an adequate supply of fuel through favorable vegetation growth

in the summer of 1993 and spring of 1994. Precipitation levels for 4 subsequent years following the fire were indicative of prolonged drought, however, ranging from 31% below average in 1997 to 8% below in 1998. (Table 2). Thus, post-fire drought was an influential factor on vegetation recovery.

Ground Cover Response

Although burned areas were lower in mean total vegetation cover in each of the 3 years after the fire, significant differences ($p < 0.05$) were limited to 1996 (Table 3). The delayed response may be linked to the extended below-normal levels of precipitation during the post-burn period. Sustained drought would impose an additive stress on plant communities, further affecting their inherent resilience.

The August 1994 wildfire significantly increased bare soil on burned areas for 3 subsequent years (Table 3). Increased bare soil likely reduced available moisture by increasing soil temperatures and surface evaporation, while reducing water infiltration.

Table 3. Effect of burning on mean cover (SE) of key ground components, including *Selaginella densa*, bare soil, and total live vegetation, within the study area during each of the first 3 years after wildfire.

Variable:	Year	Signif. Tests:		Burned ¹	Unburned ¹
		Burn	Burn x Pos.		
		----- p-values -----		----- (% cover) -----	
<i>Selaginella densa</i>	1995	NS	NS	26 (6)	28 (9)
	1996	NS	NS	30 (9)	31 (10)
	1997	NS	NS	53 (11)	41 (12)
Bare Soil	1995	p < 0.01	NS	21 (8)	2 (0.4)
	1996	p < 0.01	NS	11 (2)	2 (0.4)
	1997	p < 0.01	NS	23 (5)	7 (3)
Total Vegetation	1995	NS	NS	74 (6)	84 (6)
	1996	p < 0.05	NS	74 (6)	84 (6)
	1997	NS	NS	82 (6)	92 (3)

¹Only main effects are presented as no interactions met the 5% minimum level of significance.

Table 4. Effect of burning on mean (SE) grass and forb production, as well as accumulated litter (including standing dead) within the study area, during each of the first 3 years after wildfire. Interaction means are provided only for significant Burn x Position interactions.

Variable:	Year	Signif. Tests:		Burned			Unburned		
		Burn	Burn x Pos.	Upland	Lowland	Total	Upland	Lowland	Total
		p-values		(kg·ha ⁻¹)					
Grass	1995	p<0.01	NS	810 (83)	1050 (55)	890 (69)	1120 (212)	2166 (308)	1468 (239)
	1996	NS	NS	n/a	n/a	1053 (161)	n/a	n/a	1263 (233)
	1997	p<0.05	p<0.05	791 (50)	1288 (119)	1004 (113)	756 (70)	1838 (225)	1220 (238)
Forb	1995	NS	NS	n/a	n/a	106 (33)	n/a	n/a	151 (29)
	1996	NS	NS	n/a	n/a	70 (34)	n/a	n/a	169 (60)
	1997	NS	NS	n/a	n/a	85 (40)	n/a	n/a	180 (53)
Litter	1995	p<0.01	p<0.05	29 (29)	9 (9)	22 (19)	400 (124)	1159 (449)	653 (198)
	1997	p<0.01	NS	n/a	n/a	572 (165)	n/a	n/a	1464 (452)

tion (De Jong and MacDonald 1975, Facelli and Pickett 1991), thereby amplifying the magnitude of drought effects for 4 years. Defosse and Robberecht (1996) found soil temperatures after burning were 12 to 15°C greater due to increased absorption of solar radiation. Burning and loss of litter may also increase plant water stress through reduced snow trapping (Trlica and Schuster 1969, Redmann 1978).

In contrast to soil and vegetation, *Selaginella* cover was not affected by burning (Table 3), although some of this species was observed to die following the fire. These results contrast those of Dix (1960), who found *Selaginella* may be killed by fire.

Standing Crop Response

Graminoid production was reduced by the fire in 1995 and 1997, the first and third growing seasons, respectively (Table 4). Furthermore, the interaction between burning and topographic position was significant in 1997. While uplands recovered by 1997, grass production on lowlands remained 30% lower within burned areas, indicating wildfire reduced grass production to a greater extent and for a longer period on these areas. Lowlands were reassessed in 1998 and 4 years after the fire, grass production had recovered and was statistically similar between burned (1,380 kg·ha⁻¹, SE ± 97) and unburned (1,660 kg·ha⁻¹, SE ± 292) areas ($p > 0.10$).

These results are consistent with other studies that have found fire reduces grassland herbage production for 1 to 3 growing seasons (Dix 1960, Coupland 1973, Wright 1974a, Redmann 1978, Whisenant and Uresk 1989, Defosse and Robberecht 1996). In the study by Coupland (1973) on mesic Mixed Prairie in Saskatchewan, annual herbage production on burned areas remained 27 to 31% lower than unburned areas even after 3 years. Spring prescribed burning of Dry Mixed Prairie

in southern Alberta reduced forage yield 50% the first year and 15% the second year, with full recovery by the third (Clarke et al. 1947).

Much of the production loss may result from the removal of litter. Litter was significantly lower in the burned area throughout the monitoring period, and in 1997, remained 61% lower than the unburned area (Table 4). These findings are consistent with White and Currie (1983) and Engle and Bultsma (1984) indicating litter requires considerable time to re-accumulate in semi-arid areas. In western North Dakota, 4 growing seasons were needed for a *Stipa comata* community to recover after an August fire (Dix 1960). Full litter recovery in more northern temperate grasslands may take even longer (Redmann et al. 1993).

Litter acts as a physical barrier to heat and water flow at the soil surface (Weaver and Rowland 1952), thereby conserving soil moisture via reduced evaporation (Naeth et al. 1991). The physical removal of standing dead and surface litter over 1 to 3 years on northern Dry Mixed Prairie reduces herbage production by 25 to 56% (Willms et al. 1986, Willms et al. 1993). By removing litter, burning reduces production over an extended period in this semi-arid environment, and may increase the likelihood of yield losses during drought. The significant reduction in grass yield in 1997 may result from the loss of litter coupled with lower spring and summer precipitation that year (Table 2). Given that litter is slow to accumulate within northern Dry Mixed Prairie, management following fire should strive to enhance litter accumulation through measures such as reduced livestock stocking rates.

The variation in vegetation response to fire observed between uplands and lowlands are consistent with those of Clarke et al. (1947) who found *Stipa-Bouteloua* uplands were more resilient to prescribed burning than moister areas dominated by *Agropyron* plant communities. Similarly,

Coupland (1973) found a 3 year consecutive decline in annual herbage production of mesic *Agropyron* range in Saskatchewan after an August wildfire. Generally, lowland vegetation is expected to be more resilient than that on uplands due to a more favorable moisture regime, as lowlands accumulate snow, surface runoff and groundwater. The results found here, however, contrast the notion of enhanced resilience.

There are a number of possible explanations for the landscape-based differences in production between burned and unburned areas. One possibility is that greater fuel loads within lowlands caused greater fire intensities, which in turn led to greater damage to plants, thus offsetting any resilience to wildfire. Another explanation is that drought from 1994 to 1997 may have accentuated subsequent fire impacts by modifying local moisture regimes, further stressing vegetation. The loss of greater quantities of litter from lowlands during the fire may have played a role in further limiting subsequent herbage production. A third possibility is that carbohydrate reserve and/or morphological differences between upland and lowland vegetation resulted in differential tolerances to fire.

Carbohydrate reserves are, among other factors, a function of basic plant phenology, stresses such as fire and defoliation, and the type of plant species (White 1973). In some cases (e.g., big bluestem in Tallgrass Prairie), burning has been found to increase the carbohydrate content of plants (Rains et al. 1975), possibly due to the stimulating effect of mulch removal on regrowth (Ehrenreich 1959). Despite this, little is known about the specific response of carbohydrate levels within cool-season grasses exposed to fire. Species such as *Agropyron smithii* are considered susceptible to defoliation because of an extended V-shaped carbohydrate cycle (Menke and Trlica 1981), with heavy defoliation capable of reducing carbohydrates (Buwai and Trlica 1977).

Table 5. Effect of burning on the mean (SE) biomass of *Agropyron*, *Stipa*, and *Koeleria*, the 3 dominant graminoid components within the study area, during each of the first 3 years after wildfire. Interaction means are provided only for significant Burn x Position interactions.

Variable:	Year	Signif. Tests:		Burned			Unburned		
		Burn	Burn x Pos.	Upland	Lowland	Total	Upland	Lowland	Total
		p-values		(kg.ha ⁻¹)					
Grass	1995	p<0.01	NS1	810 (83)	1050 (55)	890 (69)	1120 (212)	2166 (308)	1468 (239)
<i>Agropyron</i> spp.	1995	NS	p<0.05	143 (21)	238 (54)	184 (30)	90 (30)	383 (34)	216 (63)
	1996	p<0.05	p<0.01	88 (43)	62 (11)	77 (24)	58 (31)	249 (25)	140 (43)
	1997	NS	NS	n/a	n/a	103 (31)	n/a	n/a	341 (227)
<i>Stipa</i> spp.	1995	p<0.01	p<0.01	164 (47)	326 (14)	233 (42)	288 (47)	966 (55)	578 (150)
	1996	NS	NS	n/a	n/a	489 (120)	n/a	n/a	608 (207)
	1997	NS	NS	n/a	n/a	378 (87)	n/a	n/a	482 (137)
<i>Koeleria</i>	1995	p<0.05	NS	178 (50)	146 (44)	164 (32)	114 (37)	24 (13)	75 (27)
<i>macrantha</i>	1996	NS	NS	141 (62)	138 (86)	140 (46)	141 (30)	48 (39)	101 (29)

Although the burned area was ungrazed in 1994 following the fire, lowland vegetation may have been more detrimentally affected by an August burn because it was more likely to be actively growing at the time of the fire, as well as more likely to regrow following burning. Throughout the fall of 1994 after the fire, visual estimates of vegetation regrowth were 2 to 4 cm and 7 to 10 cm on uplands and lowlands, respectively (Lorne Cole - Special Areas Range Manager, pers. observation). The greater regrowth on lowlands, followed by winter dormancy, would likely deplete both carbohydrate reserves and available lateral buds with minimal opportunity for replenishment, further damaging vegetation at this topographic position and effecting recovery. In contrast, low soil moisture during the summer drought of 1994 would make upland vegetation more likely to remain dormant after fire, minimizing carbohydrate loss and lateral bud death.

In contrast to grasses, wildfire did not significantly reduce peak forb production in any year (Table 4). These results are similar to Redmann et al. (1993) who found burning had little effect on forb phytomass within Mixed Prairie in Saskatchewan. In contrast, Bailey and Anderson (1978) found perennial forb cover in Fescue Prairie increased after burning, as did Engle et al. (1998) on burned mid-successional Tallgrass Prairie. Collectively, these studies suggest that forbs respond favorably to fire, but only in regions where moisture is relatively abundant.

The response of rangeland production to burning partly depends on the timing of fire. Clarke et al. (1947) found fall burning of *Stipa* rangeland reduced herbage production by 30% only in the following year, while spring burning resulted in a 50% decline the first year and a 15% decrease the second year. The 3 year response documented here on vegetation recovery is evidence of either the intense severity of this wildfire, the impact of

drought, or most likely, the interaction between wildfire and subsequent drought. Gerling et al. (1995) observed the same pattern with grass yields in Fescue Prairie, with late spring burning causing the greatest reductions, likely due to a combination of active plant growth coupled with declining soil moisture. These results indicate that although the August 1994 fire may have been detrimental to northern Dry Mixed Prairie rangeland, the impact may have been even more severe had upland plants not completed their annual growth prior to the fire.

Response of Dominant Grasses

Fire affected the amount of *Agropyron* spp. in 1995 and 1996 (Table 5), with both years showing a significant interaction between fire and topographic position. Burning reduced *Agropyron* production on lowlands while increasing it on uplands, producing a response similar to that found by other researchers (Wright 1974b, White and Currie 1983).

Agropyron spp. are normally quite resistant to fire as they have less flammable litter concentrated at the base of the plant near the meristematic tissues, and can regrow from rhizomes (Wright and Bailey 1982). These species may even be favored over others by fall burning (Wright 1974b, White and Currie 1983). The poor response observed at Buffalo, particularly in 1996, may be caused more by moisture stress, as *Agropyron* spp. frequently decrease during drought (Willms and Jefferson 1993). Although Launchbaugh and Owensby (1978) documented a decline in *Agropyron* with burning in Kansas, that fire occurred during spring when these species would have been actively growing and thus, more susceptible to fire damage.

Fire also reduced the production of *Stipa* spp. in 1995 (Table 5), with a significant

interaction of fire and topographic position again evident. Burning had a more negative effect within lowlands, but unlike the *Agropyron* spp., *Stipa* recovered by the second growing season. The shorter-term decline was unexpected as large bunch grasses have a concentration of dead material at their bases, typically resulting in relatively high temperatures for long periods when burned (Wright 1971). The decline in *Stipa* observed here is similar to those from other studies indicating fire can harm bunch grasses like *Stipa comata* (Dix 1960, Wright and Klemmedson 1965, Wright 1971). The timing of fire may also influence the magnitude and extent of *Stipa* decline. For example, Engle and Bulsma (1984) found Mixed Prairie burned in spring reduced *Stipa*, but only in the year of the burn, while in southern Idaho, *Stipa comata* was reduced by burning in June or July, but had more resistance to August fires (Wright and Klemmedson 1965). In contrast, Whisenant and Uresk (1989) found fire in either April or October reduced *Stipa comata* for up to 3 growing seasons. Based on these studies, it is apparent that even greater decreases in *Stipa* may have occurred had the wildfire taken place when vegetation was actively growing during spring or fall.

Fire significantly increased *Koeleria* production in the year following the wildfire (Table 5). The short, tufted habit of this species appears to be more resilient to burning in August than larger bunch grasses. The overall abundance of *Poa sandbergii* Vasey also appeared to increase after burning (Table 1). Short bunch grasses typically recover quickly after fire (Wright and Klemmedson 1965, Wright and Bailey 1982) as they accumulate less litter and experience lower fire intensities. Although *Bouteloua gracilis*, a warm season perennial, has been found to decrease following summer burning (Dix 1960,

Launchbaugh 1964), no notable difference was found in this species between burned and unburned areas (Table 1).

Burning also appeared to reduce the overall abundance of *Artemisia frigida* (Table 1). Several studies have documented prominent declines in sage with burning, including those by Dix (1960), Coupland (1973), and Bailey and Anderson (1978). The apparent reduction suggests that fire may have the potential for the control of this undesirable species on northern Dry Mixed Prairie rangelands.

Cattle Preference

Cattle utilized significantly more grass on burned uplands than their unburned counterparts in 1995, but not 1996 (Table 6). Burning typically increases forage preference and utilization (Barker and Erickson 1971, Willms et al. 1980).

Mixed Prairie may need 3 to 5 years to recover compared to one to three years for burned pastures that remain ungrazed. As a result, grazing management should be adjusted to account for livestock preferences, with burned areas either grazed separately from unburned areas to facilitate more uniform range use, or unburned areas within a pasture burned off to promote uniform grazing (Launchbaugh and Owensby 1978).

Conclusion

The August 1994 wildfire in northern Dry Mixed Prairie at Buffalo, Alberta, increased bare soil while reducing grass production and litter for several growing seasons. Rangeland recovery was likely impaired by 3 consecutive years of

Table 6. Evaluation of the Burn x Grazing interaction on year end mean standing crop (SE) on burned and unburned sites within the Atlee Community Pasture grazed during 1995 and 1996, the first 2 growing seasons after wildfire.

Year	Variable:	Burn x Grazing		Burned		Unburned	
		F-Value	Probability	Grazed	Ungrazed	Grazed	Ungrazed
----- (kg ha ⁻¹) -----							
1995	Grass	6.72	p<0.05	686 (128)	1206 (82)	1842 (82)	1678 (200)
	Forb	0.08	NS	247 (114)	229 (101)	288 (147)	205 (98)
	Litter	0.04	NS	0 (0)	0 (0)	826 (269)	736 (356)
1996	Grass	2.39	NS	910 (129)	2080 (460)	1400 (279)	1670 (183)
	Forb	0.95	NS	220 (194)	120 (63)	230 (106)	600 (424)
	Litter	0.26	NS	340 (128)	1070 (267)	1880 (423)	2080 (909)

Burned areas are preferred because forage is younger, more palatable, and more accessible (Coleman and Barth 1973, Wright 1974b). Post-burn vegetation can be higher in protein and lower in crude fiber (Allen et al. 1976, Willms et al. 1981). Burning also increases utilization simply by removing standing dead litter that acts as a barrier to grazing (Willms et al. 1980).

Grazing inhibits the short-term recovery of desirable forage species and slows the accumulation of litter on burned rangeland, potentially by up to several years (Dix 1960), thereby preventing the stabilization of soils and restoration of normal rangeland hydrologic functions. Many Mixed Prairie species such as *Agropyron* are strongly affected by defoliation during the growing season (Kowalenko and Romo 1998), and need more than two years rest before attaining full recovery. Given the established preference of cattle for burned areas, the findings of this study lend support to the conclusion of Clarke et al. (1947), that burned and grazed Dry

drought. Fire and subsequent drought conditions had the longest lasting impact on lowlands. Cattle preferred to forage on burned areas 1 year after the fire, which may further inhibit rangeland recovery, necessitating changes to grazing management to facilitate recovery. Given animal preferences for burned areas, as well as the reduction and slow recovery in vegetation characteristics within the study area, subsequent grazing management, including stocking rates, should be adjusted to facilitate range recovery, particularly when accompanied by extended drought.

Literature Cited

- Allen, L.J., L.H. Harbers, R.R. Schalles, C.E. Owensby and E.F. Smith. 1976. Range burning and fertilizing related to nutritive value of bluestem grass. *J. Range Manage.* 29:306-308.
- Anderson, H.G. and A.W. Bailey. 1980. Effects of annual burning on grassland in the Aspen Parkland of east-central Alberta. *Can. J. Bot.* 58:985-996.
- Bailey, A.W. 1978. Use of fire to manage grasslands of the Great Plains: Northern Great Plains and adjacent forests. pp. 691-693. *In:* D.N. Hyder (ed.). *Proc. of the First Internat. Rangeland Congress. Soc. for Range Manage.*, Denver, Colo.
- Bailey, A.W., and M.L. Anderson. 1978. Prescribed burning of a *Festuca-Stipa* grassland. *J. Range Manage.* 31:446-449.
- Barker, W.T. and D.O. Erickson. 1971. The effects of burning and mowing on utilization. *J. Anim. Sci.* 39:985.
- Buwai, M. and M.J. Trlica. 1977. Multiple defoliation effects on herbage yield, vigor, and total nonstructural carbohydrates of fire range species. *J. Range Manage.* 30:164-171.
- Clarke, S.E., E.W. Tisdale and N.A. Skoglund. 1947. The effects of climate and grazing practices on short-grass prairie vegetation in southern Alberta and southwestern Saskatchewan. *Can. Dep. Agr. Tech. Bull.* 46. 53 pp.
- Coleman, S.W. and K.M. Barth. 1973. Quality of diets selected by grazing animals and its relation to quality of available forage and species composition of pastures. *J. Anim. Sci.* 36:754-761.
- Coupland, R.T. 1961. A reconsideration of grassland classification in the Northern Great Plains of North America. *J. Ecol.* 49:135-167.
- Coupland, R.T. 1973. Producers: I. Dynamics of above-ground standing crop. *Matador Project. Canadian IBP Prog. Tech. Rep. No.* 27. Saskatoon, SK.
- Daubenmire, R. 1968. Ecology of fire in grasslands. pp. 209-266. *In:* *Advances in Ecological Research No. 5.* Academic Press, New York.
- Daubenmire, R.F. 1959. A canopy-coverage method of vegetational analysis. *Northw. Sci.* 33:43-64.
- De Jong, E. and K.B. MacDonald. 1975. The soil moisture regime under native grassland. *Geoderma* 14:207-221.
- Defosse, G.E. and R. Robberecht. 1996. Effects of competition on the postfire recovery of two bunchgrass species. *J. Range Manage.* 49:137-142.
- Dix, R.L. 1960. The effects of burning on the mulch structure and species composition of grasslands in western North Dakota. *Ecol.* 41:49-56.
- Ehrenreich, J.A. 1959. Effect of burning and clipping on growth of native prairie in Iowa. *J. Range Manage.* 12:133-137.
- Engle, D.M. and P.M. Bultsma. 1984. Burning of northern mixed prairie during drought. *J. Range Manage.* 37:398-401.
- Engle, D.M., R.L. Mitchell, and R.L. Stevens. 1998. Late growing-season fire effects in mid-successional tall-grass prairies. *J. Range Manage.* 51:115-121.

- Facelli, J.M. and S.T.A. Pickett. 1991. Plant litter: Its dynamics and effects on plant community structure. *Bot. Rev.* 57:1-32.
- Gerling, H.S., A.W. Bailey and W.D. Willms. 1995. The effects of burning on *Festuca hal-lii* in the parklands of central Alberta. *Can. J. Bot.* 73:937-942.
- Hopkins, H., F.W. Albertson and A. Riegel. 1948. Some effects of burning upon a prairie in west-central Kansas. *Kansas Acad. of Sci. Trans.* 51:131-141.
- Kowalenko, B.L. and J.T. Romo. 1998. Regrowth and rest requirements of northern wheatgrass following defoliation. *J. Range Manage.* 51:73-78.
- Launchbaugh, J.L. 1964. Effects of early spring burning on yields of native vegetation. *J. Range Manage.* 17:5-6.
- Launchbaugh, J.L. and C.E. Owensby. 1978. Kansas rangelands: their management based on a half century of research. *Kansas Agr. Exp. Sta. Bull.* 622.
- Menke, J.W. and M.J. Trlica. 1981. Carbohydrate reserve, phenology, and growth cycles of nine Colorado species. *J. Range Manage.* 34:269-277.
- Moss, E.H. 1992. *Flora of Alberta* 2nd Ed. University of Toronto Press, Toronto, Ontario. 687 pp.
- Naeth, M.A., A.W. Bailey, D.S. Chanasyk and D.J. Pluth. 1991. Water holding capacity of litter and soil organic matter in mixed prairie and fescue grassland ecosystems of Alberta. *J. Range Manage.* 44:13-17.
- Nelson, J.C. and R.E. England. 1971. Some comments on the causes and effects of fire in the northern grasslands area of Canada and the nearby United States, ca. 1750-1900. *Can. Geogr.* 15:295-306.
- Rains, J.R., C.E. Owensby, and K.E. Kemp. 1975. Effects of nitrogen fertilization, burning, and grazing on reserve constituents of big bluestem. *J. Range Manage.* 28: 358-362.
- Redmann, R.E. 1978. Plant and soil water potentials following fire in a northern mixed grassland. *J. Range Manage.* 31:443-445.
- Redmann, R.E., J.T. Romo, and B. Pylypec. 1993. Impacts of burning on primary productivity of *Festuca* and *Stipa-Agropyron* grasslands in central Saskatchewan. *Amer. Midl. Nat.* 130:262-273.
- SAS (Statistical Analysis System). 1990. *SAS/STAT User's Guide*. SAS Institute, Inc., Cary, N.C.
- Strong, W.L. and K.R. Leggat. 1992. *Ecoregions of Alberta*. Alberta Forestry, Lands and Wildlife, Edmonton, Alberta. 59 pp. plus map.
- Trlica, M.J. and J.L. Schuster. 1969. Effects of fire on grasses of the Texas high plains. *J. Range Manage.* 22:329-333.
- Weaver, J.E. and N.W. Rowland. 1952. Effects of natural mulch on development, yield, and structure of native grassland. *Bot. Gazette* 114:1-19.
- Whisenant, S.G. and E.W. Uresk. 1989. Burning upland mixed prairie in Badlands National Park. *Prairie Nat.* 21:221-227.
- White, L.M. 1973. Carbohydrate reserves of grasses: a review. *J. Range Manage.* 26:13-18.
- White, R.S. and P.O. Currie. 1983. Prescribed burning in the Northern Great Plains: yield and cover responses of three forage species in the mixed grass prairie. *J. Range Manage.* 36:179-183.
- Willms, W.D. and P.G. Jefferson. 1993. Production characteristics of the mixed prairie: constraints and potential. *Can. J. An. Sci.* 73:765-778.
- Willms, W.D., S.M. McGinn and J.F. Dormaar. 1993. Influence of litter on herbage production in the mixed prairie. *J. Range Manage.* 46:320-324.
- Willms, W.D., S. Smoliak, and A.W. Bailey. 1986. Herbage production following litter removal on Alberta native grasslands. *J. Range Manage.* 39:536-540.
- Willms, W., A.W. Bailey and A. McLean. 1980. Effect of burning or clipping *Agropyron spicatum* in the autumn on the spring foraging behavior of mule deer and cattle. *J. Appl. Ecol.* 17:69-84.
- Willms, W., A.W. Bailey, A. McLean, and C. Kalnin. 1981. Effects of fall clipping or burning on the distribution of chemical constituents in bluebunch wheatgrass in spring. *J. Range Manage.* 34:267-269.
- Wright, H.A. 1971. Why squirreltail is more tolerant to burning than needle-and-thread. *J. Range Manage.* 24:277-284.
- Wright, H.A. 1974a. Effect of fire on southern mixed prairie grasses. *J. Range Manage.* 27:417-419.
- Wright, H.A. 1974b. Range burning. *J. Range Manage.* 27:5-11.
- Wright, H.A. and A.W. Bailey. 1982. *Fire ecology United States and Southern Canada*. John Wiley and Sons, Inc. Toronto, ON. 501 pp.
- Wright, H.A. and J.O. Klemmedson. 1965. Effects of fire on bunchgrasses of the sagebrush-grass region in southern Idaho. *Ecol.* 46:680-688.
- Wroe, R.A., S. Smoliak, B.W. Adams, W.D. Willms and M.L. Anderson. 1988. *Guide to range condition and stocking rates for Alberta grasslands*. Alberta Forestry, Lands and Wildlife, Public Lands, Edmonton, AB.

Bud viability in perennial grasses: Water stress and defoliation effects

ANDREA C. FLEMMER, CARLOS A. BUSO,* AND OSVALDO A. FERNÁNDEZ

Authors are postdoctoral fellow of the Consejo Nacional de Investigaciones Científicas y Técnicas de la República Argentina (CONICET), CERZOS, Altos del Palihue, 8000 Bahía Blanca, Argentina; Full Professor, Departamento de Agronomía-CERZOS, Universidad Nacional del Sur (UNSur) and research scientist CONICET, Altos del Palihue, Bahía Blanca, and Consulting Professor, Departamento de Agronomía-CERZOS, UNSur and research scientist CONICET, Altos del Palihue, Bahía Blanca. Corresponding author: Departamento de Agronomía UNSur, Altos del Palihue, 8000-Bahía Blanca, Argentina; email=cebuso@criba.edu.ar; fax 54-291-4595127; Phone 54-0291-4595102.

Abstract

Effects of the timing and frequency of defoliation under different levels of soil water availability were evaluated on bud metabolic activity and subsequent outgrowth in the desirable (i.e., palatable) *Stipa clarazii* Ball. and *S. tenuis* Phil. in competition with the undesirable (i.e., unpalatable) *S. gynerioides* Phil. Field studies on these native, perennial tussock grasses were conducted from 1995 to 1997 in temperate, semiarid Argentina. Our working hypotheses were 1) axillary bud activation and subsequent tillering are lower under water stress than under higher soil moisture conditions in *S. clarazii*, *S. tenuis*, and *S. gynerioides*, 2) when compared to undefoliated controls, activation, and subsequent outgrowth of axillary buds reach similar or greater values in *S. clarazii* and *S. tenuis* after early (vegetative stage of development), but not late (during internode elongation) defoliations or increased defoliation frequency (vegetative+ during internode elongation) during each growing cycle. Additionally, it was expected that the greatest reduction of axillary bud metabolic activity and outgrowth would occur on plants defoliated twice, and 3) axillary bud activation and succeeding tillering are greater in the undefoliated *S. gynerioides* when the desirable species are defoliated than when they remain undefoliated. With a few exceptions, our results led us to reject all 3 hypotheses. Responses of axillary buds were in general specific to the species and treatments, to sampling time, and to the cumulative effects of previous treatments. This makes predictions of plant responses of these species under natural field conditions difficult, where they are often defoliated under water stress.

Key Words: *Stipa clarazii*, *Stipa tenuis*, *Stipa gynerioides*, bud metabolic activity, bud outgrowth, water stress, defoliation, perennial grasses, semiarid Argentina

Successive tiller production by the development of axillary buds compensates for annual tiller mortality, allowing persistence of perennial grasses (Jewis 1972). Production of new tillers, and of leaf blades, stems, and sheaths from remaining apical and intercalary meristems after defoliation contributes to reestablishment of removed plant tissues (Briske 1991). However, regrowth will depend upon activation and subsequent outgrowth of axillary buds when most, if not all, apical and intercalary meristems are

Resumen

Se evaluó el efecto de la época y la frecuencia de defoliación bajo distintos contenidos hídricos del suelo sobre la actividad metabólica de las yemas axilares y rebrote subsiguiente en las especies desables (palatables) *S. clarazii* Ball. y *S. tenuis* Phil. en competencia con la especie indeseable (no palatable) *S. gynerioides* Phil. Los estudios se efectuaron en el campo en estas especies de gramíneas perennes nativas desde 1995 a 1997 en los pastizales templados, semiáridos de Argentina. Nuestras hipótesis de trabajo fueron 1) la activación y rebrote subsiguiente de las yemas axilares son menores bajo condiciones de estrés hídrico que bajo mayores contenidos hídricos del suelo en *S. clarazii*, *S. tenuis* y *S. gynerioides*, 2) en comparación a los controles no defoliados, la activación y rebrote subsiguiente de las yemas axilares alcanzan valores similares o mayores en *S. clarazii* y *S. tenuis* después de defoliaciones tempranas (estadio fenológico vegetativo) pero no luego de defoliaciones tardías (durante la elongación de los entrenudos) o ante una mayor frecuencia de defoliación (vegetativo+elongación de entrenudos) en cada ciclo de crecimiento. Además, se esperó que la mayor reducción en la actividad metabólica de las yemas axilares y rebrote subsiguiente se produjera en las plantas defoliadas con mayor frecuencia, y 3) la activación y subsiguiente rebrote de las yemas axilares son mayores en las plantas no defoliadas de *S. gynerioides* cuando las especies deseables son defoliadas que cuando permanecen sin defoliar. Con unas pocas excepciones, las 3 hipótesis fueron rechazadas con los resultados obtenidos. Las respuestas de las yemas axilares fueron en general específicas a las especies y tratamientos, a la época de muestreo, y a los efectos acumulativos de tratamientos previos. Esto enfatiza la dificultad de predecir la respuesta de estas especies bajo condiciones naturales, en las que normalmente son defoliadas bajo condiciones de estrés hídrico.

removed by defoliation (Busso et al. 1989). Any factor, such as water stress, which decreases availability, metabolic activity or capacity to grow out of axillary buds would limit reestablishment of photosynthetic canopy of grazed perennial grasses, compromising their persistence in the plant community (Briske and Richards 1995).

Tiller production can be lower on defoliated than on undefoliated plants in perennial grasses exposed to water stress, rainfed or irrigated conditions (Busso et al. 1989, Deregibus and Trlica 1990, Bullock et al. 1994, Hendrickson and Briske 1997). Water stress can also reduce tiller production in defoliated and undefoliated plants; this response has been observed under natural droughts (Bullock et al.

1994, Briske and Hendrickson 1998) or controlled environmental conditions (Busso et al. 1989). Mueller and Richards (1986) and Busso et al. (1989) suggested that the degree of bud metabolic activity would be comparatively more important than bud number or viability in explaining reduced tiller production after defoliation with or without water stress.

Timing of defoliation can also influence tiller production. For example, tiller production was stimulated by defoliation during internode elongation, but not during earlier growth stages in *Agropyron desertorum* (Fisch. ex Link) Schult. (Olson and Richards 1988). This response is partially due to apical meristem removal which stimulates axillary bud activation after eliminating the inhibition source (Murphy and Briske 1992). However, lack of apical meristem removal has also stimulated tiller production on defoliated plants (Deregibus and Trlica 1990). In addition to direct inhibitory effects of the apical meristem on bud outgrowth, both physiological mechanisms and their interaction with environmental variables and resource availability should be considered when studying factors involved in regulating tillering in perennial grasses (Murphy and Briske 1992). For example, bud activation and subsequent outgrowth can be stimulated or suppressed by modifying light quality and quantity at the plant stem bases (Casal et al. 1986, Deregibus and Trlica 1990, Devkota et al. 1997, Gautier et al. 1999).

Knowledge of axillary bud dynamics is essential when considering production and persistence of perennial grasses in the plant community. A few studies have evaluated the effects of various biotic and abiotic factors on this important component of plant growth and development. For example, they include evaluation of defoliation at different phenological stages (*Stipa tenuis* Phil. and *Piptochaetium napostaense* (Speg.) Hack: Becker et al. 1997), water stress with or without defoliation (*Agropyron* species: Busso et al. 1989), and fire (*S. tenuis*: Busso et al. 1993; *S. tenuis*, *S. gynerioides* Phil. and *P. napostaense*: Peláez et al. 1997). The objective of this study was to evaluate the effects of defoliation at different phenological stages and under different levels of soil water availability on the degree of bud metabolic activity and bud outgrowth in 3 perennial grasses: *Stipa clarazii* Ball., *S. tenuis* and *S. gynerioides*. *Stipa clarazii* and *S. tenuis* are 2 desirable, palatable species which compete with the undesirable, unpalatable *S. gynerioides* in the semiarid, temperate rangelands of Central Argentina. We hypothesized that activation of axillary buds and succeeding tiller-

ing 1) would be lower under water stress than under more favorable soil moisture conditions in *S. clarazii*, *S. tenuis*, and *S. gynerioides*, 2) when compared with undefoliated controls, would reach similar or greater values in *S. clarazii* and *S. tenuis* after early (vegetative stage of development), but not late (during internode elongation) defoliations or increased defoliation frequency (vegetative+ during internode elongation) during each growing cycle. Additionally, we expected that the greatest reduction of the studied plant variables would occur on plants defoliated twice, and 3) would be greater in the undefoliated *S. gynerioides* when the desirable species are defoliated than when they are not. However, values for these parameters in *S. gynerioides* will be greater after late or more frequent than early defoliations of *Stipa clarazii* and *S. tenuis*. Results of this study are important to gain understanding of the

responses of these species to the most common disturbances at the study region: grazing under water stress conditions.

Materials and Methods

Study Site

This study was conducted at the research field site of the Agronomy Department-CERZOS in Bahía Blanca (38° 48'S, 62° 13'W) during 1995, 1996, and early 1997. Soil is a typical Haplustol (Luis Sánchez, Dpto. Agronomía UNSur, pers. comm.) with a petrocalcic horizon at 1.8 m depth. A meteorological station at the experimental site measured rainfall, air temperature, relative humidity, wind speed, solar radiation, and potential evapotranspiration (Fig. 1).

Fig. 1. A) Monthly rainfall (mm) and number of rainy days, B) Absolute minimum and maximum and mean monthly air temperatures (°C) to 0.25 m above the soil surface, C) Mean monthly wind speed (km hour⁻¹) to 2 m above the soil surface and mean monthly relative humidity (%), and D) Mean monthly solar radiation (cal cm⁻² day⁻¹) and potential evapotranspiration (mm, Thornthwaite) during 1995, 1996 and early 1997. Measurements were taken using a meteorological station located 100 m away from the experimental plots.

Plant material

Studies were conducted on *Stipa clarazii* Ball., *S. tenuis* Phil. and *S. gynerioides* Phil., all C₃ perennial grasses native to the South of the Calden Phytogeographical District, a region of about 4 million hectares in Central Argentina. The first 2 species have a high forage value whereas the latter is an undesirable, unpreferred tussock grass (Cano 1988). Tillering starts with fall rains in all 3 species, although it extends into winter, spring, and even summer if rainfalls are abundant (Giorgetti et al. 2000). Recent studies have shown that *S. clarazii* has a greater competitive ability and tolerance to defoliation than *S. tenuis* (Saint Pierre et al. 2000a, 2000b) and the undesirable species *Stipa trichotoma* Nees, *S. gynerioides*, and *Stipa ambigua* Speg. (Moretto and Distel 1997, Saint Pierre et al. 2000a, 2000b).

Experimental design

During December 1993–April 1994, 28 experimental plots (1.8 x 1.8 m) were established at the field site from transplants on unplowed, weeded soil. Distance among plots was 4 m. Plants were obtained from a 20 year-exclosure to domestic animals located southeast of La Pampa Province (38° 45'S, 63° 45'W) at the South of the Calden Phytogeographical Region. Plants of the 3 species were placed 30 cm from one another in intersecting rows forming a matrix where each plant of *S. clarazii* and *S. tenuis* was surrounded by 4 plants of *S. gynerioides*. Desirable species plants were always present at each plot vertex. This matrix contributed to uniform competitive effects among plants. Plant responses within a plant community are better explained by using plants growing with nearby, competitive neighbors than by utilizing plants growing in isolation (Mueggler 1972, McNaughton 1992). There were 49 plants on each plot (12 of *S. clarazii*, 12 of *S. tenuis* and 25 of *S. gynerioides*) making a total of 1372 transplants for the whole study. At the time of transplanting, plant diameters at crown level were 13.47 ± 0.56 cm ($\bar{X} \pm 1$ SE, $n = 56$) for *S. clarazii*, 10.02 ± 0.51 cm for *S. tenuis*, and 12.27 ± 0.61 cm for *S. gynerioides*. In January 1995, during the plant quiescent period, all tussocks of *S. clarazii* and *S. tenuis* were manually clipped leaving 5 cm stubble height. In this manner, only current year growth was included in subsequent harvests to determine biomass. Two experimental plots (replicates) were randomly assigned to each water level x defoliation

Fig. 2. Periods of imposition of the different water levels and timing of defoliation (indicated as vertical solid bars) at the vegetative (V), internode elongation (E) or both (VE) phenological stages in 1995 and 1996.

treatment combination, giving a total of 14 treatments (see Water levels and Defoliation treatment headings in Fig. 2).

Measurements during the 3 growing seasons were repeated measures on the same groups of plants. Thus, we report on the cumulative effects of several water and defoliation treatments. Since we worked with an enormous unit of work, labor, and budget constraints made replication of our study in space and time impossible. Despite the fact that we place emphasis on statistical differences, caution is called for extrapolating our results. These should be better viewed under the specific conditions they were obtained. However, our study provided a unique opportunity for a simultaneous comparison of plant responses to various water levels, and to the timing and frequency of defoliation on species having differences in competitive ability.

Treatments

Soil water levels

Timing of application of water level and defoliation treatments during each year is shown in Fig. 2. A set of plots received rainfall all year round (rainfed plots). Irrigated plots received rainfall plus additional water with a drip irrigation system. In the irrigated treatment, plots were watered whenever soil moisture content dropped below 60% of field capacity as determined with soil tensiometers. The amount of water added to these plots was

calculated using software (Smith 1992, 1993) which accounted for soil and climate characteristics at the study site, and plant characteristics of species similar to those investigated. Water-stressed plots were covered with transparent plastic sheets (0.2 mm thick) whenever rain fell during the vegetative (V) or early internode elongation (E) or VE phenological stage of development (Fig. 2). Plants are often exposed to water stress conditions during any of these periods in their natural environment (Busso 1997, Fernández and Busso 1999). Plastic sheets were mounted on a specially designed wooden structure that provided an open-sided rain shelter. Lateral movement of water into the water-stressed plots was prevented by surrounding these plots with plastic sheets (0.2 mm thick) up to 1.8 m depth. Plants were exposed to water stress before, during and until 3 weeks after application of the defoliation treatments.

Except for plots exposed to water stress in the VE stage, the amount of water received when the different water levels were imposed (mid-April to mid-October in 1995 and late-April to late-October in 1996) was 373.2 mm in 1995 and 305.4 mm in 1996 in the irrigated plots, 87.2 mm in 1995 and 252.4 mm in 1996 in the rainfed plots, 76.4 mm in 1995 and 172.6 mm in 1996 after alleviation of water stress in the V stage, and 22.0 mm in 1995 and 133.2 mm in 1996 before imposition

Table 1. Midday leaf water potential (MPa) on plants of *S. clarazii*, *S. gynerioides* and *S. tenuis* during 1995. *Stipa clarazii* and *S. tenuis* were either defoliated or remained undefoliated (Controls: C) at the vegetative (V), internode elongation (E) or both phenological stages (VE) under rainfed, irrigated or water stress conditions. Plants of *S. gynerioides* grew in competition with the other 2 species but remained undefoliated. Each value is the mean (+/-SE) of n=2. Values without SE come from n=1.

Treatments			1995					
Water levels	Defoliation		1 Apr	17 May	31 Aug	26 Sep	24 Oct	29 Nov
(MPa)								
<i>S. clarazii</i>	Irrigation	C	-1.00 -	-2.10 (0.20)	-3.33 (0.28)	-3.33 (0.08)	-3.60 (0.40)	-1.98 (0.78)
		V	-0.88 (0.23)	-2.30 (0.00)	-2.75 (0.25)	-3.05 (0.55)	-3.28 (0.13)	-1.83 (0.83)
		E	-1.30 (0.40)	-2.65 -	-2.78 (0.28)	-3.28 (0.73)	-2.78 (0.38)	-2.00 (0.65)
		VE	-0.85 (0.55)	-2.33 (0.38)	-2.55 (0.10)	-2.95 (0.15)	-2.80 (0.30)	-2.03 (0.88)
	Rainfed	C	-1.75 (0.05)	-2.83 (0.38)	-2.33 (0.18)	-1.40 (0.10)	-1.43 (0.13)	-2.50 (0.55)
		V	-1.58 (0.43)	- -	-1.35 (0.15)	-1.28 (0.58)	-0.65 (0.15)	-1.30 (0.10)
		E	-1.43 (0.38)	-2.60 -	-2.03 (0.03)	-0.85 (0.35)	-1.18 (0.53)	-1.75 (0.15)
		VE	-1.68 (0.03)	-1.30 -	-1.63 (0.28)	-1.38 (0.58)	-1.10 (0.00)	-1.90 (0.10)
	Water stress V	C	-0.65 -	-2.80 (0.10)	-3.13 (0.03)	-3.25 (0.30)	-4.15 (0.80)	-2.28 (0.08)
		V	-1.65 (0.25)	-2.63 (0.43)	-2.93 (0.13)	-3.83 (0.38)	-3.78 (0.13)	-1.85 (0.15)
	Water stress E	C	-0.80 -	-2.60 (0.20)	-2.08 (0.08)	-3.33 (0.08)	-2.35 (0.15)	-2.50 (0.05)
		E	-1.10 (0.10)	-3.00 -	-3.80 (1.60)	-3.35 (1.00)	-2.03 (0.23)	-2.23 (0.23)
	Water stress VE	C	-0.80 -	-2.08 (0.98)	-2.85 (0.05)	-3.85 (0.55)	-1.83 (0.83)	-2.75 (0.25)
		VE	-1.25 (0.55)	-2.35 (0.45)	-2.45 (0.05)	-2.83 (0.18)	-2.13 (0.18)	-3.10 (0.45)
<i>S. gynerioides</i>	Irrigation	C	-0.50 -	-1.95 (0.85)	-3.28 (0.18)	-2.88 (0.18)	-3.60 (0.60)	-1.65 (0.35)
		V	-1.55 (0.75)	-1.70 (0.60)	-3.00 (0.05)	-3.05 (0.25)	-2.95 (0.15)	-2.40 (0.25)
		E	-0.70 (0.10)	-2.60 -	-2.50 (0.00)	-2.38 (0.68)	-3.25 (0.05)	-1.93 (0.23)
		VE	-0.35 (0.15)	-1.50 (0.60)	-2.50 (1.20)	-3.70 (0.70)	-3.15 (0.25)	-1.88 (0.63)
	Rainfed	C	-1.75 (0.75)	-2.88 (0.23)	-2.75 (0.45)	-1.83 (0.58)	-1.58 (0.28)	-1.63 (0.28)
		V	-1.80 (0.80)	- -	-2.10 (0.40)	-1.23 (0.28)	-1.25 (0.05)	-1.55 (0.85)
		E	-1.85 (0.95)	-2.30 -	-2.10 (0.60)	-1.08 (0.63)	-1.35 (0.15)	-1.73 (0.48)
		VE	-1.20 (0.70)	-2.80 -	-1.90 (0.70)	-1.05 (0.20)	-1.50 (0.10)	-1.28 (0.08)
	Water stress V	C	-1.80 -	-1.75 (0.55)	-2.90 (0.50)	-4.53 (0.73)	-2.88 (0.23)	-2.75 (0.25)
		V	-2.60 (0.70)	-2.58 (0.23)	-3.08 (0.63)	-3.45 (0.20)	-3.53 (0.08)	-2.33 (0.03)
	Water stress E	C	-0.30 -	-1.45 (0.95)	-2.10 (1.00)	-2.33 (0.88)	-2.05 (0.30)	-2.13 (0.28)
		E	-1.65 (0.85)	-2.90 -	-2.38 (0.73)	-2.60 (0.60)	-2.08 (0.18)	-2.25 (0.35)
	Water stress VE	C	-2.70 -	-2.08 (1.08)	-4.13 (0.23)	-3.60 (0.10)	-2.90 (0.90)	-1.80 (0.20)
		VE	-1.30 (1.10)	-1.45 (0.95)	-2.08 (0.63)	-2.35 (0.40)	-2.28 (0.03)	-2.38 (0.33)
<i>S. tenuis</i>	Irrigation	C	-1.20 -	-2.60 (0.60)	-2.75 (0.50)	-2.93 (0.18)	-2.90 (0.40)	-1.53 (0.48)
		V	-2.00 (0.30)	-2.35 (0.25)	-2.80 (0.35)	-2.63 (1.03)	-2.53 (0.43)	-2.10 (0.45)
		E	-1.70 (0.10)	-2.40 -	-2.28 (0.28)	-2.65 (0.10)	-2.75 (0.05)	-2.50 (0.15)
		VE	-1.95 (0.05)	-1.78 (0.28)	-3.15 (0.10)	-2.95 (0.45)	-3.00 (0.10)	-2.68 (0.13)
	Rainfed	C	-2.05 (0.05)	-2.45 (0.95)	-1.45 (0.35)	-1.20 (0.25)	-1.15 (0.05)	-1.18 (0.13)
		V	-1.78 (0.68)	- -	-2.68 (0.13)	-1.73 (0.78)	-1.48 (0.38)	-1.65 (0.00)
		E	-1.45 (0.25)	-2.10 -	-2.43 (0.23)	-1.73 (0.38)	-1.60 (0.50)	-1.20 (0.10)
		VE	-1.75 (0.15)	-1.10 -	-1.45 (0.10)	-1.88 (0.38)	-1.70 (0.50)	-1.23 (0.28)
	Water stress V	C	-1.90 -	-2.88 (0.53)	-4.00 (0.80)	-3.65 (0.15)	-3.03 (0.78)	-2.33 (0.48)
		V	-1.65 (0.75)	-2.05 (0.05)	-2.80 (0.30)	-3.05 (0.40)	-2.88 (0.58)	-1.78 (0.93)
	Water stress E	C	-1.60 -	-2.25 (0.15)	-3.13 (0.48)	-3.43 (0.23)	-2.78 (0.93)	-1.65 (0.55)
		E	-1.85 (0.05)	-2.40 -	-2.10 (0.60)	-2.78 (0.23)	-2.20 (0.40)	-1.75 (0.35)
	Water stress VE	C	-1.30 -	-1.65 (0.55)	-4.15 (0.75)	-2.80 (0.10)	-2.30 (0.20)	-2.10 (0.85)
		VE	-1.70 (0.10)	-1.95 (0.85)	-3.58 (0.53)	-3.43 (0.03)	-2.53 (1.53)	-2.23 (0.13)

of water stress at the E stage. Thereafter, all 28 experimental plots received 313.7 mm from mid-October 1995 to late-April 1996, and 487.8 mm from late-October 1996 to March 1997.

Defoliation treatments

Within each water level, plants of *S. clarazii* and *S. tenuis* remained undefoliated (Controls: C) or were defoliated at either V or E or VE stage of development during 1995 and 1996. Clipping left 5–7

cm stubble height on 23 May (V) or 27 September (E) in 1995, and 12 June (V) or 20 September (E) in 1996 (Fig. 2). *Stipa gynerioides* was not defoliated in 1995 and 1996 since it is not consumed by cattle (Cano 1988, Moretto and Distel 1997). However, all plants of this species were clipped to 5–7 cm stubble height at the end of the study (12 March 1997) to determine biomass production in the different treatments.

Leaf water potential

Determinations of leaf water potential provided a measure of plant water stress. Mid-day leaf water potential was periodically measured in all species using a pressure chamber during 1995, 1996, and early 1997 (Waring and Cleary 1967). Youngest, fully expanded leaves were taken for these measurements; one tiller was used per species and replicate on each sampling date. Leaves were kept in a plastic bag from excision to end of each determination to reduce water loss (Turner 1987).

Table 2. Midday leaf water potential (MPa) on plants of *S. clarazii*, *S. gynerioides* and *S. tenuis* during 1996 and early 1997. *Stipa clarazii* and *S. tenuis* were either defoliated or remained undefoliated (Controls: C) at the vegetative (V), internode elongation (E) or both phenological stages (VE) under rainfed, irrigated or water stress conditions during 1996. These plants had been defoliated under these water levels during 1995. Plants of *S. gynerioides* grew in competition with the other 2 species but remained undefoliated. Plants of all 3 species received natural rainfall during early 1997. Each value is the mean (+/-SE) of n=2.

Treatments			1996						1997
Water levels	Defoliation		19 Apr	11 Jun	15 Aug	22 Sep	14 Nov	21 Dec	22 Feb
-(MPa)									
<i>S. clarazii</i>	Irrigation	C	-1.88 (0.08)	-0.85 (0.45)	-1.80 (0.45)	-2.03 (0.13)	--	-2.38 (0.18)	-2.55 (0.25)
		V	-1.40 (0.10)	-1.13 (0.13)	-1.15 (0.15)	-2.13 (0.38)	--	-2.45 (0.10)	-2.40 (0.30)
		E	-1.68 (0.08)	-1.43 (0.73)	-1.68 (0.23)	-2.25 (0.35)	--	-2.48 (0.38)	-2.45 (0.05)
		VE	-1.30 (0.20)	-1.43 (0.53)	-1.98 (0.28)	-1.95 (0.55)	--	-2.10 (0.70)	-2.35 (0.05)
	Rainfed	C	-1.53 (0.28)	-0.98 (0.28)	-1.65 (0.65)	-1.70 (0.10)	-3.10 (0.40)	-1.95 (0.45)	-2.95 (0.45)
		V	-1.73 (0.28)	-1.68 (0.43)	-1.85 (0.15)	-1.90 (0.00)	-3.63 (1.03)	-2.65 (0.55)	-2.40 (0.40)
		E	-2.05 (0.25)	-1.25 (0.45)	-0.95 (0.25)	-2.35 (0.05)	-3.10 (0.20)	-2.55 (0.55)	-2.75 (0.75)
		VE	-1.93 (0.23)	-0.88 (0.28)	-1.30 (0.70)	-2.10 (0.10)	-2.40 (0.25)	-2.10 (0.20)	-2.25 (0.05)
	Water stress V	C	-2.38 (0.18)	-3.95 (0.35)	-2.38 (0.28)	-2.60 (0.30)	--	-2.83 (0.43)	-3.05 (0.25)
		V	-2.15 (0.35)	-4.68 (0.48)	-2.18 (0.33)	-2.40 (0.20)	--	-2.75 (0.20)	-3.15 (0.45)
	Water stress E	C	-2.00 (0.00)	-1.45 (0.20)	-2.30 (0.10)	-3.65 (0.05)	-6.15 (0.35)	-2.30 (0.30)	-2.90 (0.10)
		E	-1.85 (0.50)	-1.65 (0.15)	-1.73 (0.18)	-4.05 (1.65)	-3.60 (0.80)	-2.15 (0.35)	-2.75 (0.25)
	Water stress VE	C	-2.48 (0.33)	-3.28 (0.03)	-3.50 (0.10)	-3.35 (0.05)	-5.20 (0.50)	-2.88 (0.28)	-2.65 (0.15)
		VE	-1.68 (0.44)	-3.63 (0.38)	-2.73 (0.03)	-2.53 (0.18)	-4.38 (0.23)	-2.75 (0.30)	-2.50 (0.20)
<i>S. gynerioides</i>	Irrigation	C	-1.38 (0.13)	-1.58 (1.18)	-2.80 (0.60)	-2.63 (0.03)	--	-2.85 (0.15)	-2.60 (0.30)
		V	-1.70 (0.10)	-1.55 (0.05)	-1.65 (0.85)	-2.40 (0.20)	--	-2.50 (0.05)	-2.15 (0.05)
		E	-1.95 (0.80)	-2.25 (0.55)	-1.43 (0.60)	-2.48 (0.18)	--	-3.00 (0.15)	-1.85 (0.45)
		VE	-1.25 (0.15)	-2.05 (0.65)	-2.83 (0.68)	-2.33 (0.03)	--	-2.83 (0.38)	-2.40 (0.40)
	Rainfed	C	-1.48 (0.23)	-3.10 (0.00)	-1.85 (0.45)	-2.00 (0.30)	-3.03 (0.08)	-2.45 (0.45)	-2.90 (0.30)
		V	-1.78 (0.38)	-1.00 (0.10)	-1.00 (0.00)	-2.50 (0.20)	-2.85 (0.65)	-3.10 (0.00)	-2.40 (0.30)
		E	-2.33 (0.13)	-1.08 (0.38)	-1.93 (0.08)	-2.25 (0.15)	-2.55 (0.35)	-2.45 (0.55)	-2.20 (0.80)
		VE	-1.43 (0.43)	-1.08 (0.38)	-2.43 (0.23)	-1.65 (0.05)	-2.15 (0.45)	-2.63 (0.03)	-1.70 (0.20)
	Water stress V	C	-2.25 (0.15)	-4.25 (0.75)	-2.73 (0.23)	-2.83 (0.08)	--	-2.63 (0.03)	-2.45 (0.65)
		V	-1.43 (0.18)	-4.10 (0.60)	-1.70 (0.50)	-2.93 (0.03)	--	-2.70 (0.20)	-3.10 (0.40)
	Water stress E	C	-1.45 (0.35)	-1.18 (0.08)	-2.40 (0.30)	-3.70 (0.10)	-4.08 (0.28)	-2.88 (0.13)	-2.75 (0.35)
		E	-1.85 (0.05)	-1.28 (0.13)	-2.60 (0.50)	-4.95 (2.45)	-3.50 (0.60)	-2.73 (0.43)	-2.88 (0.28)
	Water stress VE	C	-1.80 (0.60)	-3.75 (0.15)	-4.05 (0.15)	-3.85 (0.75)	-6.08 (1.33)	-2.38 (0.13)	-2.60 (0.30)
		VE	-2.15 (0.55)	-2.15 (0.85)	-4.65 (0.15)	-4.20 (1.00)	-4.35 (0.35)	-2.65 (0.15)	-1.35 (0.75)
<i>S. tenuis</i>	Irrigation	C	-1.95 (0.05)	-1.30 (0.45)	-2.48 (0.03)	-2.40 (0.10)	--	-1.88 (0.18)	-2.33 (0.13)
		V	-2.10 (0.05)	-1.80 (0.70)	-2.20 (0.10)	-2.30 (0.30)	--	-1.85 (0.05)	-1.90 (0.70)
		E	-2.08 (0.18)	-1.63 (0.33)	-1.55 (0.45)	-2.15 (0.05)	--	-2.38 (0.13)	-1.85 (0.35)
		VE	-1.85 (0.45)	-1.63 (0.78)	-1.75 (0.60)	-1.80 (0.00)	--	-1.55 (0.30)	-2.10 (0.00)
	Rainfed	C	-2.10 (0.30)	-1.78 (0.83)	-1.35 (0.35)	-1.55 (0.25)	-2.80 (1.20)	-2.00 (0.25)	-2.45 (0.35)
		V	-1.63 (0.28)	-1.43 (0.38)	-1.10 (0.00)	-1.80 (0.00)	-2.50 (0.70)	-1.66 (0.28)	-2.25 (0.15)
		E	-2.00 (0.20)	-2.25 (0.05)	-1.40 (0.45)	-1.90 (0.20)	-2.60 (0.20)	-2.13 (0.13)	-2.40 (0.00)
		VE	-2.40 (0.50)	-1.20 (0.05)	-1.85 (0.35)	-1.90 (0.20)	-1.80 (0.50)	-2.03 (0.33)	-1.98 (0.28)
	Water stress V	C	-2.13 (0.13)	-3.35 (0.10)	-1.38 (0.13)	-1.80 (0.10)	--	-1.70 (0.30)	-2.48 (0.68)
		V	-1.60 (0.20)	-4.75 (0.45)	-1.93 (0.28)	-1.98 (0.28)	--	-2.05 (0.20)	-3.35 (1.05)
	Water stress E	C	-2.30 (0.20)	-1.33 (0.03)	-2.28 (0.13)	-4.35 (0.05)	-5.65 (0.65)	-2.10 (0.25)	-3.00 (0.50)
		E	-2.10 (0.35)	-1.73 (0.03)	-1.98 (0.03)	-3.35 (1.25)	-3.93 (0.73)	-1.70 (0.10)	-2.82 (0.29)
	Water stress VE	C	-1.90 (0.10)	-2.70 (0.50)	-2.75 (0.35)	-2.45 (0.15)	-3.75 (1.75)	-2.15 (1.15)	-2.10 (0.00)
		VE	-2.05 (0.55)	-2.40 (0.60)	-3.13 (0.38)	-2.63 (0.63)	-4.38 (0.13)	-2.20 (0.10)	-1.60 (0.30)

Bud metabolic activity and axillary bud outgrowth

These variables were evaluated on parent tillers produced during each growing season. At each observation date, 2 to 4 tillers were harvested per plant of *S. clarazii*, *S. tenuis*, or *S. gynerioides*; one plant was used per replicate in all treatments. Crown samples were maintained at 4°C until dissection. Number, metabolic activity, and outgrowth of axillary buds were determined on each tiller under a

binocular microscope. Three bud categories were considered: metabolically active (MAB), dormant or dead (DDB), and buds which grew out originating daughter tillers (DT). Total bud number (TBN) was calculated as MAB+DDB+DT. The potential maximum number of buds per stem base (total node number = TN) was calculated as MAB+DDB+DT+number of foliar scars. Font Quer (1982) reported that this number is equivalent to the number of produced leaves. Foliar

scars indicate presence of leaves which do not have buds or daughter tillers in their axilla (Hendrickson and Briske 1997).

Metabolic activity of axillary buds was determined using Triphenyl Tetrazolium Chloride (TTC) following Busso et al. (1989). Each stem base was longitudinally cut leaving entire buds at both sides of the cutting. Both halves were maintained in a solution of 0.6% (weight/volume) TTC-0.05 M Phosphate buffer (pH = 7.38) during 15 hours in darkness at 30°C.

Metabolically active buds were those whose apex stained pink or red indicating enzymatic reduction of colourless tetrazolium salt to red, insoluble formazan. Buds not-stained with TTC were considered dormant or dead.

Statistical analysis

Leaf water potentials were analyzed separately for each date using ANOVA. A split plot design was used with treatments (14 combinations of water x defoliation levels) as main factors and species as secondary factors. One-way ANOVA was used to analyze the bud metabolic activity data; analysis was performed separately for each date and species using a completely randomized design with 14 treatments. Whenever F tests were significant at $p < 0.05$, means were separated using Fisher LSD or Tukey-Kramer test for balanced or unbalanced data, respectively. Values for MAB and DDB were transformed to $\sqrt{x+1}$ to improve normality assumptions (Steel and Torrie 1985). Non-transformed values are presented in Figures.

Results and Discussion

Leaf water potentials

During 1995, 1996, and early 1997, leaf water potentials were similar ($p > 0.25$) among defoliation treatments within each water level in all 3 species (Tables 1 and 2). These results are similar to those of Becker et al. (1997) and Busso and Richards (1993) in these and other perennial grasses. Other studies, however, have reported higher leaf water potentials on defoliated than on undefoliated perennial tussock grasses (Briske and Anderson 1990, Brown 1995, Williams et al. 1998). This positive response to herbivory has been attributed to a reduced transpiratory leaf surface area after defoliation which would conserve soil water (Anderson and Briske 1995, Brown 1995).

At the beginning and end of each growing cycle, leaf water potential was similar ($p > 0.25$) among water levels in *S. clarazii*, *S. tenuis* and *S. gynerioides*. In August, September, and October 1995, however, these species had lower ($p < 0.05$) leaf water potentials under water stress than under irrigated conditions. Similar results were obtained in 1996 during this period, except on plants of the desirable species by the end of September ($p > 0.15$). Leaf water potentials were more variable on plants of the 3 species in the rainfed plots. Under these conditions, leaf

Table 3. Number of total nodes (TN), buds which originated daughter tillers (DT), and metabolically active (MAB) and dead and dormant (DDB) buds on parent tillers of *S. gynerioides* at the different treatments in 1995, 1996 and early 1997. C: Undefoliated controls, and defoliation at the vegetative (V), internode elongation (E) or both phenological stages (VE). Each value is the mean (+/-SE) of n=2.

Dates	Treatments		TN	DT	MAB	DDB
	Water levels	Defoliation				
23/5/95	Irrigation	C	6.25 (0.75)	3.00 (0.00)	1.25 (0.25)	0.25 (0.25)
		V	5.75 (0.75)	2.00 (0.50)	0.50 (0.00)	1.00 (1.00)
		VE	8.00 (0.00)	5.00 (0.00)	1.00 (0.00)	0.00 (0.00)
	Rainfed	C	7.00 (0.00)	3.50 (0.00)	0.50 (0.00)	0.00 (0.00)
		V	7.75 (1.25)	3.00 (1.00)	0.75 (0.25)	0.50 (0.00)
		VE	7.25 (1.25)	2.25 (0.25)	0.75 (0.25)	1.75 (0.75)
	Water stress V	C	6.75 (0.75)	3.75 (1.25)	0.75 (0.75)	0.75 (0.75)
		V	7.75 (0.25)	3.75 (0.25)	1.00 (0.00)	0.25 (0.25)
	Water stress VE	C	8.25 (0.75)	4.00 (1.00)	0.50 (0.00)	1.00 (1.00)
		VE	6.25 (0.75)	3.25 (0.75)	1.00 (0.00)	0.00 (0.00)
	7/9/95	C	7.13 (0.13)	2.63 (0.13)	0.88 (0.13)	2.00 (0.00)
		V	7.25 (2.00)	2.88 (1.13)	0.88 (0.38)	1.00 (0.75)
		VE	6.25 (0.50)	3.13 (0.13)	0.88 (0.38)	0.25 (0.00)
27/9/95	Rainfed	C	7.25 (0.75)	3.00 (0.25)	0.50 (0.25)	1.75 (1.50)
		V	5.88 (0.63)	2.25 (0.50)	0.75 (0.00)	1.63 (0.38)
		VE	7.13 (1.13)	2.83 (1.17)	0.71 (0.04)	1.25 (0.25)
	Water stress V	C	6.50 (0.00)	2.50 (0.00)	1.50 (0.50)	0.75 (0.50)
		V	8.08 (0.58)	3.38 (0.63)	0.79 (0.46)	1.38 (0.38)
	Water stress VE	C	6.42 (0.08)	2.71 (0.04)	1.09 (0.42)	0.88 (0.13)
		VE	7.75 (0.00)	3.13 (0.13)	0.88 (0.38)	1.00 (0.75)
	Irrigation	C	7.38 (0.38)	3.38 (0.38)	0.38 (0.13)	2.00 (0.50)
		E	7.88 (0.13)	3.13 (0.63)	0.88 (0.38)	1.25 (0.00)
		VE	8.88 (0.13)	3.75 (0.50)	1.00 (0.00)	1.50 (0.50)
	Rainfed	C	8.00 (0.75)	2.88 (0.38)	0.50 (0.50)	2.38 (0.63)
		E	9.13 (0.38)	4.00 (0.25)	0.88 (0.13)	2.00 (0.00)
		VE	8.50 (1.00)	3.38 (0.13)	1.25 (0.25)	2.00 (1.00)
	Water stress E	C	7.75 (0.50)	2.88 (0.13)	0.25 (0.00)	1.88 (0.63)
		E	7.88 (0.38)	3.00 (0.75)	0.63 (0.13)	1.00 (0.00)
	Water stress VE	C	7.50 (0.50)	2.75 (0.25)	1.38 (0.13)	1.38 (0.63)
		VE	9.63 (0.13)	4.00 (0.25)	0.63 (0.38)	1.50 (0.25)
	14/12/95	C	6.88 (0.13)	2.75 (1.25)	0.00 (0.00)	2.13 (0.63)
		E	7.75 (0.75)	2.38 (0.38)	0.00 (0.00)	3.00 (0.00)
		VE	7.13 (0.38)	2.63 (0.63)	0.00 (0.00)	2.13 (0.38)
	Rainfed	C	7.63 (0.63)	3.00 (0.50)	0.13 (0.13)	2.25 (0.25)
		E	8.63 (1.38)	3.50 (0.25)	0.25 (0.25)	2.63 (1.63)
	Water stress E	C	7.88 (0.63)	3.88 (1.13)	0.00 (0.00)	2.50 (0.50)
		E	7.88 (0.63)	2.88 (0.63)	0.00 (0.00)	2.50 (0.25)
	Water stress VE	C	8.25 (0.50)	4.13 (0.38)	0.00 (0.00)	2.13 (0.63)
		VE	6.88 (0.63)	2.50 (0.75)	0.00 (0.00)	2.63 (0.38)
	25/4/96	C	9.00 (0.00)	3.00 (0.50)	1.75 (0.25)	2.00 (0.00)
		V	7.25 (0.25)	0.75 (0.25)	1.75 (0.25)	3.25 (1.25)
		E	6.50 (0.00)	1.50 (0.50)	1.75 (0.25)	2.00 (0.00)
	Rainfed	VE	8.25 (0.25)	1.25 (0.25)	0.75 (0.25)	3.25 (1.25)
		C	6.75 (0.25)	1.50 (0.00)	1.00 (0.00)	2.50 (0.50)
		V	7.00 (0.50)	1.75 (0.25)	2.00 (0.00)	0.75 (0.25)
	Water stress V	E	7.25 (1.25)	1.50 (1.00)	1.25 (0.25)	3.00 (0.50)
		VE	7.75 (0.25)	1.50 (0.00)	1.50 (0.50)	2.25 (0.25)
		C	6.75 (0.25)	2.25 (0.25)	1.00 (0.50)	1.50 (0.50)
	Water stress VE	V	7.00 (1.00)	2.50 (0.50)	0.50 (0.50)	2.25 (0.25)
		C	7.00 (0.00)	2.00 (0.00)	1.75 (0.25)	1.50 (0.50)
		VE	7.50 (1.00)	2.00 (1.00)	1.25 (0.25)	2.75 (0.25)
	12/6/96	C	8.13 (0.13)	1.75 (0.75)	2.13 (0.13)	2.63 (0.38)
		V	10.00 (0.25)	2.50 (0.75)	1.50 (0.25)	3.75 (0.50)
		VE	8.63 (0.13)	1.13 (0.13)	1.13 (0.13)	3.25 (0.25)
	Rainfed	C	7.63 (0.50)	1.63 (0.25)	1.50 (0.50)	2.88 (0.13)
		V	8.63 (0.88)	1.88 (0.63)	1.13 (0.63)	3.50 (0.50)
		VE	8.50 (0.00)	2.50 (0.25)	1.38 (0.63)	2.88 (0.63)
	Water stress V	C	8.25 (0.50)	1.13 (0.38)	1.38 (0.13)	3.13 (0.13)
		V	8.50 (1.00)	1.75 (0.25)	1.00 (0.75)	3.63 (1.13)

(Continued on page 156)

Table 3. Continued.

Dates	Treatments		TN	DT	MAB	DDB
	Water levels	Defoliation				
30/7/96	Water stress VE	C	7.88 (0.38)	2.00 (0.50)	1.63 (0.13)	2.50 (0.25)
		VE	9.38 (0.88)	3.13 (1.13)	1.00 (0.00)	2.00 (0.50)
	Irrigation	C	8.00 (0.00)	1.38 (0.88)	1.75 (0.00)	3.38 (0.63)
		V	8.25 (0.00)	1.75 (0.75)	1.25 (0.00)	3.38 (0.38)
		VE	7.63 (0.38)	2.25 (0.25)	1.13 (0.38)	2.00 (0.25)
	Rainfed	C	8.25 (0.75)	2.50 (0.00)	0.88 (0.13)	2.13 (0.88)
		V	8.88 (0.63)	2.75 (1.00)	1.25 (0.25)	2.50 (1.00)
		VE	8.25 (1.00)	1.88 (0.63)	0.75 (0.50)	4.13 (0.88)
	Water stress V	C	8.00 (0.00)	2.25 (0.00)	0.88 (0.63)	3.13 (0.63)
		V	7.63 (0.13)	1.88 (0.38)	1.13 (0.88)	3.00 (1.25)
21/9/96	Water stress VE	C	9.25 (1.25)	2.50 (1.00)	1.00 (0.25)	4.25 (0.00)
		VE	8.25 (0.50)	2.63 (0.63)	1.38 (0.13)	2.13 (0.13)
	Irrigation	C	8.13 (0.63)	1.50 (0.75)	0.38 (0.13)	3.88 (0.88)
		E	8.13 (0.38)	1.88 (0.88)	0.38 (0.13)	3.63 (1.38)
		VE	8.00 (0.25)	2.88 (0.13)	0.25 (0.25)	2.38 (0.13)
	Rainfed	C	8.75 (0.25)	3.13 (0.13)	0.13 (0.13)	3.25 (0.25)
		E	8.13 (0.13)	1.88 (0.13)	0.25 (0.25)	2.25 (1.25)
		VE	8.88 (0.13)	2.38 (0.13)	0.63 (0.63)	3.63 (0.63)
	Water stress E	C	9.63 (0.63)	3.38 (0.88)	1.13 (0.13)	2.13 (0.38)
		E	8.25 (0.25)	2.38 (0.13)	0.63 (0.63)	2.75 (1.00)
30/10/96	Water stress VE	C	8.88 (0.13)	2.75 (1.25)	1.13 (0.63)	1.63 (0.63)
		VE	7.88 (0.38)	2.13 (0.63)	0.75 (0.25)	3.13 (0.63)
	Irrigation	C	7.88 (0.13)	1.38 (0.13)	0.00 (0.00)	4.50 (0.00)
		V	8.63 (0.63)	2.00 (0.75)	0.38 (0.13)	4.25 (1.00)
		E	—	—	—	—
		VE	7.75 (0.50)	2.25 (0.50)	0.00 (0.00)	3.13 (0.63)
	Rainfed	C	7.88 (0.13)	2.25 (0.25)	0.00 (0.00)	3.75 (0.00)
		V	7.50 (0.25)	2.13 (0.13)	0.13 (0.13)	2.38 (0.63)
		E	8.50 (0.75)	1.63 (0.88)	0.38 (0.38)	4.00 (1.00)
		VE	9.63 (0.38)	2.63 (0.13)	0.13 (0.13)	4.75 (0.00)
	Water stress V	C	7.63 (0.38)	2.00 (0.50)	0.00 (0.00)	3.50 (0.00)
		V	8.63 (0.13)	4.38 (0.38)	0.25 (0.00)	2.00 (0.50)
7/1/97	Water stress VE	C	8.25 (0.00)	2.13 (0.13)	0.75 (0.25)	4.00 (0.75)
		VE	8.63 (0.38)	2.13 (1.13)	0.13 (0.13)	4.88 (1.38)
	Irrigation	C	6.88 (0.13)	2.13 (0.13)	0.00 (0.00)	2.88 (0.13)
		V	6.38 (0.13)	2.13 (0.63)	0.00 (0.00)	2.13 (0.63)
		E	6.50 (0.50)	1.25 (0.25)	0.00 (0.00)	2.25 (0.00)
		VE	6.75 (0.25)	1.50 (0.00)	0.13 (0.13)	2.63 (0.13)
	Rainfed	C	6.75 (0.75)	2.00 (0.25)	0.13 (0.13)	2.50 (0.75)
		V	7.63 (0.63)	2.63 (0.13)	0.00 (0.00)	2.75 (0.75)
		E	6.88 (0.88)	0.88 (0.13)	0.00 (0.00)	4.00 (0.50)
		VE	6.75 (0.75)	1.50 (1.00)	0.13 (0.13)	3.50 (0.25)
	Water stress V	C	6.63 (0.88)	1.63 (0.38)	0.00 (0.00)	3.00 (1.00)
		V	6.25 (0.25)	2.38 (0.13)	0.25 (0.25)	1.63 (0.38)
12/3/97	Water Stress E	C	7.25 (0.25)	2.00 (0.25)	0.00 (0.00)	2.50 (0.25)
		E	8.13 (1.38)	2.13 (0.63)	0.13 (0.13)	3.25 (1.00)
	Water stress VE	C	9.46 (1.21)	3.04 (0.29)	0.29 (0.04)	1.96 (0.29)
		VE	9.09 (0.58)	2.50 (0.50)	0.00 (0.00)	3.54 (0.21)
	Irrigation	C	7.13 (0.38)	3.38 (1.13)	0.00 (0.00)	1.75 (0.25)
		V	6.75 (0.00)	1.88 (0.13)	0.00 (0.00)	2.50 (0.00)
		E	6.96 (0.29)	2.00 (0.00)	0.25 (0.25)	1.71 (0.04)
		VE	6.63 (0.38)	2.25 (0.00)	0.13 (0.13)	1.38 (1.13)
	Rainfed	C	6.13 (0.13)	2.13 (0.63)	0.13 (0.13)	1.50 (1.00)
		V	6.88 (0.63)	1.75 (0.25)	0.63 (0.38)	2.00 (0.25)
		E	7.00 (0.75)	2.13 (0.63)	0.13 (0.13)	2.13 (0.13)
		VE	6.25 (0.25)	1.63 (0.38)	0.25 (0.25)	1.88 (0.13)
	Water stress V	C	6.25 (0.25)	2.63 (0.13)	0.25 (0.25)	1.38 (0.13)
		V	7.38 (0.13)	2.75 (0.25)	0.00 (0.00)	2.25 (0.75)
	Water stress E	C	6.63 (0.13)	2.25 (0.25)	0.00 (0.00)	2.00 (0.50)
		E	7.50 (0.50)	2.00 (0.50)	0.13 (0.13)	3.13 (0.88)
	Water stress VE	C	7.38 (0.38)	3.00 (0.00)	0.13 (0.13)	1.75 (0.25)
		VE	7.50 (0.75)	2.75 (1.25)	0.00 (0.00)	2.25 (0.50)

water potentials were lower ($p < 0.05$) than those in the irrigated plots in 1995, and higher ($p < 0.05$) than those in the water-stressed plots in 1996 (Tables 1 and 2). This was very likely due to the lower annual rainfall in 1995 (447.2 mm) than in 1996 (621.3 mm) (Fig. 1).

In 1995, leaf water potential on average for all treatments was similar ($p > 0.25$) among species, except in April when this variable was higher ($p < 0.05$) in *S. clarazii* than in *S. tenuis*. Plants of the desirable species had higher ($p < 0.05$) leaf water potentials than *S. gynerioides* in mid-August, September, and December in 1996 (Tables 1 and 2).

Bud metabolic activity and axillary bud outgrowth

On average for each date and species, between 62 and 82% of the total number of nodes had daughter tillers, metabolically active buds or dormant or dead buds on parent tillers. This indicates that not all leaves possess axillary buds which is similar to results of Mueller and Richards (1986) and Hendrickson and Briske (1997) on other perennial grasses.

Numbers of total nodes, daughter tillers, and metabolically active or dormant or dead buds were similar ($p > 0.10$) between defoliation treatments and water levels during 1995, 1996, and early 1997 on parent tillers of *S. gynerioides* (Table 3). This implies that neither axillary bud activation nor initial outgrowth would contribute to explain the observed release from competition of *S. gynerioides* after selective defoliation of *S. clarazii* (Moretto and Distel 1999) and *S. clarazii* and *S. tenuis* (Flemmer 2000). These results also show the lack of sensitivity of axillary buds in *S. gynerioides* to water stress, a common abiotic factor to which plants are exposed in the temperate, central semiarid rangelands of Argentina (Busso 1997, Fernández and Busso 1999). Axillary buds of this species, however, are susceptible to fire (Distel and Bóo 1996, Peláez 2000).

Total node number, and numbers of daughter tillers, and metabolically active or dormant or dead buds were also similar ($p > 0.25$) in all water level and defoliation treatments on parent tillers of *S. tenuis* during 1995 (Table 4). These results indicate that the degree of metabolic activity and outgrowth capacity of axillary buds are maintained on parent tillers of this species after a one-year-exposure to the combined or separate influence of water stress and defoliation. Similar results ($p > 0.25$) were obtained for most sampling dates in 1996 (Table 4).

Table 4. Number of total nodes (TN), buds which originated daughter tillers (DT), and metabolically active (MAB) and dead and dormant (DDB) buds on parent tillers of *S. tenuis* at the different treatments in 1995, 1996 and early 1997. I: Irrigation, R: Rainfed, WS: Water stress, C: Undeveloped controls, and defoliation at the vegetative (V), internode elongation (E) or both phenological stages (VE). Each value is the mean (+/-SE) of n=2. Values without SE come from n=1.

Dates	Treatments		TN	DT	MAB	DDB
	Water levels	Defoliation				
23/5/95	Irrigation	C	7.25 (0.25)	2.75 (1.75)	2.25 (1.25)	0.25 (0.25)
		V	7.00 (1.00)	3.00 (0.00)	1.75 (0.25)	0.50 (0.50)
		VE	6.00 (0.00)	2.00 (0.00)	1.50 (0.00)	1.00 (0.00)
	Rainfed	C	7.00 (0.00)	5.00 (0.00)	0.00 (0.00)	0.50 (0.00)
		V	7.00 (0.50)	3.00 (0.50)	1.25 (0.75)	0.75 (0.25)
		VE	5.00 (1.00)	2.50 (0.50)	0.50 (0.50)	1.00 (1.00)
	Water stress V	C	10.00 (1.00)	4.00 (1.00)	3.50 (1.50)	0.00 (0.00)
		V	5.25 (0.25)	3.25 (0.25)	0.50 (0.50)	0.00 (0.00)
	Water stress VE	C	6.75 (0.25)	3.25 (0.75)	0.00 (0.00)	1.00 (1.00)
		VE	7.00 (2.00)	1.50 (0.50)	1.75 (0.25)	0.50 (0.50)
7/9/95	Irrigation	C	9.00 (1.25)	2.88 (1.38)	1.50 (1.00)	2.13 (0.63)
		V	8.71 (1.04)	3.92 (0.58)	1.50 (0.50)	1.75 (0.25)
		VE	8.00 (1.25)	3.25 (0.50)	1.75 (1.50)	1.50 (0.00)
	Rainfed	C	8.00 (2.00)	4.50 (1.50)	1.13 (0.13)	0.38 (0.38)
		V	7.13 (0.88)	3.38 (0.63)	2.25 (0.75)	0.42 (0.08)
		VE	7.46 (0.79)	2.50 (0.50)	2.38 (0.38)	1.29 (0.04)
	Water stress V	C	9.25 (0.25)	3.88 (1.63)	3.25 (1.25)	0.50 (0.00)
		V	7.33 (1.00)	3.17 (1.17)	1.00 (0.67)	1.17 (0.83)
	Water stress VE	C	7.21 (0.54)	2.33 (0.33)	2.21 (1.54)	1.46 (1.21)
		VE	8.04 (1.71)	3.58 (0.08)	1.58 (0.92)	1.04 (0.71)
27/9/95	Irrigation	C	10.13 (0.88)	3.38 (1.38)	1.75 (0.25)	3.38 (0.88)
		E	9.83 (0.83)	3.79 (0.46)	1.58 (1.08)	1.08 (0.42)
		VE	10.00 (1.00)	3.63 (0.13)	2.50 (1.00)	2.25 (0.50)
	Rainfed	C	8.75 (1.25)	2.75 (1.00)	2.88 (0.63)	1.25 (0.50)
		E	9.75 (1.00)	4.50 (0.25)	2.13 (0.38)	1.88 (1.13)
		VE	8.88 (1.63)	3.25 (0.25)	2.50 (1.25)	1.38 (0.38)
	Water stress E	C	9.00 (1.75)	4.25 (0.50)	1.38 (0.63)	2.00 (1.75)
		E	8.88 (0.63)	3.25 (0.25)	3.00 (0.50)	1.25 (0.75)
	Water stress VE	C	8.75 (0.25)	3.88 (0.13)	1.50 (0.00)	1.50 (0.50)
		VE	9.75 (1.00)	2.75 (0.50)	3.75 (0.25)	2.00 (0.25)
14/12/95	Irrigation	C	8.75 (0.25)	3.63 (0.88)	1.00 (0.50)	2.63 (0.63)
		E	7.50 (2.50)	1.75 (1.00)	1.00 (0.75)	2.88 (2.13)
		VE	9.00 (1.75)	3.50 (0.25)	0.63 (0.13)	3.63 (1.63)
	Rainfed	C	8.63 (0.88)	3.88 (1.38)	2.00 (0.00)	1.50 (0.50)
		E	8.25 (3.00)	3.88 (2.38)	1.00 (0.25)	2.00 (0.75)
		VE	9.63 (0.88)	4.25 (0.25)	0.75 (0.25)	2.88 (1.38)
	Water Stress E	C	8.75 (0.75)	4.25 (0.50)	0.63 (0.13)	2.38 (0.13)
		E	9.25 (0.75)	4.38 (0.38)	1.25 (1.00)	2.00 (0.75)
	Water stress VE	C	8.25 (1.00)	3.88 (0.13)	1.50 (1.00)	1.25 (0.75)
		VE	9.38 (1.38)	3.63 (0.38)	0.25 (0.25)	4.00 (1.50)
25/4/96	Irrigation	C	6.50 (0.00)	2.75 (0.75)	0.75 (0.75)	1.25 (1.25)
		V	9.50 (0.50)	3.50 (1.50)	1.75 (0.75)	3.00 (0.00)
		E	6.00 (0.50)	1.50 (0.00)	1.75 (0.25)	0.75 (0.75)
		VE	7.00 (0.00)	0.00 (0.00)	3.00 (0.00)	2.00 (0.00)
	Rainfed	C	8.00 (1.00)	3.25 (0.75)	1.00 (0.50)	1.25 (1.25)
		V	7.50 (1.50)	3.25 (0.75)	0.25 (0.25)	1.50 (1.50)
		E	7.00 (0.00)	2.75 (0.75)	1.25 (1.25)	0.50 (0.50)
		VE	7.00 (2.00)	3.75 (0.75)	1.75 (1.75)	0.25 (0.25)
	Water stress V	C	9.25 (1.25)	4.00 (0.00)	1.25 (0.75)	1.25 (1.25)
		V	7.50 (0.00)	3.75 (0.75)	2.00 (0.50)	0.25 (0.25)
	Water stress E	C	7.50 (1.00)	2.25 (0.25)	3.25 (1.25)	0.50 (0.50)
		E	7.25 (2.25)	2.75 (1.25)	2.00 (0.50)	0.25 (0.25)
	Water stress VE	C	8.75 (0.25)	3.00 (2.00)	3.25 (1.25)	0.50 (0.50)
		VE	8.00 (0.00)	2.75 (1.25)	1.50 (1.00)	2.00 (1.50)

(Continued on page 158)

However, defoliation affected bud metabolic activity of *S. tenuis* independently of plant water status in June 1996 (before defoliation at V). While defoliated and undeveloped plants of this species had a similar ($p > 0.25$) total bud number, numbers of metabolically active buds were lower ($p < 0.05$) and those of dormant or dead buds were higher ($p < 0.05$) on plants defoliated at the vegetative and vegetative + early internode elongation stages in the previous year than on undeveloped controls under all water levels (Table 4). Despite this lower degree of metabolic activity, defoliated and undeveloped plants of *S. tenuis* had a similar ($p \geq 0.10$) number of daughter tillers. Busso et al. (1989) also reported a reduction in the number of metabolically active buds on plants of *Agropyron spicatum* (Pursh) Scribn. and Smith (Syn: *Pseudoroegneria spicata* (Pursh) A. Löve ssp. *spicata*) under the simultaneous influence of defoliation and water stress during 2 consecutive years. At the same time in June 1996, daughter tiller production (DT) was greater ($p < 0.05$) on plants defoliated twice than on those defoliated at the vegetative stage under rainfed and irrigated conditions in *S. tenuis*; this was associated with a lower ($p < 0.01$) number of metabolically active buds. A greater defoliation frequency has increased daughter tiller production in other perennial grasses by modifying both light quantity and quality at stem bases (Deregibus et al. 1983, Casal et al. 1985, Gautier et al. 1999).

In June 1996, plants of *S. tenuis*, whether defoliated or not during the previous year, had a greater ($p < 0.05$) number of daughter tillers and total nodes after exposure to water stress in the vegetative+early internode elongation than in the vegetative stage. It is likely that accumulation of total nonstructural carbohydrates in the stem bases increased as the period of exposure to water stress also increased. Since this species remains dormant during dry summers (Distel and Fernández 1986), these carbohydrates may be utilized for rapid regrowth during the next growing season. Various studies have reported that accumulation of total nonstructural carbohydrates in the stem bases of perennial grasses during periods of water stress resulted in greater tillering responses (Busso et al. 1990, Fulkerson and Slack 1995, Volaire 1995, Oosthuizen and Snyman 1999). Also by mid-year 1996, numbers of dormant or dead buds were greater ($p < 0.01$) under irrigated than under rainfed or water stress conditions on plants of *S. tenuis* which had been defoliated

Table 4 Continued.

Dates	Treatments		TN	DT	MAB	DDB
	Water levels	Defoliation				
12/6/96	Irrigation	C	11.50 (0.25)	4.75 (0.25)	4.38 (0.38)	0.25 (0.25)
		V	11.00 (0.00)	3.25 (0.00)	2.00 (0.00)	4.00 (0.00)
		VE	10.00 (0.00)	5.63 (0.38)	0.50 (0.00)	2.38 (0.13)
	Rainfed	C	8.88 (0.88)	3.88 (0.38)	3.38 (0.63)	0.38 (0.13)
		V	9.75 (1.50)	4.13 (0.13)	1.38 (0.38)	1.38 (0.13)
		VE	10.75 (0.00)	5.25 (1.50)	0.88 (0.88)	2.75 (0.50)
	Water stress V	C	8.25 (0.00)	3.63 (0.63)	2.63 (0.13)	0.25 (0.00)
		V	8.88 (0.38)	4.13 (0.38)	1.00 (0.50)	2.00 (0.50)
	Water stress VE	C	10.50 (0.00)	4.50 (0.00)	4.25 (0.00)	0.25 (0.00)
		VE	10.92 (0.58)	5.96 (0.29)	0.46 (0.21)	2.96 (0.29)
30/7/96	Irrigation	C	9.88 (0.38)	3.25 (0.75)	1.88 (1.38)	2.75 (2.25)
		V	10.63 (1.88)	5.38 (0.63)	2.75 (2.25)	1.25 (0.75)
		VE	12.25 (0.75)	3.50 (0.50)	5.00 (1.00)	2.13 (1.13)
	Rainfed	C	10.00 (1.00)	5.00 (2.25)	1.88 (1.38)	1.25 (0.75)
		V	9.50 (1.00)	3.38 (0.88)	1.50 (1.50)	2.75 (2.25)
		VE	11.00 (0.00)	4.75 (0.25)	2.13 (1.63)	1.63 (1.13)
	Water stress V	C	8.63 (0.13)	4.00 (0.00)	2.00 (0.25)	0.63 (0.13)
		V	9.25 (0.00)	3.38 (0.13)	0.75 (0.75)	2.25 (1.25)
	Water stress VE	C	7.25 (0.00)	3.00 (0.00)	3.25 (0.00)	0.00 (0.00)
		VE	9.25 (0.00)	3.63 (0.13)	2.50 (1.50)	1.63 (1.63)
21/9/96	Irrigation	C	9.88 (0.38)	4.00 (0.75)	2.25 (0.25)	1.88 (1.13)
		E	10.63 (0.13)	5.13 (1.13)	2.50 (1.75)	1.50 (1.25)
		VE	10.50 (1.50)	4.00 (0.25)	1.38 (1.38)	3.38 (0.63)
	Rainfed	C	12.00 (1.50)	5.25 (2.00)	0.63 (0.38)	4.38 (0.38)
		E	10.63 (1.38)	4.38 (0.13)	0.75 (0.75)	3.63 (2.13)
		VE	9.50 (1.00)	4.63 (0.63)	0.00 (0.00)	3.00 (0.50)
	Water stress E	C	10.75 (0.25)	6.00 (0.25)	1.13 (0.63)	2.00 (0.25)
		E	9.88 (0.38)	4.75 (0.50)	2.25 (0.75)	1.13 (1.13)
	Water stress VE	C	10.00 (0.00)	5.75 (0.00)	2.25 (0.00)	0.75 (0.00)
		VE	9.63 (0.88)	4.25 (1.50)	0.38 (0.38)	2.25 (0.00)
30/10/96	Irrigation	C	9.88 (0.13)	5.00 (0.25)	0.88 (0.38)	2.00 (0.00)
		V	8.38 (0.88)	3.13 (0.13)	1.13 (0.88)	2.25 (0.50)
		E	--	--	--	--
		VE	11.50 (1.50)	5.50 (0.75)	1.00 (1.00)	3.00 (0.25)
	Rainfed	C	8.88 (0.63)	4.25 (1.25)	0.00 (0.00)	2.88 (1.38)
		V	9.63 (0.13)	4.75 (0.75)	0.13 (0.13)	3.13 (0.63)
		E	9.50 (0.25)	4.00 (0.25)	0.50 (0.50)	3.38 (0.13)
		VE	8.75 (1.25)	3.38 (1.63)	0.83 (0.13)	3.50 (0.50)
	Water stress V	C	10.75 (0.25)	5.88 (0.38)	0.38 (0.13)	2.50 (0.00)
		V	10.50 (0.75)	4.88 (0.63)	0.25 (0.25)	3.63 (0.38)
	Water stress E	C	10.50 (0.50)	6.13 (0.38)	0.13 (0.13)	2.25 (0.00)
		E	10.00 (2.00)	3.75 (1.75)	1.63 (0.63)	2.50 (0.00)
	Water stress VE	C	11.67 (0.00)	4.33 (0.00)	0.33 (0.00)	6.00 (0.00)
		VE	10.25 (0.75)	3.75 (0.25)	1.88 (1.88)	3.50 (2.50)
7/1/97	Irrigation	C	9.63 (0.13)	4.25 (1.25)	0.50 (0.50)	2.25 (0.25)
		V	9.25 --	2.75 --	2.00 --	1.25 --
		E	10.00 --	4.50 --	0.00 --	3.00 --
		VE	10.17 (0.83)	2.75 (0.75)	0.83 (0.17)	3.96 (0.29)
	Rainfed	C	10.63 (0.13)	5.75 (0.75)	1.25 (0.75)	2.13 (0.13)
		V	10.50 (0.00)	5.25 (0.50)	1.00 (0.75)	2.63 (0.13)
		E	7.00 --	3.00 --	0.75 --	1.25 --
		VE	11.25 (2.50)	3.88 (2.13)	1.38 (0.88)	3.88 (1.13)
	Water stress V	C	9.50 (0.25)	3.75 (1.00)	0.13 (0.13)	2.63 (0.13)
		V	9.88 (1.63)	3.75 (0.00)	0.13 (0.13)	3.38 (0.88)
	Water stress E	C	8.63 (2.63)	3.25 (1.75)	1.38 (0.88)	0.75 (0.75)
		E	8.00 (1.50)	3.13 (0.38)	0.50 (0.25)	2.25 (0.50)
	Water stress VE	C	11.00 --	6.50 --	0.50 --	2.00 --
		VE	6.50 --	1.25 --	0.00 --	3.25 --

(Continued on page 159)

ed at the vegetative stage the previous year, although numbers of daughter tillers were similar ($p > 0.25$) among water levels.

Axillary bud activation and outgrowth in *S. tenuis* were not affected by any treatment ($p > 0.25$) after defoliation at the vegetative stage in July 1996 (Table 4). Numbers of total nodes in this species, however, were on average lower ($p < 0.01$) under water stress than under better moisture levels. Reduction of leaf production (equal to number of TN) is a common response in plants of perennial grasses exposed to water stress (Brown 1995, Busso and Richards 1995, Volaire 1995).

At the end of the 1996 growing cycle, total bud number was similar ($p > 0.15$) among treatments. However, numbers of dormant or dead buds in *S. tenuis* were greater ($p < 0.05$) on plants defoliated twice under rainfed or irrigated conditions, and on those defoliated once or twice under water stress, than on undefoliated controls (Table 4). Defoliation under water stress also lowered metabolic activity on buds of *A. spicatum* (Busso et al. 1989). The observed response resulted in a lower number of daughter tillers on plants defoliated twice than on undefoliated controls under all water levels, although differences were not significant ($p > 0.25$). At the same time, numbers of dormant or dead buds were greater ($p < 0.05$) when defoliated and undefoliated plants of *S. tenuis* were exposed to water stress at the vegetative or vegetative+early internode elongation than at the early internode elongation stage. This indicates that early (i.e., at V) or prolonged (i.e., at VE) water stress can be more detrimental on the degree of bud metabolic activity than late water stress (i.e., at E) in *S. tenuis*.

By early September 1995, responses in *S. clarazii* differed among water levels depending on whether plants were defoliated or not. Numbers of daughter tillers were 50% greater ($p < 0.05$) under rainfed than under irrigated or water stress conditions on undefoliated plants of this species (Table 5). When plants were defoliated, however, numbers of daughter tillers were on average 50% greater ($p < 0.01$) in the water stress than in the other water availability treatments. In comparison to values obtained before defoliation at the vegetative stage, subsequent responses can be explained, at least partially, through a greater bud activation and outgrowth on undefoliated, rainfed plants; a greater suppression of bud activation on defoliated, irrigated plants, and a greater bud outgrowth on plants defoliated at the vegetative stage under water stress.

Table 4 Continued.

Dates	Treatments		TN	DT	MAB	DDB
	Water levels	Defoliation				
12/3/97	Irrigation	C	7.00 –	3.33 –	0.00 –	1.00 –
		V	9.00 –	4.00 –	0.50 –	2.00 –
		E	0 –	0 –	0 –	0 –
		VE	5.00 –	3.00 –	0.00 –	0.00 –
	Rainfed	C	7.25 –	3.00 –	0.00 –	2.75 –
		V	6.50 (0.00)	3.50 (0.00)	0.00 (0.00)	1.13 (0.38)
		E	6.50 –	3.00 –	0.25 –	0.75 –
		VE	10.13 (3.88)	5.63 (2.38)	0.50 (0.50)	0.63 (0.63)
	Water stress V	C	6.88 (0.63)	3.13 (1.13)	0.25 (0.25)	1.75 (0.75)
		V	6.75 –	3.75 –	0.00 –	0.75 –
	Water stress E	C	6.50 (0.75)	3.50 (0.00)	0.25 (0.25)	0.63 (0.38)
		E	6.88 (0.13)	3.63 (0.38)	0.00 (0.00)	0.75 (0.25)
	Water stress VE	C	9.50 –	6.00 –	0.00 –	1.00 –
		VE	7.63 (1.63)	3.00 (2.00)	0.13 (0.13)	3.00 (1.00)

With a few exceptions, all studied variables showed similar ($p > 0.10$) values in all defoliation and water level treatments at each sampling date in 1996 on parent tillers of *S. clarazii* (Table 5). Early in 1996, variations observed on numbers of daughter tillers in response to treatments were associated with variations on numbers of dormant or dead buds. This means that treatment effects on investigated variables were observed earlier in *S. clarazii*

than in *S. tenuis* after the first year of treatment application. Numbers of daughter tillers were greater ($p < 0.05$) and those of dormant or dead buds were lower ($p < 0.05$) on *S. clarazii* plants defoliated twice than on those defoliated at the vegetative stage or nondefoliated during the previous year under rainfed conditions (Table 5). Increases in defoliation frequency have stimulated tillering through changes in light quality and/or quantity reaching stem

bases in perennial grasses (Deregibus et al. 1983, Casal et al. 1985, Gautier et al. 1999). However, numbers of dormant or dead buds were greater ($p < 0.05$) on plants defoliated twice than on undefoliated controls under irrigation in *S. clarazii* (Table 5); this contributed to a lower number of daughter tillers, although differences were not significant ($p > 0.10$). At the same time, numbers of daughter tillers were greater ($p < 0.05$) on plants defoliated at the vegetative than at the early internode elongation or vegetative + early internode elongation stage in *S. clarazii* under irrigated conditions. Defoliated plants of this species, however, had a lower ($p < 0.05$) number of daughter tillers than undefoliated controls under water stress; this was associated with a greater number of dormant or dead buds, although differences were not significant ($p > 0.12$). Late or frequent defoliations have reduced daughter tiller production on several perennial grass species exposed to irrigated or water stress conditions (Busso et al. 1989, Simoes and Baruch 1991). This response has been associated with direct effects of defoliation in suppressing bud activation or to a low remaining photosynthetic leaf surface area after defoliation

Fig. 3. Number of total nodes (TN), buds which originated daughter tillers (DT), and metabolically active (MAB) and dead and dormant (DDB) buds on average for all parent tillers of *S. clarazii* (Sc), *S. gynerioides* (Sg), and *S. tenuis* (St) observed at each date during the study period. Each symbol is an average of $n=29-112$. Vertical bars represent one S.E.M.

Table 5. Number of total nodes (TN), buds which originated daughter tillers (DT), and metabolically active (MAB) and dead and dormant (DDB) buds on parent tillers of *S. clarazii* at the different treatments in 1995, 1996 and early 1997. I: Irrigation, R: Rainfed, WS: Water stress, C: Undeveloped controls, and defoliation at the vegetative (V), internode elongation (E) or both phenological stages (VE). Each value is the mean (+/-SE) of n=2.

Dates	Treatments		TN	DT	MAB	DDB	
	Water levels	Defoliation					
------(number)-----							
23/5/95	Irrigation	C	7.25 (0.25)	2.50 (0.00)	2.00 (0.50)	0.50 (0.50)	
		V	7.00 (0.50)	1.25 (0.25)	2.75 (1.75)	0.00 (0.00)	
		VE	8.50 (0.00)	2.50 (0.00)	2.50 (0.00)	0.00 (0.00)	
	Rainfed	C	8.00 (0.00)	2.00 (0.00)	1.50 (0.00)	1.00 (0.00)	
		V	7.25 (0.75)	3.00 (1.50)	1.75 (0.25)	0.25 (0.25)	
		VE	6.25 (1.75)	2.25 (0.75)	1.75 (0.25)	0.25 (0.25)	
	Water stress V	C	7.25 (0.75)	2.00 (1.00)	1.50 (0.50)	0.25 (0.25)	
		V	8.50 (0.50)	3.25 (0.25)	2.75 (0.25)	0.00 (0.00)	
	Water stress VE	C	6.25 (0.25)	2.25 (1.25)	2.25 (0.75)	0.25 (0.25)	
		VE	7.50 (1.50)	4.00 (2.00)	1.00 (0.00)	0.50 (0.50)	
7/9/95	Irrigation	C	9.25 (1.00)	2.75 (0.25)	2.38 (0.13)	0.83 (0.13)	
		V	7.67 (0.33)	1.25 (0.75)	3.08 (0.58)	1.00 (1.00)	
		VE	7.63 (0.13)	1.63 (0.38)	3.00 (0.25)	0.75 (0.25)	
	Rainfed	C	8.50 (0.00)	4.50 (0.00)	2.50 (0.00)	0.00 (0.00)	
		V	7.88(1.38)	2.13 (0.13)	2.25 (0.50)	0.50 (0.00)	
		VE	7.13 (0.13)	2.13 (1.13)	2.75 (0.25)	0.38 (0.13)	
	Water stress V	C	7.25 (0.25)	2.13 (0.38)	2.00 (0.25)	0.88 (0.13)	
		V	8.75 (1.00)	4.25 (0.50)	1.38 (0.13)	0.50 (0.50)	
	Water stress VE	C	6.83 (0.17)	1.79 (0.54)	2.46 (0.79)	0.33 (0.33)	
		VE	8.63 (0.63)	4.38 (0.38)	1.25 (0.25)	0.75 (0.75)	
	27/9/95	Irrigation	C	9.25 (1.50)	3.75 (0.50)	2.50 (1.50)	0.50 (0.25)
			E	9.42 (1.92)	3.04 (0.71)	3.33 (1.33)	1.25 (0.75)
			VE	8.13 (0.38)	1.88 (0.13)	3.50 (0.25)	0.25 (0.00)
		Rainfed	C	11.25 (1.75)	3.42 (0.08)	2.71 (0.96)	1.88 (0.13)
E			8.21 (0.46)	1.88 (0.13)	3.46 (0.21)	0.29 (0.04)	
VE			8.63 (0.13)	2.88 (1.13)	2.88 (1.38)	0.38 (0.13)	
Water stress E		C	9.04 (0.29)	4.17 (0.17)	1.54 (0.21)	0.63 (0.38)	
		E	10.38 (0.38)	3.13 (0.38)	2.63 (0.38)	1.38 (0.38)	
Water stress VE		C	9.25 (0.75)	4.63 (0.88)	1.88 (0.38)	0.50 (0.50)	
		VE	9.25 (0.50)	3.75 (1.00)	3.00 (1.50)	0.75 (0.50)	
14/12/95		Irrigation	C	7.38 (2.13)	2.50 (0.25)	0.63 (0.38)	1.25 (1.00)
			E	9.38 (0.38)	4.38 (0.63)	0.25 (0.25)	1.13 (0.13)
	VE		8.63 (0.13)	1.75 (0.25)	2.13 (0.88)	2.50 (0.50)	
	Rainfed	C	9.25 (0.75)	3.88 (0.13)	0.63 (0.38)	1.92 (0.58)	
		E	8.75 (1.75)	3.13 (0.63)	2.25 (0.75)	0.88 (0.13)	
		VE	8.50 (0.75)	3.00 (1.00)	0.75 (0.75)	2.38 (0.88)	
	Water stress E	C	8.00 (0.25)	4.38 (1.38)	0.25 (0.00)	0.88 (0.63)	
		E	10.25 (1.50)	3.88 (0.63)	1.63 (0.88)	2.13 (1.13)	
	Water stress VE	C	8.88 (1.13)	4.25 (0.75)	0.38 (0.13)	2.00 (0.00)	
		VE	9.88 (0.13)	4.88 (0.63)	0.25 (0.00)	2.38 (0.63)	
	25/4/96	Irrigation	C	7.25 (0.25)	1.75 (0.25)	2.50 (0.50)	0.25 (0.25)
			V	7.50 (0.00)	2.25 (0.25)	2.75 (0.75)	1.25 (0.75)
			E	5.75 (1.25)	0.50 (0.50)	2.75 (0.25)	0.50 (0.00)
			VE	8.00 (0.00)	0.75 (0.25)	2.75 (1.25)	2.00 (1.00)
Rainfed		C	8.75 (2.25)	1.00 (0.50)	2.00 (0.00)	2.75 (0.75)	
		V	11.25 (1.75)	1.25 (0.75)	5.25 (2.75)	2.50 (0.50)	
		E	8.50 (0.50)	2.00 (0.00)	2.25 (0.25)	1.50 (0.50)	
		VE	8.75 (0.25)	2.75 (0.75)	4.25 (0.75)	0.50 (0.00)	
Water stress V		C	7.50 (0.00)	3.50 (0.50)	1.50 (0.00)	0.25 (0.25)	
		V	7.75 (0.25)	1.75 (0.25)	4.00 (1.00)	0.50 (0.50)	
Water stress E		C	8.50 (1.00)	1.50 (0.50)	4.00 (1.00)	1.25 (0.75)	
		E	8.25 (0.25)	1.25 (0.25)	3.25 (0.25)	2.50 (0.50)	
Water stress VE		C	8.75 (0.75)	2.00 (1.00)	2.75 (0.25)	2.00 (0.00)	
		VE	9.00 (1.00)	1.25 (0.25)	2.25 (0.75)	2.75 (0.75)	
12/6/96	Irrigation	C	9.13 (0.38)	2.00 (0.75)	4.00 (0.75)	0.25 (0.25)	
		V	9.25 (1.25)	2.50 (0.50)	2.38 (0.13)	1.38 (1.13)	
		VE	9.00 (1.50)	2.13 (0.63)	3.50 (0.25)	0.63 (0.13)	

(Continued on page 161)

which is insufficient to maintain a high degree of bud metabolic activity under different levels of soil water availability (Busso et al. 1989). As mentioned previously, the opposite response was observed under rainfed conditions. Photosynthetically active radiation at crown level of the desirable grasses under irrigation was 70% of that under rainfed conditions (Flemmer 2000). Greater shading effects by *S. gynerioides* under higher soil water availability levels, and greater leaf water potentials in the rainfed than in the water stress treatment (Tables 1 and 2), may help explain the greater number of daughter tillers and the lower number of dormant or dead buds on defoliated than on undefoliated plants under rainfed than under irrigated or water stress conditions.

At the beginning of 1996, defoliated and undefoliated plants of *S. clarazii* had more daughter tillers ($p < 0.05$) and fewer dormant or dead buds ($p < 0.01$) after exposure to water stress at the vegetative than at the early internode elongation or vegetative + internode elongation stage. Contrary to that found in *S. tenuis*, water stress had a less detrimental impact on the degree of bud metabolic activity and subsequent outgrowth in *S. clarazii* when it occurred early (i.e., at V) than when it was present late (i.e., at E), or was prolonged (i.e., VE) during the growing season. Jamieson et al. (1995) reported a lower leaf senescence associated with a higher light interception on plants exposed to early rather than late water stress.

In October 1996, numbers of total nodes were lower ($p < 0.05$) on plants of *S. clarazii* defoliated at either the early internode elongation stage under water stress, or at the vegetative and vegetative+early internode elongation stages under irrigation than on undefoliated controls (Table 5). At the same time, however, plants of this species showed a greater ($p < 0.01$) number of total nodes under water stress when they were defoliated at the vegetative + early internode elongation stage than when they remained undefoliated. Reduction of transpiratory leaf surface areas after defoliation may have reduced detrimental effects of water stress on plant growth in comparison to undefoliated controls (Mohammad et al. 1982, Simoes and Baruch 1991).

At the end of the 1996 growing cycle, the greatest ($p < 0.05$) number of total nodes in *S. clarazii* was observed on defoliated and undefoliated plants which had been exposed to water stress at the vegetative+early internode elongation stage (Table 5). The amount of rainfall from the

Table 5. Continued.

Dates	Treatments		TN	DT	MAB	DDB	
	Water levels	Defoliation					
------(number)-----							
30/7/96	Rainfed	C	9.00 (1.00)	2.13 (0.63)	3.50 (0.50)	1.50 (0.00)	
		V	9.63 (0.38)	2.75 (0.50)	3.50 (0.25)	1.00 (0.00)	
		VE	9.50 (0.25)	2.63 (0.38)	2.88 (0.88)	1.63 (0.13)	
	Water stress V	C	9.13 (0.63)	3.75 (0.50)	2.38 (0.38)	1.13 (0.88)	
		V	8.75 (0.00)	2.75 (1.00)	1.75 (1.25)	1.38 (1.38)	
	Water stress VE	C	9.38 (0.13)	3.50 (0.25)	3.38 (0.13)	0.63 (0.38)	
		VE	9.75 (0.00)	2.63 (0.13)	3.25 (0.25)	2.63 (0.13)	
	Irrigation	C	10.38 (1.38)	4.25 (0.25)	2.13 (0.13)	0.13 (0.13)	
		V	9.13 (0.63)	2.88 (0.13)	2.75 (0.50)	1.38 (0.88)	
		VE	10.00 (0.25)	3.75 (1.00)	1.13 (0.88)	1.63 (1.38)	
	Rainfed	C	8.88 (0.63)	1.50 (0.25)	2.13 (0.63)	2.38 (0.13)	
		V	9.88 (0.63)	3.75 (1.00)	3.38 (0.13)	1.13 (1.13)	
		VE	9.50 (0.50)	3.75 (0.00)	1.38 (1.13)	1.63 (0.38)	
	Water stress V	C	9.00 (0.50)	3.25 (0.50)	2.38 (0.88)	1.13 (0.88)	
		V	9.00 (0.75)	3.00 (0.00)	2.50 (0.50)	1.88 (0.63)	
	Water stress VE	C	9.13 (1.63)	2.88 (0.13)	2.38 (0.13)	1.50 (1.25)	
		VE	9.25 (1.00)	3.00 (0.75)	2.63 (0.38)	1.50 (0.50)	
	21/9/96	Irrigation	C	9.50 (0.00)	5.13 (1.13)	1.13 (0.38)	0.88 (0.88)
E			10.25 (1.00)	3.63 (0.38)	1.25 (0.00)	2.00 (0.25)	
VE			9.75 (1.00)	4.00 (1.00)	0.88 (0.13)	2.13 (0.13)	
Rainfed		C	8.38 (0.88)	2.25 (0.50)	1.63 (1.13)	2.00 (1.50)	
		E	8.88 (1.63)	3.25 (0.50)	0.25 (0.25)	2.25 (0.50)	
		VE	10.75 (0.50)	3.00 (0.75)	0.63 (0.38)	4.25 (1.75)	
30/10/96	Water stress E	C	11.00 (1.25)	4.00 (1.00)	1.25 (1.00)	1.38 (0.38)	
		E	8.25 (0.50)	3.00 (0.25)	1.38 (0.63)	1.13 (0.38)	
	Water stress VE	C	11.88 (1.38)	4.13 (0.38)	3.38 (1.13)	2.00 (0.75)	
		VE	9.25 (1.00)	2.00 (0.00)	2.38 (0.13)	2.50 (0.75)	
	Irrigation	C	10.50 (1.25)	3.50 (0.00)	0.38 (0.13)	1.75 (0.25)	
		V	7.75 (0.25)	3.63 (0.63)	0.75 (0.00)	0.38 (0.13)	
		E	—	—	—	—	
		VE	8.00 (0.50)	3.50 (0.25)	0.38 (0.13)	0.88 (0.38)	
	Rainfed	C	8.75 (0.50)	3.50 (0.50)	0.13 (0.13)	1.75 (0.25)	
		V	8.50 (0.50)	2.25 (0.00)	0.38 (0.38)	3.13 (0.38)	
		E	9.13 (0.38)	3.88 (1.88)	1.88 (0.88)	1.00 (0.25)	
		VE	9.38 (0.13)	3.25 (0.00)	0.13 (0.13)	3.25 (0.50)	
	Water stress V	C	8.50 (0.25)	4.13 (0.88)	0.13 (0.13)	1.50 (0.75)	
		V	9.38 (0.63)	4.00 (0.75)	0.63 (0.38)	1.75 (0.25)	
	Water stress E	C	10.75 (0.25)	4.25 (0.25)	0.75 (0.75)	2.25 (2.00)	
		E	8.88 (0.13)	3.50 (0.50)	0.63 (0.13)	2.38 (0.38)	
	7/1/97	Water stress VE	C	8.38 (0.38)	2.63 (0.13)	1.38 (0.38)	1.88 (0.88)
			VE	12.63 (0.13)	3.75 (0.50)	2.13 (1.38)	4.25 (0.50)
Irrigation		C	7.63 (0.88)	2.88 (1.63)	0.13 (0.13)	1.50 (0.25)	
		V	7.63 (1.38)	3.13 (0.88)	0.25 (0.00)	0.63 (0.38)	
		E	6.75 (0.50)	1.75 (0.25)	0.88 (0.38)	1.00 (0.25)	
		VE	7.38 (1.38)	2.38 (0.88)	0.25 (0.25)	1.38 (0.63)	
Rainfed		C	7.13 (1.38)	2.38 (1.13)	0.38 (0.13)	1.13 (0.38)	
		V	8.00 (0.50)	2.38 (0.13)	0.63 (0.13)	1.00 (0.75)	
		E	10.13 (0.63)	3.88 (1.38)	0.88 (0.63)	2.25 (0.75)	
		VE	8.88 (0.88)	3.00 (1.00)	0.13 (0.13)	2.63 (0.13)	
Water stress V		C	7.63 (0.13)	2.63 (0.38)	0.25 (0.25)	0.88 (0.13)	
		V	7.00 (0.50)	2.50 (0.25)	0.13 (0.13)	0.63 (0.13)	
Water stress E		C	8.13 (0.13)	3.75 (0.25)	0.25 (0.25)	0.75 (0.25)	
		E	7.50 (0.75)	2.63 (1.63)	0.88 (0.63)	1.88 (1.13)	
Water stress VE		C	10.88 (1.13)	5.13 (0.63)	0.50 (0.50)	3.13 (0.13)	
		VE	11.38 (1.38)	3.75 (1.00)	1.75 (0.25)	3.63 (0.63)	
12/3/97		Irrigation	C	6.13 (0.63)	1.75 (0.25)	0.00 (0.00)	1.75 (0.25)
			V	7.13 (0.38)	2.50 (0.00)	0.50 (0.25)	1.88 (0.63)
	E		7.75 —	1.75 —	0.25 —	2.00 —	
	VE		7.63 (0.63)	1.63 (0.63)	0.50 (0.00)	2.63 (0.13)	

(Continued on page 162)

end of the water stress treatment at the vegetative + early internode elongation stage to sampling at the end of the growing cycle in 1996 was high (221 mm). This and total nonstructural carbohydrates which may have accumulated during the long water stress period (i.e., VE) may have resulted in such a high number of total nodes at the end of the second year of successive treatments. Numbers of dormant or dead buds, however, were greater ($p < 0.01$) on plants exposed to water stress at the vegetative + early internode elongation than at the vegetative or early internode elongation stage. Similar to that found in other perennial grasses (Busso et al. 1989), prolonged water stress stimulated suppression of bud activation in *S. clarazii*.

At the beginning of 1997, after 2 years of successive treatments, numbers of total nodes and bud metabolic activity and outgrowth were similar ($p > 0.25$) between defoliation treatments or water levels on parent tillers of *S. clarazii* and *S. tenuis* (Tables 4 and 5). A similar response was reported on *S. tenuis* and *P. napostaense*: these species did not modify their potential regrowth capacity after rainfed plants were defoliated at different phenological stages during 2 consecutive years (Becker et al. 1997). The degree of metabolic activity and outgrowth of axillary buds has also been similar on perennial grass plants coming from sites with very different grazing histories (Hendrickson and Briske 1997). Potential regrowth capacity of *S. tenuis*, *P. napostaense* and *S. gynerioides*, however, is reduced by fire (Peláez et al. 1997, Peláez 2000).

Numbers of total nodes, daughter tillers, and metabolically active buds tended to be similar or greater on the desirable than on the undesirable species when averaging values for all parent tillers within each species and sampling date (Fig. 3). Numbers of daughter tillers tended to be greater in *S. tenuis* than in *S. clarazii* during 1996. On the other hand, *S. gynerioides* appeared to have a greater number of dormant or dead buds than *S. clarazii* in 1995, and than both desirable species in 1996 (Fig. 3). Early in 1997, greatest numbers of metabolically active buds and daughter tillers were observed on parent tillers of *S. clarazii* and *S. tenuis*, respectively. Thus, *S. clarazii* showed a greater potential regrowth capacity than *S. tenuis*, whereas *S. tenuis* was able to activate a greater bud number and produce more new tillers than *S. clarazii* after 2 years of treatment. Recent studies have indicated a greater competitive ability and tolerance to defoli-

Table 5. Continued.

Treatments						
Dates	Water levels	Defoliation	TN	DT	MAB	DDB
----- (number) -----						
Rainfed		C	7.50 (0.50)	1.75 (0.25)	0.50 (0.25)	1.75 (0.25)
		V	8.88 (1.63)	2.38 (1.13)	1.25 (1.25)	2.25 (1.75)
		E	6.63 (0.13)	1.38 (0.38)	0.63 (0.63)	1.63 (0.13)
		VE	8.21 (1.46)	1.38 (0.63)	2.29 (1.04)	2.13 (0.13)
Water stress V		C	7.63 (0.88)	1.25 (0.25)	2.25 (1.25)	1.63 (1.38)
		V	8.00 (0.25)	0.75 (0.50)	0.50 (0.00)	3.13 (0.13)
Water stress E		C	6.88 (1.13)	1.38 (0.38)	0.75 (0.50)	1.13 (0.88)
		E	7.13 (0.13)	0.88 (0.38)	0.88 (0.13)	2.50 (0.00)
Water stress VE		C	9.13 (1.38)	2.38 (1.13)	0.88 (0.38)	3.38 (0.13)
		VE	11.50 (4.25)	2.75 (1.50)	1.00 (0.50)	4.63 (2.38)

ation in *S. clarazii* than in *S. tenuis* (Saint Pierre et al. 2000a, 2000b). Our results show that plant traits which make *S. clarazii* a superior competitor and more tolerant to defoliation are not linked to producing more daughter tillers.

As the growing season progressed in 1995 and 1996, numbers of metabolically active buds decreased and those of dormant or dead buds increased on parent tillers of the 3 species (Fig. 3). Bud senescence or necrosis may increase suppression of bud activation towards the end of a growing season in perennial grasses (Mitchell 1953). With the advancement of the growing season, however, signs of bud senescence were minor with most buds looking viable in *A. desertorum* and *A. spicatum* (Mueller and Richards 1986). Low percentages of metabolically active buds at the end of 1996 were confirmed early in 1997 indicating a decreased potential regrowth capacity in all 3 species in comparison to previous years, probably because of cumulative treatment effects.

During 1995 in all 3 species and *S. clarazii* and *S. tenuis* in 1996, approximately 50-60% of the entire bud pool (DT+MAB+DDB) was able to grow out and produce new tillers. However, less than 41% of all buds grew out into daughter tillers on parent tillers of *S. gynerioides* in 1996. Percentage of buds which grew out and produced tillers from the entire bud pool is greater than that reported for other perennial grasses of semiarid regions (Mueller and Richards 1986, Busso et al. 1989, Hendrickson and Briske 1997).

Despite some transitory effects of defoliation on axillary bud dynamics, rapid photosynthetic canopy reestablishment after defoliation under all water levels was not limited by availability and/or regrowth capacity of axillary buds in *S. clarazii* and *S. tenuis*. These results do not support hypothesis 2. The only exception, and in

agreement with this hypothesis, was observed after defoliation at the vegetative stage in 1995 on parent tillers of *S. clarazii*: these tillers had a greater number of daughter tillers after being defoliated than remaining undefoliated under water stress. At the same time, however, numbers of daughter tillers were lower on defoliated than on undefoliated plants of this species when exposed to rainfed or irrigated conditions. Lack of consistent responses to defoliation have been attributed, at least partially, to the complexity of physiological mechanisms (i.e., see Murphy and Briske 1992) and the great number of potentially intervening factors (i.e., abiotic variables, phenological stage of development, and frequency and intensity of defoliation) which can regulate bud metabolic activity and subsequent regrowth in perennial grasses (Briske and Richards 1995). In our study, responses were specific to the species, imposed treatments, sampling times, and cumulative treatment effects. This makes prediction of plant responses under natural conditions difficult, a conclusion similar to that reported by Haferkamp and Karl (1999) or Allen et al. (1989) after studying the effects of defoliation on plant growth of an annual brome grass or the degree of colonization of perennial grass roots by arbuscular-vesicular mycorrhiza, respectively.

Literature Cited

- Allen, M.F., J.H. Richards and C.A. Busso. 1989. Influence of clipping and soil water status on vesicular-arbuscular mycorrhizae of two semi-arid tussock grasses. *Biol. Fert. Soils* 8: 285-289.
- Anderson, V.J. and D.D. Briske. 1995. Herbivore-induced species replacement in grasslands: Is it driven by herbivory tolerance or avoidance?. *Ecol. Appl.* 5: 1014-1024.

- Becker, G.F., C.A. Busso, and T. Montani. 1997. Effects of defoliating *Stipa tenuis* and *Piptochaetium napostaense* at different phenological stages: axillary bud viability and growth. *J. Arid Environ.* 35: 233-250.
- Briske, D.D. 1991. Developmental morphology and physiology of grasses. In: R.K. Heitschmidt and J.W. Stuth (eds) *Grazing Management: an ecological perspective*. pp.85-108. Timber Press, Portland, Ore.
- Briske, D.D. and V.J. Anderson. 1990. Competitive ability of the bunchgrass *Schizachyrium scoparium* as affected by grazing history and defoliation. *Vegetatio* 103:41-49.
- Briske, D.D. and J.R. Hendrickson. 1998. Does selective defoliation mediate competitive interactions in a semiarid savanna? A demographic evaluation. *J. Veg. Sci.* 9: 611-622.
- Briske, D.D. and J.H. Richards. 1995. Plant responses to defoliation: a physiological, morphological and demographic evaluation. In: D.J. Bedunah and R.E. Sosebee (eds) *Wildland Plants: Physiological Ecology and Developmental Morphology*. pp. 635-710. Soc. for Range Manage., Denver, Colo.
- Brown, R.W. 1995. The water relations of range plants: adaptations to water deficits. In: D.J. Bedunah and R.E. Sosebee (eds) *Wildland Plants: Physiological Ecology and Developmental Morphology*. pp. 291-413. Soc. for Range Manage., Denver, Colo.
- Bullock, J.M., B. Clear Hill, and J. Silvertown. 1994. Tiller dynamics of two grasses - responses to grazing, density and weather. *J. Ecol.* 82: 331-340.
- Busso, C.A. 1997. Towards an increased and sustainable production in semiarid rangelands of Central Argentina: Two decades of research. *J. Arid Environ.* 36: 197-210.
- Busso, C.A. and J.H. Richards. 1993. Leaf extension rate in two tussock grasses: effects of water stress and clipping. *Acta Oecol.* 14: 3-15.
- Busso, C.A. and J.H. Richards. 1995. Drought and clipping effects on tiller demography and growth of two bunch grasses in Utah. *J. Arid Environ.* 29: 239-251.
- Busso, C.A., R.M. Bóo, and D.V. Peláez. 1993. Fire effects on bud viability and growth of *Stipa tenuis* in semiarid Argentina. *Ann. Bot.* 71:377-381.
- Busso, C.A., R.J. Mueller, and J.H. Richards. 1989. Effects of drought and defoliation on bud viability in two caespitose grasses. *Ann. Bot.* 63: 477-485.
- Busso, C.A., J.H. Richards, and N.J. Chatterton. 1990. Nonstructural carbohydrates and spring regrowth of two cool-season grasses: Interaction of drought and clipping. *J. Range Manage.* 43: 336-343.
- Cano, E. 1988. Pastizales Naturales de La Pampa. Descripción de las especies más importantes. Tomo I. Convenio AACREA-Provincia de La Pampa, Capital Federal, Buenos Aires.
- Casal, J.J., V.A. Deregibus, and R.A. Sánchez. 1985. Variation in tiller dynamics and morphology in *Lolium multiflorum* Lam. vegetative and reproductive plants as affect-

- ed by differences in red far-red irradiation. *Ann. Bot.* 56: 553–559.
- Casal, J.J., R.A. Sánchez, and V.A. Deregibus. 1986.** The effect of plant density on tillering: the involvement of R/FR ratio and the proportion of radiation intercepted per plant. *Environ. Exp. Bot.* 26: 365–371.
- Deregibus, V.A. and M.J. Trlica. 1990.** Influence of defoliation upon tiller structure and demography in two warm-season grasses. *Acta Oecol.* 11: 693–699.
- Deregibus, V.A., R.A. Sánchez, and J.J. Casal. 1983.** Effects of light quality on tiller production in *Lolium* spp. *Plant Physiol.* 72: 900–902.
- Devkota, N.R., P.D. Kemp, and J. Hodgson. 1997.** Screening pasture species for shade tolerance. *Proc. Agron. Soc. of New Zealand* 27:119–128.
- Distel, R.A. and R.M. Bóo. 1996.** Vegetation States and Transitions in Temperate Semiarid Rangelands of Argentina. In: N.E. West (ed) *Rangelands in a Sustainable Biosphere*, Proc. Symp. Vth Internat. Rangeland Congr., 23–28 July. pp. 117–118. Salt Lake City, Utah
- Distel, R.A. and O.A. Fernández. 1986.** Productivity of *Stipa tenuis* Phil. and *Piptochaetium napostaense* (Speg.) Hack in semi-arid Argentina. *J. Arid Environ.* 11: 93–96.
- Flemmer, A.C. 2000.** Influencia simultánea del estrés hídrico y la defoliación en distintos momentos del desarrollo de *Stipa clarazii* y *Stipa tenuis* en competencia con *Stipa gynerioides*. MSc Thesis, Departamento de Agronomía, Universidad Nacional del Sur, Bahía Blanca, Argentina.
- Fernández, O.A. and C.A. Busso. 1999.** Arid and semi-arid rangelands: two thirds of Argentina. In: O. Arnalds and S. Archer (eds) *Case Studies of Rangeland Desertification*, Proc. Internat. Workshop. Agr. Res. Institute, 16–19 September 1997. pp. 41–60. Reykjavik, Iceland.
- Font Quer, P. 1982.** Diccionario de Botánica. Labor S.A., Barcelona.
- Fulkerson, W.J. and K. Slack. 1995.** Leaf number as a criterion for determining defoliation time for *Lolium perenne*: 2. Effect of defoliation frequency and height. *Grass Forage Sci.* 50:16–20.
- Gautier, H., C. Varlet-Grancher, and L. Hazard. 1999.** Tillering responses to the light environment and defoliation in populations of perennial ryegrass (*Lolium perenne* L.) selected for contrasting leaf length. *Ann. Bot.* 83:423–429.
- Giorgetti, H.D., Z. Manuel, O.A. Montenegro, G.D. Rodríguez, and C.A. Busso. 2000.** Phenology of some herbaceous and woody species in central, semiarid Argentina. *Phyton* 69:91–108.
- Haferkamp, M.R. and M.G. Karl. 1999.** Clipping effects on growth dynamics of Japanese brome. *J. Range Manage.* 52:339–345.
- Hendrickson, J.R. and D.D. Briske. 1997.** Axillary bud banks of two semiarid perennial grasses: occurrence, longevity, and contribution to population persistence. *Oecologia* 110:584–591.
- Jamieson, P.D., R.J. Martin, GS Francis, and D.R. Wilson. 1995.** Drought effects on biomass production and radiation-use efficiency in barley. *Field Crops Res.* 43:77–86.
- Jewis, O.R. 1972.** Tillering in grasses - its significance and control. *J. British Grass. Soc.* 27: 65–82.
- McNaughton, S.J. 1992.** Laboratory-simulated grazing: interactive effects of defoliation and canopy closure on Serengeti grasses. *Ecol.* 73:170–182.
- Mitchell, K.J. 1953.** Influence of light and temperature on the growth of ryegrass (*Lolium* sp.) II. The control of lateral bud development. *Physiol. Plant.* 6: 425–43.
- Mohammad, N., D.D. Dwyer, and F.E. Busby. 1982.** Responses of crested wheatgrass and Russian wildrye to water stress and defoliation. *J. Range Manage.* 35:227–320.
- Moretto, A.S. and R.A. Distel. 1997.** Competitive interactions between palatable and unpalatable grasses native to a temperate semi-arid grassland of Argentina. *Plant Ecol.* 130:155–161.
- Moretto, A.S. and R.A. Distel. 1999.** Effects of selective defoliation on the competitive interaction between palatable and unpalatable grasses native to a temperate semi-arid grassland of Argentina. *J. Arid Environ.* 42:167–175.
- Mueggler, W.F. 1972.** Influence of competition on the response of bluebunch wheatgrass to clipping. *J. Range Manage.* 25: 88–92.
- Mueller, R.J. and J.H. Richards. 1986.** Morphological analysis of tillering in *Agropyron spicatum* and *Agropyron desertorum*. *Ann. Bot.* 58:911–921.
- Murphy, J.S. and D.D. Briske. 1992.** Regulation of tillering by apical dominance: Chronology, interpretive value, and current perspectives. *J. Range Manage.* 45:419–429.
- Olson, B.E. and J.H. Richards. 1988.** Tussock regrowth after grazing: intercalary meristem and axillary bud activity of tillers of *Agropyron desertorum*. *Oikos* 51:374–382.
- Oosthuizen, I.B. and H.A. Snyman. 1999.** The influence of water stress on the growth reserves of *Themeda triandra* Forssk. in the semi-arid grasslands of South Africa. In: D. Eldridge and D. Freudenberger (eds) *People and Rangelands Building the Future*, Proc. Symp. VIth Internatio. Rangeland Congress, 19–23 July. pp. 209. Townsville, Australia.
- Peláez, D.V. 2000.** Respuesta de gramíneas perennes nativas del Caldenal a distintas intensidades de fuego. PhD Thesis, Departamento de Agronomía, Universidad Nacional del Sur, Bahía Blanca, Argentina.
- Peláez, D.V., R.M. Bóo, O.R. Elía, and M.D. Mayor. 1997.** Effect of fire intensity on bud viability of three grass species native to central semi-arid Argentina. *J. Arid Environ.* 37: 309–317.
- Saint Pierre, C., C.A. Busso, O.A. Montenegro, G.D. Rodríguez, H.D. Giorgetti, and T. Montani. 2000a.** Producción de materia seca en especies de gramíneas perennes nativas del centro de Argentina. XVI Reunión Latinoamericana de Producción Animal, III Congreso Uruguayo de Producción Animal. Montevideo, Uruguay. Available on CD-ROM.
- Saint Pierre, C., C.A. Busso, O.A. Montenegro, G.D. Rodríguez, H.D. Giorgetti, and T. Montani. 2000b.** Demografía y crecimiento en especies de gramíneas nativas del Sur de la Provincia Fitogeográfica del Monte. XVI Reunión Latinoamericana de Producción Animal, III Congreso Uruguayo de Producción Animal. Montevideo, Uruguay. Available on CD-ROM.
- Simoes, M. and Z. Baruch. 1991.** Responses to simulated herbivory and water stress in two tropical C₄ grasses. *Oecologia* 88:173–180.
- Smith, M. 1992.** CROPWAT-A computer program for irrigation planning and management. FAO Irrigation and Drainage Paper No. 46. FAO, Rome.
- Smith, M. 1993.** CLIMWAT for CROPWAT - A climatic database for irrigation planning and management. FAO Irrigation and Drainage Paper No. 49. FAO, Rome.
- Steel, R.G.D. and J.H. Torrie. 1985.** *Bio Estadística: principios y procedimientos*. McGraw-Hill.
- Turner, N.C. 1987.** The use of the pressure chamber in studies of plant water status. *Proceedings International Conference on Measurements of Soil and Plant Water Status*. pp. 13–24. Logan, Utah.
- Volaire, F. 1995.** Growth, carbohydrate reserves and drought survival strategies of contrasting *Dactylis glomerata* populations in a Mediterranean environment. *J. Appl. Ecol.* 32:56–66.
- Waring, R.H. and B.D. Cleary. 1967.** Plant moisture stress: evaluation by pressure bomb. *Science* 155:1248–1254.
- Williams, K.J., B.J. Wilsey, S.J. McNaughton, and F.F. Banyikwa. 1998.** Temporally variable rainfall does not limit yields of Serengeti grasses. *Oikos* 81:463–470.

Day and night grazing by cattle in the Sahel

AUGUSTINE. A. AYANTUNDE, SALVADOR FERNÁNDEZ-RIVERA, PIERRE. H. HIERNAUX, HERMAN VAN KEULEN, AND HENK M. J. UDO

Authors are former graduate Fellow, Animal Scientist and Range Ecologist, International Livestock Research Institute, ILRI/ICRISAT, B.P. 12404, Niamey, Niger, professor and Associate Professor, Animal Production Systems Group, Wageningen Agricultural University, P.O. Box 338, 6700 AH Wageningen, The Netherlands. The correspondence author is Henk Udo.

Abstract

The influence of night grazing on feeding behavior, nutrition and performance of cattle was studied. Twenty-four steers weighing 367 kg (SD = 76) grazed either from 0900 to 1900 (day grazers), 2100 to 0700 (night grazers) or 0900 to 1900 and 2400 to 0400 (day-and-night grazers) during 13 weeks. Four esophageally fistulated steers were used in a cross-over design to sample the diet selected during the day and at night. No differences ($P > 0.05$) were observed in the diet selected in the day or at night. As the season progressed the fiber components of the diet increased ($P < 0.01$) significantly while nitrogen and in sacco dry matter disappearance declined ($P < 0.01$). Actual grazing time (min day⁻¹, SE = 16) were 352, 376, and 476 for day, night, and day-and-night grazers, respectively. Day-and-night grazers had a higher intake of organic matter than either day or night grazers. Night grazers had the lowest forage intake and also the slowest rate of consumption. Steers that grazed in the night had the lowest water intake: 22.7 liter day⁻¹ (SE = 1.5) in week 4; 19.9 liter day⁻¹ (SE = 1.1) in week 8. Average weight changes (g day⁻¹, SE = 62) were -435, -548 and -239 for day, night, and day-and-night grazers, respectively. These results show that during the dry season, grazing exclusively in the night cannot substitute for day time grazing, but that it is rather complementary to the latter. Timing (day or night) of grazing did not affect diet selection but nocturnal grazing decreased the need for water.

Key Words: cattle, forage intake, night grazing, Sahel

Night grazing is a common herd management practice in the West African Sahel, especially at the end of the dry season (Dicko-Touré 1980, Powell et al. 1996). This practice has also been reported for herded animals in the sub-humid zone of West Africa (Bayer 1986), East Africa (Wigg and Owen 1973, Nicholson 1987) and for free ranging sheep and cattle in the USA and Australia (Vallentine 1990). In addition to the advantage of increased grazing time, King (1983) reported that night grazing helps to reduce heat stress on the animals and may increase forage intake. It has the benefit of manure deposition on rangelands rather than in the enclosed sites (Wigg and Owen 1973). However, this is in conflict with the practice of corralling the animals on cropland for depositing manure (Powell et al. 1996). Previous research (Fernández-Rivera et al. 1996) on night grazing

Resumen

El objetivo del presente trabajo fue estudiar la influencia del pastoreo nocturno sobre el comportamiento alimenticio, el consumo de forraje, la excreción fecal y los cambios de peso en bovinos. Veinticuatro novillos con un peso inicial de 367 kg (desviación estándar = 76) pastorearon de 0900 a 1900 (pastoreo diurno), 2100 a 0700 (pastoreo nocturno) o de 0900 a 1900 y de 2100 a 0700 (pastoreo día y noche) durante 13 semanas. Cuatro novillos con fístula esofágica fueron utilizados en un diseño reversible para muestrear la dieta seleccionada durante el día y en la noche. No se observaron diferencias ($P > 0.05$) en la dieta seleccionada en el día o en la noche. A medida que la estación seca avanzó los componentes de fibra de la dieta aumentaron ($P < 0.01$), mientras que el contenido de nitrógeno y la desaparición *in sacco* de la materia seca disminuyeron ($P < 0.01$). El tiempo de pastoreo propiamente dicho (i.e. tiempo de consumo) fue 352, 376 y 476 min día⁻¹ (SE = 16) para novillos con pastoreo nocturno, pastoreo diurno o con pastoreo el día y la noche, respectivamente. Los novillos con pastoreo el día y la noche tuvieron un mayor consumo de materia orgánica que aquellos que pastorearon el día o la noche. Los novillos con pastoreo nocturno tuvieron los niveles y tasas de consumo de forraje más bajos. El consumo de agua fue también más bajo en los novillos que pastorearon durante la noche 22.7 liter día⁻¹ (SE = 1.5) en la semana 4 y 19.9 liter día⁻¹ (SE = 1.1) en la semana 8. El cambio promedio de peso fue -435, -548 y -239 g día⁻¹ (SE = 62) para los novillos con pastoreo nocturno, pastoreo diurno o con pastoreo el día y la noche, respectivamente. Estos resultados indican que durante la estación seca el pastoreo exclusivamente durante la noche no puede ser sustituto, sino más bien complemento del pastoreo durante el día. El momento (día o noche) de pastoreo no afectó la selección de la dieta, pero el pastoreo nocturno disminuyó el requerimiento de agua.

by cattle showed that diet selection during the day and at night were not different. However, the steers that grazed during the day consumed more forage and water than those that grazed in the night. Further studies on the influence of night grazing on feeding behavior, nutrition and performance of cattle are needed to improve understanding of the nutrition of grazing cattle and cattle's role in nutrient transfer processes in the landscape.

The objective of this study was to determine the effects of night grazing on diet selection, forage and water intake, fecal excretion, feeding behavior and performance of cattle.

Material and Methods

Study site

The experiment was conducted over 13 weeks at the end of the dry season (February to May) of 1995 at International Crop Research Institute for the Semi-Arid Tropics (ICRISAT-SC) in Sadorè (13° 14' N 2° 16' E), Niger.

Treatments, pasture and animals

Twenty-four intact steers with a body weight (W) of 367 (SD = 76) kg were randomly allotted to 3 treatments: grazing either from 0900 to 1900 (day grazing), 2100 to 0700 (night grazing) or 0900 to 1900 and 2400 to 0400 (day-and-night grazing). After return from the pasture, the steers were kept in individual pens in a barn located 150 m from the paddock. The animals grazed the same pasture in the day and at night, i.e. a fallow of 5.5 ha, dominated by annual grasses mainly *Ctenium elegans* Kunth, *Diheteropogon hagerupii* Hitchc., *Pennisetum pedicellatum* Trin. and forbs mainly *Borreria stachydea* (DC.) Hutch. & Dalz. and *Hibiscus sabdarifa* Linn. At the beginning of the trial, the standing herbage and litter mass of the pasture were estimated at 828 and 1,070 kg DM ha⁻¹, respectively (Table 1). The herbage mass consisted of standing hay composed of 59% grasses and 41% forbs.

The study included 2 periods of collection of feces and extrusa which started in weeks 4 and 8 of the experiment. Each period included 9 days of fecal collection. The animals were accustomed to carrying fecal collection bags during the last week before the collection started. In each collection period, fecal bags were emptied and the feces weighed, before and after grazing. Ten percent of the fecal excretion was sampled and frozen for subsequent analysis. Water intake was also measured in weeks 4 and 8 of the trial. All the animals were watered in the morning (0800) before grazing started. Water intake was measured daily during the collection periods, for which all animals had access to

water for 30 min. In week 8 of the experiment the grazing activities of all steers were observed. Observation was made every 5 min (24 hour/day) for 3 consecutive days by 6 observers. The observation was instantaneous and the recording included one of the following activities: searching for food, prehending, masticating, ruminating, walking, drinking, sleeping, and idling. Grazing time was defined as the time spent prehending, masticating and searching for food. Idling included time spent neither for grazing, ruminating, sleeping, walking, nor drinking. Activities such as drinking, fighting, and socializing were referred to as 'other'.

In the 2 collection periods, four esophageally fistulated steers were randomly grouped into 2 pairs and were used in a cross-over design for sampling the diet selected during the day and at night. The 2 pairs either grazed in the day (0900 to 1900) or at night (2100 to 0700). During the data collection period in weeks 4 and 8, samples of the diet selected by the fistulated steers (extrusa) were collected in the morning (1000) and afternoon (1500) for the day grazing pair, and at night (2200) and at dawn (0300) for the night grazing pair, for 3 consecutive days. At the end of the 3 days collection period, the 2 groups were switched. After switching the grazing schedule, the animals were allowed 3 days for adaptation after which extrusa samples were collected for another 3 days following the same collection schedule. The extrusa samples were frozen immediately after collection.

Sample processing and laboratory analyses

The daily fecal sub-samples were bulked by time of collection (before or after grazing) and analyzed for dry (DM) and organic matter (OM). The extrusa samples were dried at 55° C for 48 hours and were ground to pass a 1-mm screen. They were analyzed for DM, OM, nitrogen (N), ashless neutral detergent fiber (NDF), ashless acid detergent fiber (ADF)

and ashless lignin (Van Soest et al. 1991). Hemicellulose and cellulose were calculated as the differences NDF-ADF and ADF-lignin, respectively. Samples ground to pass a 2-mm screen were incubated in duplicate for 48 hours in 3 ruminally fistulated steers to determine in sacco DM (DMD) and OM (OMD) disappearance, treating the residues from the nylon bags in a HCl-pepsin solution for 24 hours. Samples collected from vegetation mass measurement, representing the available feed, were subdivided by functional group (grasses or forbs) and dominant species within a group for standing herbage and litter separately. These were analyzed for DM, OM, N, phosphorus (P), DMD, and OMD.

Animal measurements

Animals were weighed every two weeks for 3 consecutive days. Average daily gain (ADG) was estimated by regression of individual body weight (W) data over time. Individual animal feed intake was determined from individual data on fecal output and group (day or night schedule) means of OMD.

Statistical analysis

Data analysis were performed with SAS (Statistical Analysis System Institute 1987) using the General Linear Model (GLM) procedure for the variance and regression analyses. An analysis of variance model including treatments as fixed effects, was used to analyze data on fecal output, forage and water intake, and animal behavior (time spent grazing, ruminating, idling, walking, sleeping, and drinking). The model for analysis of water intake included live weight and dry matter intake in addition to the treatments studied. Multiple comparisons of treatment means (Day vs Night grazing and Day vs Day-and-night grazing) within and between the collection periods (weeks 4 and 8) were performed by contrasts. Extrusa components of diet selected in the day and at night were analyzed using the Cochran procedure for the t-test. Unless it is specified differently, the level of significance was declared at P < 0.05.

Results

There were no differences in the quality of diet (extrusa) selected (Table 2) in the day or at night for both collection periods (weeks 4 and 8), the only exception was observed in week 4 when the NDF (SE =

Table 1. Nutritional quality of standing herbage and litter mass at the beginning of the experiment (March 1995).

Component	Standing herbage	Litter	SE
	----- g kg ⁻¹ DM -----		
Organic matter	949	938	6
Nitrogen	3.5	3.4	0.5
Phosphorus	1.2	1.1	0.2
Dry matter digestibility	426	412	18
Organic matter digestibility	400	391	19
Digestible organic matter	380	367	13

Table 2. Chemical composition of forage selected (extrusa) by esophageally fistulated steers grazing in the day or at night.

Component	Week 4		Week 8		SE
	Day	Night	Day	Night	
	g kg ⁻¹ DM				
Organic matter	894	883	881	889	4
Nitrogen	9.0 ^a	8.1 ^a	7.5 ^b	7.1 ^b	0.4
NDF	649 ^a	675 ^a	817 ^b	821 ^b	6
ADF	507 ^a	521 ^a	635 ^b	637 ^b	6
Lignin	134 ^a	129 ^a	178 ^b	187 ^b	5
Cellulose	373 ^a	393 ^a	460 ^b	450 ^b	6
Hemicellulose	143 ^a	154 ^a	182 ^b	184 ^b	5
DMD ²	533 ^a	524 ^a	486 ^b	478 ^b	8
OMD ²	469	455	459	444	8
DOM ²	419	402	404	395	6

¹Values with different superscripts denote significant difference ($P < 0.05$) between means within rows.

²DMD=Dry matter digestibility; OMD = Organic matter digestibility; and DOM = Digestible organic matter (i.e. OMD x OM).

6) of the diet selected by night grazers (675 g kg⁻¹ DM) was significantly higher than that of the day grazers (649 g kg⁻¹ DM). As the dry season progressed (week 4 vs week 8, Table 2) diet's NDF, ADF, cellulose, hemicellulose and lignin increased significantly ($P < 0.01$) while nitrogen concentration (SE = 0.4) declined from 8.5 in week 4 to 7.3 g kg⁻¹ DM in week 8 and DMD (g kg⁻¹ DM, SE = 8) also declined significantly (week 4 = 529; week 8 = 482).

Steers grazing in the day, night, and day-and-night spent 352, 376, and 476 min day⁻¹ respectively for grazing (Table 3). Night grazers spent less time ruminating and walking than day grazers. Day-and-night grazers spent 124 minutes grazing more than day-grazers. The hourly distribution of time expenditure (Fig. 1.) for different activities showed that day grazers had 2 distinct grazing periods with the first in the morning till mid-day and the second before the sunset. The second grazing period accounted for over 60% of total time spent grazing. Day-and-night grazers also had 2 grazing periods in the day similar to day grazers with one additional period in the night of about 2 hours. Night grazers had 2 grazing periods with the initial period accounting for about 75% of the total grazing time. Steers that grazed in the day-and-night had lower time for resting (time spent sleeping + idling) than steers that grazed in the day (421 vs 560, SE = 25, $P < 0.05$) but there was no difference in resting time by day grazers compared to night grazers (560 vs 614, SE = 25).

Day, and day-and-night grazing steers consistently consumed more forage (g DM kg^{-0.75} W) than steers that grazed at night (Table 4). In weeks 4 and 8, day-and-night grazers consumed daily 93.2 and 67.1 g DM kg^{-0.75} W respectively whereas night

grazers consumed 62.5 g DM kg^{-0.75} W in week 4 and 53.6 g DM kg^{-0.75} W in week 8. Day grazers consumed significantly more digestible organic matter (g DOM kg^{-0.75} W) than night grazers (Week 4: 30.2 vs 20.4, SE = 1.6; week 8: 22.7 vs 18.3, SE = 1.4), but the differences between day grazers and day-and-night grazers were not statistically significant. Forage intake declined significantly from week 4 to week 8 for day grazers, and day-and-night grazers. Intake rate (mg OM kg^{-0.75} W min⁻¹) in week 8 (SE = 7) were 142 for day grazers, 110 for night grazers and 113 for day-and-night grazers.

There was a significant difference in water intake between steers that grazed in

Fig. 1. Hourly distribution of time expenditure for different activities by (a) day, (b) night, and (c) day-and-night grazing steers in the dry season in the Sahel.

Table 3. Time expenditure on different activities in Week 8 (May 1995) of the experiment by day, night, and day-and-night grazing steers.

Activity	Day	Night	Day-and-night	SE
	----- (min day ⁻¹) -----			
Grazing ²	352 ^a	376 ^a	476 ^b	16
Ruminating	463 ^a	389 ^b	447 ^a	21
Sleeping	88 ^a	99 ^a	50 ^b	12
Walking	37 ^a	28 ^a	55 ^b	3
Idling ²	472 ^a	519 ^a	371 ^b	27
Other	30	29	43	10

¹Values with different superscripts denote significant difference ($P < 0.05$) between means within rows.

²Grazing includes prehension, mastication and search for food; Idling includes time spent neither for grazing, ruminating, sleeping, walking nor drinking; and Other includes activities such as drinking, fighting and socializing.

the night and those that grazed either in the day or in the day-and-night in both periods of measurement (Table 4). As the season progressed water intake of day grazers (week 4 = 35.5, week 8 = 27.6 liter day⁻¹) and day-and-night grazers (week 4 = 35.5, week 8 = 27.6 liter day⁻¹) declined significantly but that of night grazers (week 4 = 22.7, week 8 = 19.9 liter day⁻¹) remained fairly constant. Relative to forage intake water consumption (liter kg⁻¹ forage DM) was constant for all treatments regardless of the period of measurement. Regression analyses of water intake on metabolic weight ($W^{0.75}$) and dry matter intake (DMI, kg DM day⁻¹) showed that water intake (ml day⁻¹) was correlated with metabolic weight in all treatments and with DMI for day grazers (equation 1), and day-and-night grazers (equation 3) but not for night grazers (equation 2). The following regression equations were estimat-

ed from the pooled data of weeks 4 and 8:

$$\text{water intake} = 148 (\text{SE} = 26) W^{0.75} + 3243 (\text{SE} = 343) \text{ DMI} (r^2 = 0.99, P < 0.01) \quad (1)$$

$$\text{water intake} = 263 (\text{SE} = 6) W^{0.75} (r^2 = 0.99, P < 0.01) \quad (2)$$

$$\text{water intake} = 126 (\text{SE} = 34) W^{0.75} + 3412 (\text{SE} = 429) \text{ DMI} (r^2 = 0.99, P < 0.01) \quad (3)$$

In week 4, fecal excretion by day grazers, night grazers, and day-and-night grazers were 9.3, 6.9, and 10.3 g DM kg⁻¹ W day⁻¹ (SE = 0.7), respectively. In week 8 (SE = 0.6), day grazers excreted 7.6 g DM kg⁻¹ W day⁻¹, the fecal output by night grazers was 6.9 g DM kg⁻¹ W day⁻¹ and day-and-night grazers voided 8.3 g DM kg⁻¹ W day⁻¹. A significant decrease in fecal excretion was observed in day grazers, and day-and-night grazers as the season progressed, whereas that of night graz-

ers remained essentially the same.

Average weight changes (g day⁻¹, SE = 62) was -435 for day grazers, -548 for night grazers and -239 for day-and-night grazers. There was no significant difference in weight changes between day grazers and night grazers.

Discussion

The results on diet (extrusa) quality show that the time (day or night) of grazing had no significant influence on dietary selection, which supports the findings by Arnold (1966) that sight does not play a major role in the selection of plant parts by grazing animals. Similar results were observed by Fernández-Rivera et al. (1996). However, there may be differences between the quality of diet selected during the day and at night if the grazing sites and species composition are different, which is often the case when the animals are herded during night grazing. The declining quality of the diet selected as the season progressed, as observed in this study, has also been reported by Schlecht (1995) for steers and by Becker et al. (1996) for zebu cows grazing natural pastures in the region. Nitrogen concentration (7.1–9.0 g kg⁻¹ DM) in the diet selected was similar to values reported in the dry season by Schlecht (1995) in Mali (53–82 g CP kg⁻¹ OM) and Becker et al. (1996) in Niger (64–75 g CP kg⁻¹ OM) for extrusa samples taken in the same season. The digestibility of OM (444–469 g kg⁻¹ DM) was similar to that observed by the latter authors and by Fernández-Rivera et al. (1996) in the region.

Regardless of the time of grazing, the steers spent about 60% of the time allowed for grazing (i.e. prehension, mastication, and searching for food). The actual grazing times of 5.9, 6.3, and 7.9 hours for day, night, and day-and-night grazing, respectively, compare well with reported values in the dry season of 6.3 hours for a day grazing herd in Kenya by Coppock et al. (1988); 7 to 8 hours for day-and-night grazers in Uganda by Harker et al. (1954) and 7.4 to 10.4 hours reported by Dicko-Touré (1980) for day-and-night grazers in Mali. The ruminating time (6.5 to 7.7 hours) also agrees with those reported by Dicko-Touré (1980) and Harker et al. (1954). Night grazers spent less time ruminating than either day grazers or day-and-night grazers, because they had a lower forage intake. This might also be associated with the natural inclination to ruminate in the night. The lower walking time for

Table 4. Daily intake of dry matter (DM), digestible organic matter (DOM) and intake rate, and water intake by day, night, and day-and-night grazing steers in the dry season in the Sahel.

Variable	Day	Night	Day-and-night	SE
Week 4				
Forage intake				
g DM kg ^{-0.75} W	86.3 ^{a†}	62.5 ^b	93.2 ^{a†}	4.8
g DOM kg ^{-0.75} W	30.2 ^{a†}	20.4 ^b	31.9 ^{a†}	1.6
Water intake				
liter animal ⁻¹ day ⁻¹	36.0 ^{a†}	22.7 ^b	35.5 ^{a†}	1.5
liter kg ⁻¹ forage DM	5.1 ^a	4.4 ^b	4.9 ^a	0.2
ml kg ⁻¹ W day ⁻¹	100 ^{a†}	62 ^b	105 ^{a†}	5
Week 8				
Forage intake				
g DM kg ^{-0.75} W	62.9 ^a	53.6 ^b	67.1 ^a	4
g DOM kg ^{-0.75} W	22.7 ^a	18.3 ^b	24.3 ^a	1.4
Intake rate				
g DM min ⁻¹	14.4 ^a	11.2 ^b	11.0 ^b	0.7
mg OM kg ^{-0.75} W min ⁻¹	142 ^a	110 ^b	113 ^b	7
Water intake				
liter animal ⁻¹ day ⁻¹	27.1 ^a	19.9 ^b	27.6 ^a	1.1
liter kg ⁻¹ forage DM	5.5 ^a	4.8 ^b	5.3 ^a	0.3
ml kg ⁻¹ W day ⁻¹	80 ^a	59 ^b	82 ^a	3

¹Values with different superscripts denote significant difference ($P < 0.05$) between means within rows.

²Different symbols (†) following the same variable in Weeks 4 and 8 within a treatment group (column) denote significant difference ($P < 0.05$) between values in the 2 periods.

steers that grazed in the night compared to the other groups, even though they grazed in the same pasture, supports the findings of Arnold (1966) that sight impairment (poor visibility) causes orientation problems, which limits the area for selective grazing by the animals. The cost of grazing in the night in addition to day grazing is a reduction in resting time as observed for day-and-night grazers. The general pattern of 2 grazing periods during the day, separated by a mid-day rest observed in day grazers, and day-and-night grazers has also been reported by Coppock et al. (1988) for Turkana cattle in Kenya. Night grazers had a longer initial grazing period (4.5 vs 2.7 hours) than day grazers, probably because they were not constrained by heat and high radiation. Resting between the grazing periods by night grazers may likely be induced by rumen fill or fatigue. Similar findings were reported by Fernández-Rivera et al. (1996) in a preliminary study on nocturnal grazing by cattle in the region.

Forage intake, in both weeks 4 and 8, was lower for night grazers than day grazers, which supports previous findings by Fernández-Rivera et al. (1996). This was due to a slow intake rate. Forage intake by day grazers ($64.6 \text{ g OM kg}^{-0.75} \text{ W}$), and day-and-night grazers (69.0 g) in week 4 falls within the range of 63–83 g reported by Schlecht (1995) for unsupplemented steers in Mali and the values reported by Becker et al. (1996) for unsupplemented cows in Niger. The intake values in week 8, however, are lower than those reported by these authors. Day-and-night grazers spent longer time grazing than day grazers but intake was not significantly different. This means that in the day-and-night grazing group, intake (and intake rate) during the day decreased due to night grazing. The fecal excretion values found in this study ($6.3\text{--}11.0 \text{ g DM kg}^{-1} \text{ W day}^{-1}$) is similar to those reported by Schlecht (1995). Collectable manure, i.e. the amount of feces excreted while not in the pastures (manure excreted while in the corralling site), was higher than the feces deposited in the rangelands by day grazers (week 4: 1,786 vs 1,521, week 8: 1,322 vs 1,236 g DM animal⁻¹ day⁻¹). The reverse was the case for the animals that grazed in the night, i.e. night grazers (week 4: 1,058 vs 1,385, week 8: 953 vs 1,304 g DM animal⁻¹ day⁻¹) and day-and-night grazers (week 4: 1,126 vs 2,326, week 8: 932 vs 1,836 g DM animal⁻¹ day⁻¹). This shows that more manure could be collected from animals that did not graze in the night compared to those that did. The amounts

of collectable manure estimated in this study fall within the range of 600 to 1,500 g DM TLU⁻¹ (TLU is Tropical Livestock Unit, animal of 250 kg body weight) reported by Khombe et al. (1992) and Fernández-Rivera et al. (1995).

Consumption of water relative to forage intake (liter kg⁻¹ forage DM) found in this study agrees with the value of $4.5 \text{ liter kg}^{-1}$ forage DM reported by King (1983). The day, and day-and- night grazers, that consumed more forage drank more water than the night grazers. High water consumption by the former could also be associated with high temperatures during the day, as reported by Nicholson (1987) and King (1983), the latter suggesting an extra water cost of $0.35 \text{ liter km}^{-1}$ for walking in high solar heat. The range in water consumption ($56\text{--}110 \text{ ml kg}^{-1} \text{ W day}^{-1}$) observed in this study is below the theoretical maximum ($160 \text{ ml kg}^{-1} \text{ BW day}^{-1}$) suggested by King (1983) for cattle grazing tropical pastures. The lower water intake observed in the second period of measurement (week 8) could be attributed to an unexpected rainfall during the period and the concomitant fall in daily temperature for some days and the low ingestion of forage. Low water consumption by the night grazers observed in this study and the previous one (Fernández-Rivera et al. 1996) suggests that during a period of water scarcity, the water needs of grazing cattle could be reduced if nocturnal grazing is practiced without day grazing and the animals are restricted and protected from sunlight during the day.

Steers that grazed in the day-and-night had lower weight loss (239 g day^{-1}) than either day grazers (435 g day^{-1}) or night grazers (548 g day^{-1}). Similar results were reported by Wigg and Owen (1973) and Khombe et al. (1992) for steers that grazed day and night. These findings and that of the present study show that grazing exclusively in the night cannot substitute for day grazing. It rather complements day grazing and leads to better animal performance especially in the dry season. From the data on weight change and intake, day-and-night grazers lost significantly less weight than day grazers but had the same diet quality and intake, whereas day grazers had higher intake than night grazers but had the same weight loss. This discrepancy could be due to differential gut fill which might have influenced live weight measurement (t' Mannetje et al. 1976). The differential gut fill could be associated with the time of the day (0730 to 0800) at which all the animals were weighed. This implies that the night grazers were

weighed almost immediately after grazing, about 4 hours after night grazing for day-and-night grazers and 12 hours after grazing for day grazers. Perhaps, the weight loss for night grazers and day-and-night grazers could have been higher than the reported values if they had been weighed at the same time difference after grazing as the day grazers. However, this is not feasible due to the experimental design.

The results also show that the traditional practice of night corralling (i.e. no night grazing) of cattle in West African Sahel put a nutritional stress on the animals (by decreasing forage intake), thereby increasing weight losses especially in the dry season. It also increases the needs for supplementation. To resolve the conflict between night grazing and night corralling, it is necessary to determine the optimum use of the animal's time for grazing and manuring. Therefore, further research on combinations of timing (day and/or night) and duration of grazing is needed to identify practical and feasible recommendations on how to resolve the conflict.

Literature Cited

- Arnold, G.W. 1966.** The special senses in grazing animals. I. Sight and dietary habits in sheep. *Aust. J. Agr. Res.* 17:521–529.
- Bayer, W. 1986.** Agropastoral herding practices and grazing behaviour of cattle in the subhumid zone of Nigeria. *ILCA Bull.* 24:8–13.
- Becker, K., C. Gall, A. Susenbeth, and T. Rath. 1996.** Nutrition and productivity of milking cattle on a semi-arid rangeland in West Africa, p. 153–184. *In: Adapted farming in West Africa. Rep. on results, Interim Rep. 1994 - 1996; Special programme 308, Univ. Hohenheim, Hohenheim, Germany.*
- Coppock, D.L., J.E. Ellis, and D.M. Swift. 1988.** Seasonal patterns of activity, travel and water intake for livestock in south Turkana, Kenya. *J. Arid Environ.* 14:319–331.
- Dicko-Touré, M.S. 1980.** The contribution of browse to cattle fodder in the sedentary system of the Office du Niger, p. 313–319. *In: H. N. Le HouËrou (ed.), Browse in Africa: the current state of knowledge. International Livestock Center for Africa, Addis Ababa, Ethiopia.*
- Fernández-Rivera, S., A. Ayantunde, P.H.Y. Hiernaux, and M. Turner. 1996.** Nocturnal grazing effects on the nutrition of cattle. *J. Anim. Sci.* 74 (Suppl. 1) 200 (abstr.).
- Fernández-Rivera, S., T. O. Williams, P. Hiernaux, and J. M. Powell. 1995.** Fecal excretion by ruminants and manure availability for crop production in semi-arid West Africa, p. 149–169. *In: J. M. Powell, S. Fernández-Rivera, T. O. Williams, and C. Renard (eds.), Livestock and sustainable nutrient cycling in mixed farming systems of*

- sub-saharan Africa. Volume II: Technical papers. International Livestock Center for Africa, Addis Ababa, Ethiopia.
- Harker, K.W., J.I. Taylor, and D.H.L. Rollinson. 1954.** Studies on habits of zebu cattle. I. Preliminary observations on grazing habits. *J. Agr. Sci. (Camb.)*. 44:193–198.
- Khombe, C.T., I.A. Dube, and P. Nyathi. 1992.** The effects of kraaling and stover supplementation during the dry season on body weight and manure production of Mashona steers in Zimbabwe. *African Livestock Res.* 1:18–23.
- King, J.M. 1983.** Livestock water needs in pastoral Africa in relation to climate and forage. ILCA (International Livestock Center for Africa) Res. Rep. 7, Addis Ababa, Ethiopia.
- t'Mannetje, L., R.J. Jones, and T.H. Stobbs. 1976.** Pasture evaluation by grazing experiments, p. 194–234. *In*: Shaw N.H and W.W. Bryan (eds.), *Tropical pasture research: principles and methods*. Commonwealth bureau of pastures and field crops, Hurley, Berkshire.
- Nicholson, M.J. 1987.** Effects of night enclosure and extensive walking on the productivity of zebu cattle. *J. Agr. Sci. (Camb.)*. 109:445–452.
- Powell, J. M., S. Fernández-Rivera, P. Hiernaux, and M.D. Turner. 1996.** Nutrient cycling in integrated rangeland/cropland systems of the Sahel. *Agr. Sys.* 52:143–170.
- Schlecht, E. 1995.** The influence of different levels of supplementation on feed intake and nutrient retention of grazing zebu cattle in Sahelian agro-pastoral systems. Ph.D Thesis, Univ. Hohenheim, Hohenheim, Germany.
- Statistical Analysis System Institute. 1987.** SAS/STAT guide for personal computers. SAS Institute Inc., Cary, N.C.
- Vallentine, J.F. 1990.** Grazing management. Academic Press, San Diego, Calif.
- Van Soest, P.J., J.B. Robertson, and B.A. Lewis. 1991.** Methods for dietary fiber, and nonstarch polysaccharides in relation to animal nutrition. *J. Dairy Sci.* 74:3583–3597.
- Wigg, P.M. and M.A. Owen. 1973.** Studies on water consumption, night grazing and growth of Boran and crossbreed steers at Kongwa, Tanzania. *East African Agr. and Fores. J.* 38:361–366.

Nutritional value and intake of prickly pear by goats

ZENO McMILLAN, CODY B. SCOTT, CHARLES A. TAYLOR, JR., AND J. ED HUSTON

Authors are former Graduate Assistant, Associate Professor, Department of Agriculture, Angelo State University, San Angelo, Tex.; Supervisor, Texas Agricultural Experiment Station, Sonora, Tex; and Professor, Texas Agricultural Experiment Station, San Angelo, Tex.

Abstract

Prickly pear (*Opuntia* sp.) is both a benefit and hindrance to the livestock industry in the southwestern U.S. It competes with herbaceous forage but is sometimes used as emergency feed during drought. Spineless prickly pear (*O. fiscus-indica* Engelm. and *O. rufida* Engelm.) has been planted in some regions of the southwest but little is known about its nutritional value. Our objectives were to determine: (1) the nutritional value of both spined (*O. macrorhiza* Engelm.) and spineless prickly pear (*O. rufida* Engelm.); (2) if goats can be conditioned to eat prickly pear after prescribed burning; and, (3) if goats would consume prickly pear when alternative forage was available. In Experiment 1, 8 goats were placed in metabolism stalls and fed either spineless or spined prickly pear with singed spines in both summer and winter. Intake, digestibility, and nitrogen balance were measured. In Experiment 2, 18 goats were placed in individual pens, and 9 were fed spineless prickly pear to determine if this increased acceptance of spined prickly pear with singed spines. In the third experiment, we varied the amount of alfalfa pellets fed to goats (below, near, and above maintenance) to determine if level of alfalfa intake affected prickly pear intake. Spineless prickly pear was higher ($P < 0.05$) in digestibility and crude protein than singed prickly pear, but nitrogen balance was similar for goats consuming the 2 species. Goats ate more spineless prickly pear on an as fed basis, but on a dry basis, intake was similar. Familiarity with spineless prickly pear increased ($P < 0.05$) subsequent intake of singed prickly pear. Level of alfalfa intake did not affect prickly pear intake. We concluded that both species are moderately nutritious, spineless prickly pear is more digestible than spined prickly pear, and once a preference for prickly pear has developed, goats may continue to eat prickly pear even though other forage is available.

Key Words: *Opuntia*, food novelty, learning, diet preference, browsing, protein, nitrogen balance, forage digestibility

The perceived value of prickly pear (*Opuntia* sp.) varies depending on geographic location and species. Most livestock producers in the southwestern United States attempt to control prickly pear because of its competitive nature with herbaceous forages (Mayeux and Johnson 1989, Ueckert et al. 1988). Most species of prickly pear also contain spines that cause injury to

Resumen

El "Prickly pear" (*Opuntia* sp.) es benéfico pero a la vez también es un estorbo para la ganadería del sudeste de los Estados Unidos. El compite con la vegetación forrajera herbácea, pero en ocasiones es utilizado como forraje de emergencia durante la sequía. En algunas regiones del sudeste se ha plantado una especie de "Prickly pear" sin espinas (*O. fiscus-indica* Engelm. and *O. rufida* Engelm.), pero poco se sabe acerca de su valor nutricional. Nuestros objetivos fueron determinar (1) el valor nutricional del "Prickly pear" con espinas (*O. macrorhiza* Engelm.) y sin espinas (*O. rufida* Engelm.); (2) si las cabras pueden ser acondicionadas para comer "Prickly pear" después de un fuego prescrito y (3) si las cabras consumirían "Prickly pear" cuando otro forraje alternativo esta disponible. En el experimento 1, 8 cabras se colocaron en jaulas metabólicas individuales y durante el invierno y verano fueron alimentadas con "Prickly pear" sin espinas o con espinas marcadas y se midió el consumo, la digestibilidad y el balance de nitrógeno. En el experimento 2, 18 cabras fueron colocadas en corrales individuales y 9 se alimentaron con "Prickly pear" sin espinas para determinar si esto incrementa la aceptación sobre el "Prickly pear" con espinas marcadas. En el tercer experimento variamos la cantidad de pelets de alfalfa con la que se alimento a las cabras (abajo, cerca y arriba del nivel de mantenimiento) para determinar si el nivel de consumo de alfalfa afectó el consumo de "Prickly pear". La especie de "Prickly pear" sin espinas fue mayor en digestibilidad y proteína cruda ($P < 0.05$) que la especie con espinas marcadas, pero el balance de nitrógeno fue similar en cabras consumiendo las 2 especies. En base al alimento, las cabras consumieron mas "Prickly pear" sin espinas, pero en base de materia seca el consumo fue similar. La familiaridad del "Prickly pear" sin espinas incremento ($P < 0.05$) el consumo subsecuente de "Prickly pear" con espinas marcadas. El nivel de consumo de alfalfa no afecto el consumo de "Prickly pear". Concluimos que ambas especies son moderadamente nutritivas, que el "Prickly pear" sin espinas es mas digestible que la especie con espinas y que una vez que la preferencia por "Prickly pear" ha sido desarrollada las cabras pueden continuar comiendo "Prickly pear" aunque otro forraje este disponible.

livestock after ingestion (Ueckert et al. 1990). In other areas, spineless prickly pear (*Opuntia fiscus-indica* Engelm. and *O. ficus-indica* (L.) Miller) has been introduced as an alternative feed (Brutsch and Zimmerman 1993). Spined prickly pear is used as forage for livestock, especially during droughts (Griffiths 1905, Bement 1969, Lehman 1969, Hanselka and Paschal 1991). Before feeding or grazing prickly pear, the pads are generally singed with a propane burner to remove the spines thereby improving acceptance and reducing the health hazards (i.e., phys-

Funding was provided by the Management, Instruction, and Research Center, Angelo State University, San Angelo, Tex.; Texas Agricultural Experiment Station, Sonora, Tex. The authors would like to acknowledge B.S. Engdahl for her assistance with laboratory analysis.

Manuscript accepted 8 Jul. 01.

ical damage to the lips, mouth, and upper gastrointestinal tract) (Ueckert et al. 1990, Hanselka et al. 1993).

Throughout most of western and central Texas, prescribed burning is used to reduce prickly pear abundance, but mortality rates are low unless winter burning is followed with herbicide application (Ueckert 1997, Ueckert et al. 1988). The high cost of herbicides limits the economic feasibility of controlling prickly pear. Given that livestock will consume prickly pear after the spines have been removed, prescribed burning could be followed by livestock grazing. Grazing after burning may also reduce prickly pear density because the plant does not tolerate heavy defoliation (Maltsberger 1989).

Prickly pear species are common throughout the southwestern U.S. and many produce substantial phytomass that can serve as emergency forage (Garcia de Cortazar and Nobel 1992). Prickly pear is moderately high in sugars, starch, ether extract, crude protein, amino acids, and fiber (Teles et al. 1984, Retamal et al. 1987). However, the availability of nutrients for ruminant animals has not been assessed. To assess the potential value of singing prickly pear as an emergency forage resource, it is important to know its forage value. Thus, the first objective of this study was to quantify *in vivo* digestibility of prickly pear and nitrogen balance of goats consuming prickly pear.

Our second objective was to determine if we could improve acceptance of prickly pear as a forage. Recent studies on livestock training have suggested that previous experiences with certain foods increases intake, and preferences may develop and persist (Provenza 1994). Thus, it may be possible to train livestock to consume more prickly pear, thereby increasing the effectiveness of livestock herbivory after prescribed burning as a biological control. We hypothesized that feeding spineless prickly pear immediately after weaning would improve acceptance of singed (spined) prickly pear.

Given the presence of spines, livestock generally avoid eating prickly pear when other forage is available. However, livestock have been observed to eat prickly pear throughout the year even though they develop health problems and alternative forage is available (Hanselka et al. 1993). Our third objective was to determine how dietary feed level affected intake of prickly pear by goats. We hypothesized that goats meeting or exceeding maintenance requirements would avoid eating prickly pear while goats unable to meet maintenance

requirements because of limited feed intake would consume prickly pear.

Methods

All experiments were conducted at the Texas Agricultural Experiment Station, Sonora, Tex. (30° N, 100° W) beginning in June 1999. Spined (*O. macrohiza* Engelm.) and spineless (*O. rufida* Engelm.) prickly pear were fed to goats in 3 studies. The spineless prickly pear was grown on site under ambient conditions, and the spined prickly pear was harvested from a natural stand nearby. The spined prickly pear was singed with a propane burner in the field each day immediately before harvesting to remove all spines. Both types of prickly pear were cut into 5 cm wide strips, and fed fresh to individual goats in each of the 3 experiments.

Metabolism Study

Eight female Boer-Spanish cross goats (11 months-old and weighing about 45 kg) were randomly allocated to 1 of 2 treatments in a Latin square design. Goats were housed in an open-air building in individual 2.4 x 1.1 x 1.7 m metabolism stalls with expanded steel floors to allow feces and urine separation and collection. Goats were given *ad libitum* access to either spined prickly pear with singed spines or spineless prickly pear daily. Intake, fecal output and urine output were recorded daily. All goats used in this study were accustomed to the stalls from a previous experiment.

Treatments consisted of feeding either singed or spineless prickly pear to individual goats (8 goats/treatment). Two periods were conducted with treatments reversed (i.e., 4 goats fed spineless prickly pear in Period 1 were fed singed prickly pear in Period 2). Period 2 was initiated 10 days after the completion of Period 1. Goats were maintained on alfalfa pellets (15 g kg⁻¹) between periods. Goats were fed the appropriate prickly pear during a 3-day adjustment period followed by a 5-day collection period. Relatively short adjustment and collections periods were used because of the short retention time of goats (Huston et al. 1986). A 2 x 2 Latin square design was used for Experiment 1 because of a limited number of metabolism stalls.

Feces and urine were collected daily during each 5-day collection period for each trial. Ten ml of 25% H₂SO₄ was added to 1-gallon plastic collection containers to prevent volatilization of ammo-

nia from urine (A.O.A.C. 1984). Urine and feces were frozen at -26°C until analysis. Composite diet and fecal samples were dried at 60°C for 48 hours, ground to pass through a 1 mm screen, dried at 105°C, and ashed at 600°C to determine percent dry matter and organic matter, respectively. Nitrogen contents of prickly pear, feces, and urine were analyzed using standard micro-Kjeldahl procedures (Holechek et al. 1982). The fecal and urinary nitrogen content was subtracted from the nitrogen intake from the prickly pear to estimate nitrogen balance (Boutouba et al. 1990). Dry matter and organic matter digestibility of prickly pear were estimated using *in vivo* techniques and compared between prickly pear species (Holechek et al. 1982, Nunez-Hernandez et al. 1992).

Preliminary evidence suggested that nutrient content of prickly pear varied among seasons (Huston et al. 1981, Retamal et al. 1987). The metabolism trial was repeated in winter (December) to estimate differences in prickly pear quality between summer and winter. The same goats and protocol used in the summer trial were used in the winter trial.

Previous Dietary Experiences

In Experiment 2, 9 intact male and 9 female Boer-Spanish cross goats, 4-5 months of age, and weighing 20 kg, were used to determine how experience with spineless prickly pear at weaning affected intake of singed prickly pear. Goats were placed in individual pens and allocated randomly to 1 of 2 treatments (9 goats/treatment). Four males were assigned to Treatment 1 with 5 females, and 5 males and 4 females were assigned to the other Treatment 2.

Treatments consisted of goats either naive or familiar with spineless prickly pear. All goats were raised in pens to control exposure to prickly pear before the test period, and all goats were naive to prickly pear before initiation of the study. The naive goats received only alfalfa pellets (15 g kg⁻¹ BW) to meet maintenance requirements (NRC 1981). In addition to feeding alfalfa pellets at maintenance levels, experienced goats were also fed spineless prickly pear in excess for 1 hour daily until consumption leveled off (8 days). After the initial 8 days, all naive and experienced goats were fed singed prickly pear for 1 hour daily over 4 days, and intake was recorded daily. Prickly pear was harvested fresh daily, spines were singed, and pads were chopped into 5 cm wide strips to facilitate feeding. All goats continued to receive fresh water and 15 g kg⁻¹ BW of alfalfa daily throughout the study.

Feed and Prickly Pear Intake

Experiment 3 began 14 days after the completion of Experiment 2. Goats from Experiment 2 were re-randomized to 1 of 3 treatments and placed in individual pens. An equal number of goats from Treatments 1 and 2 used in Experiment 2 were assigned to treatments for Experiment 3 to minimize the effect of previous experience with prickly pear. Goats were fed a maintenance diet of alfalfa pellets (15 g kg⁻¹ BW) until the experiment began (14 days).

For this experiment, goats were allocated to 1 of 3 treatment groups. Treatment 1 was fed 10 g kg⁻¹ BW of alfalfa pellets daily to represent a diet below maintenance, Treatment 2 was fed 20 g kg⁻¹ BW of alfalfa pellets daily to represent a near maintenance diet, while Treatment 3 was fed 30 g kg⁻¹ BW of alfalfa pellets daily to exceed maintenance requirements. Freshly chopped singed prickly pear was fed to all 3 groups for 2 hours each morning before they were fed their pre-assigned alfalfa diet. Singed prickly pear intake was recorded daily over 5 days. The effects of basal diet feeding level on prickly pear consumption were compared among the 3 treatments.

Statistical Analysis

For each experiment, data were analyzed using analysis of variance (Hicks 1993). A 2 x 2 Latin square design (2 treatments and 2 periods) was used in Experiment 1. A nested design was used in all experiments with goats nested within treatments as replicates. Treatment (naive vs. familiar) served as the primary effect and sex as the secondary effect in Experiment 2. For Experiment 3, level of alfalfa intake was the primary effect and familiarity with prickly pear (from Exp. 2) was the secondary effect. Intake data for all 3 experiments were converted to g kg⁻¹ body weight (BW) on a dry matter basis to eliminate the effects of moisture content

and body size on intake data. Data from Experiments 2 and 3 were analyzed using repeated measures analysis of variance because intake was measured for individual goats daily. Means were separated using least significant difference (LSD) when $P < 0.05$ (Gomez and Gomez 1984). Data were analyzed using the statistical computer package JMP (SAS 1994).

Results

Metabolism Trial

Goats readily consumed both prickly pear species. Goats consumed more ($P < 0.05$) spineless prickly pear on an as fed basis (g kg⁻¹ BW), whereas dry matter intake was similar for both species of prickly pear (Table 1). Moisture content of prickly pear was high for both species and for both seasons (summer 95% and 90%; winter 90% and 75% for spineless and spined prickly pear, respectively).

Digestibility varied between prickly pear species, but was similar between seasons. Digestibility of spineless prickly pear was greater than singed prickly pear for both dry matter ($P < 0.05$) and organic matter ($P < 0.07$) when data were combined across seasons (Table 1). Percent crude protein was also greater ($P < 0.05$) for spineless prickly pear.

Nitrogen balance of goats did not differ when fed spined or spineless prickly pear (Table 1). Values were negative for both species in the summer (-0.21 g vs -0.42 g for spined and spineless, respectively). During the winter, nitrogen balance for goats consuming spined prickly pear were 0.36 g while goats consuming spineless prickly had a positive nitrogen balance of 4.0 g.

Previous Dietary Experiences

During the 8-day familiarization period, goats ate on average 1.3 g kg⁻¹ BW DM of

spineless prickly pear. Following initial exposure to spineless prickly pear, goats familiar with spineless prickly pear ate more ($P < 0.05$) singed prickly pear than naive goats (3.1 vs. 1.0 g kg⁻¹ BW for goats familiar vs. naive to prickly pear). Intake of prickly pear differed ($P < 0.05$) among days over the 4-days of feeding (Fig. 1). Nevertheless, familiar goats consistently ate more singed prickly pear than naive goats. Intake of prickly pear was similar ($P > 0.05$) between males and females.

Feed and Prickly Pear Intake

Varying intake of alfalfa did not affect intake of singed prickly pear ($P > 0.05$, 3.2 ± 0.6 , 3.3 ± 0.6 , 3.5 ± 1.3 , g kg⁻¹ BW for below, near, and above maintenance, respectively). Goats familiar with spineless prickly pear in the previous experiment continued to eat more ($P < 0.08$) singed prickly pear than naive goats (4.2 vs. 2.5 g kg⁻¹ BW, for familiar vs. naive goats, respectively), regardless of the amount of alfalfa fed.

Discussion

Nutritive Value of Prickly Pear

Both species were moderately digestible (58–85% DMD) and met nitrogen requirements for goats during the winter (Exp. 1). Goats readily consumed both species of prickly pear and consumed some prickly pear when another forage was fed to meet or exceed nutrient requirements (Exp. 3). We contend that prickly pear can be a viable alternative forage, especially when used as an emergency feed. Producers typically rely on prickly pear when other forage sources are depleted or dormant. Under these circumstances and given the negative nitrogen balance values during the summer trial (Exp. 1), protein supplementation may be required in addition to feeding prickly pear.

The prickly pear used in this study was only collected from 1 site and may vary nutritionally in other areas. Future studies should identify variations in nutritional value of prickly pear growing on different soil types and in different locations.

Consumption of spined prickly pear after singeing the spines suggests strongly that goats will consume prickly pear after prescribed burning. Prescribed burning or singeing spines with a propane torch would be required to reduce health hazards (Ueckert et al. 1990). In addition, livestock herbivory after burning should reduce prickly pear cover and density

Table 1. Mean nutritional parameters of spine (singed) and spineless prickly pear fed to goats for Experiment 1. Crude protein values were measured using the 2 outermost prickly pear cladodes.

Parameter	Singed	SEM	Spineless	SEM
Dry matter (%)	11.5		23.7	
Organic Matter (%)	74.0		71.0	
Intake, as fed basis (g kg ⁻¹ BW)	91.0 ^b	4.1	154.0 ^a	3.9
Dry matter intake (g kg ⁻¹ BW)	14.0	1.3	12.0	1.3
Fecal Output (g day ⁻¹)	462.5 ^a	20.3	304.8 ^b	19.5
Dry matter digestibility (%)	58.0 ^b	0.1	79.0 ^a	0.1
Organic matter digestibility (%)	70.0 ^b	1.0	83.0 ^a	1.0
Crude protein (%)	4.8 ^b	0.9	8.1 ^a	0.5
Nitrogen balance (g/d)	0.4	0.2	1.8	0.2

^{a,b}Means within rows with different superscripts differ (Intake $P < 0.05$; DMD, $P < 0.05$; OMD, $P < 0.07$; CP, $P < 0.05$).

Fig. 1. Intake ($\text{g kg}^{-1} \text{ BW}$) of singed prickly pear by goats familiar or naïve with spineless prickly pear over a 4 days (days 9 through 12) in Experiment 2. The first 8 days involved the familiarization period when experienced goats were fed spineless prickly pear. Average consumption of spineless prickly pear for the familiarization period was $1.3 \text{ g kg}^{-1} \text{ BW}$ on dry basis.

given that this plant has a low tolerance to herbivory (Griffiths 1905). However, goat herbivory may need to occur quickly after burning before pads begin to spoil from heat damage (Ueckert pers. comm.).

Spineless prickly pear was more digestible and had a higher crude protein content than spined prickly pear. Thus, spineless prickly pear could serve as a palatable and nutritious alternative feed source for livestock and wildlife. Establishing spineless prickly pear can be highly successful, but requires at least 4 years to accumulate sufficient biomass (Turpin and Gil, 1928). Palatability of spineless prickly pear will necessitate fencing to reduce herbivory until establishment. Providing spineless prickly pear as a forage may be more cost effective than burning spined prickly pear when forage is limited because of the high cost of labor and propane fuel for burning.

Spineless prickly pear also could be established in food plots to serve as emergency forage for wildlife. Most forages grown on food plots for deer in central and western Texas were developed in areas that receive higher and more consistent precipitation, and most are not adapted to xeric climates. Because spineless prickly pear evolved in dry conditions, it should remain productive even during drought.

Previous Dietary Experiences

Previous foraging experiences improve acceptance, foraging skills, and may result in physiological adaptations to metabolize some toxins (Distel and Provenza 1991, Provenza 1994, Bisson et al. 2001). Foraging experiences are particularly

important in the formation of dietary preferences when forages are nutritious and nonaversive (Villalba and Provenza 1997a, 1997b, 1997c, 1999). Prickly pear is moderately nutritious (Exp. 1) and lacks mechanical defenses after singeing. Feeding of spineless prickly pear increased consumption of singed prickly pear (Exp. 2), and this acceptance persisted (Exp. 3).

Weaning may be an important time for molding diet selection because of limited maternal influences on dietary habits (Hinch et al. 1987, Howery et al. 1998). Conditioning the acceptance of prickly pear could be accomplished during weaning when replacement animals are separated from their dams and housed in separate facilities. Once goat kids acquire a preference for spineless prickly pear, the acceptance of singed prickly pear is easily attainable as observed in Experiment 2. As an alternative to growing and hand-feeding spineless prickly pear, producers could wean goat kids in a pasture after singeing prickly pear spines.

Prickly Pear Intake

Level of alfalfa intake did not affect intake of prickly pear in this study. Goats consumed prickly pear at a constant rate regardless of the level of intake of the basal diet. Goats may have consumed prickly pear because of an innate desire to consume a variety of foods. In another study, when lambs were offered 3 rations varying in nutrient quality (high, medium, and low), they consistently ate all 3 even though the high quality ration met all of their dietary requirements (Provenza et al.

1996). Food preferences change within meals often to less nutritious foods (Newman et al. 1994, Early and Provenza 1998) and ruminants prefer alternatives to forages they have consumed for several days (Newman et al. 1992, 1994, Ramos and Tennesen 1993) or even several hours (Parsons et al. 1994).

Prickly pear also may provide other essential nutrients that may be limited. Other studies have reported that livestock and wildlife often consume prickly pear even when forage quantity is not limited (Taylor et al. 1980, Fontenot et al. 1991). Phosphorous often is limited on central and western Texas rangelands. Ruminants occasionally consume atypical dietary items to rectify deficiencies (Provenza 1994).

Implications

Most southwestern livestock producers consider spined prickly a hindrance to forage production; spined prickly pear has increased in cover in the last 100 years because of overgrazing and the lack of fire. Controlling spined prickly pear in the southwestern U.S. is often not practical because of economic restraints, its use as emergency feed during droughts, and its importance for wildlife habitat.

Spineless prickly pear has the potential as an alternative forage for goats or other domestic livestock or deer. Nutritionally, it yields enough protein to meet protein requirements of goats under some levels or stages of production. In addition, for most current management systems, spined prickly pear is an unused forage source. However, combining prescribed burning with goat herbivory would allow prickly pear to be used as a forage resource without jeopardizing the animal health and reduce prickly pear cover and density.

Literature Cited

- A.O.A.C. 1984. Official Methods of Analysis (14th Ed.). Association of Official Analytical Chemists, Washington D.C.
- Bement, R.E. 1969. Plains pricklypear: relation to grazing intensity and blue grama yield on central Great Plains. *J. Range Manage.* 21:83–86.
- Bisson, M.G., C.B. Scott, C.A. Taylor, Jr., and R.A. Moen. 2001. Activated charcoal and experience affect intake of juniper by goats. *J. Range Manage.* 54:274–278.
- Boutouba, A., J.L. Holecchek, M.L. Galyean, G. Nunez-Hernandez, J.D. Wallace, and M. Cardenas. 1990. Influence of two native shrubs on goat nitrogen status. *J. Range Manage.* 43:530–534.

- Brutsch, M.O. and H.G. Zimmerman. 1993.** The prickly pear (*Opuntia ficus-indica* [Cactaceae]) in South Africa: utilization of the naturalized weed and of cultivated plants. *Econ. Bot.* 47:154-162.
- Distel, R.A. and F.D. Provenza. 1991.** Experience early in life affects voluntary intake of blackbrush by goats. *J. Chem. Ecol.* 17:431-450.
- Early, D.M. and F.D. Provenza. 1998.** Food flavor and nutritional characteristics alter dynamics of food preference in lambs. *J. Anim. Sci.* 76:728-734.
- Fontenot, N.J., G.R. Engdahl, G.L. Holland, and W.H. Schacht. 1991.** Seasonal diet selection of white-tailed deer (*Odocoileus virginianus*) in relation to forage availability in west central Texas. *MIR Prog. Rep.* No. R-5:8-9.
- Garcia de Cortazar, V. and P.S. Nobel. 1992.** Biomass and fruit production for the prickly pear cactus, *Opuntia ficus-indica*. *J. Amer. Soc. Hort. Sci.* 117:558-562.
- Gomez, K.A. and A.A. Gomez. 1984.** Statistical Procedures for Agricultural Research. pp. 187-207. John Wiley and Sons, New York.
- Griffiths, D. 1905.** The prickly pear and other cacti as food for stock. *USDA Bureau of Plant Industries Bull.* 74:46.
- Hanselka, C.W. and J.C. Paschal. 1991.** Prickly pear cactus: an important rangeland resource. *In: Progress Report*, pp. 141-143. Texas Agr. Exp. Sta., U.S.A.
- Hanselka, C.W., R.Q. Landers, and J.C. Paschal. 1993.** Prickly pear: friend or foe. *Texas Agri. Ext. Ser.* at Corpus Christi. Technical Rept. B-5046.
- Hicks, C.R. 1993.** Fundamental Concepts in the Design of Experiments. p. 201. Saunders College Publishing, New York.
- Hinch, G.N., E. Lecrivain, J.J. Lynch, and R.L. Elwin. 1987.** Changes in maternal-young associations with increasing age of lambs. *Appl. Anim. Behav. Sci.* 17:305-318.
- Howery, L.D., F.D. Provenza, R.E. Banner, and C.B. Scott. 1998.** Social and environmental factors influence cattle distribution on rangeland. *Appl. Anim. Behav. Sci.* 55:231-244.
- Holecchek, J.L., M. Vavra, and R.D. Pieper. 1982.** Methods of determining the nutritive quality of range ruminant diets: a review. *J. Anim. Sci.* 53:291-302.
- Huston, J.E., B.S. Rector, W.C. Ellis, M.L. Allen. 1986.** Dynamics of digestion in cattle, sheep, goats and deer. *J. Anim. Sci.* 62:208-215.
- Huston, J.E., B.S. Rector, L.B. Merrill, and B.S. Engdahl. 1981.** Nutritional Value of Range Plants in the Edwards Plateau Region of Texas. *Texas Agr. Exp. Sta. Bull.* B-1357.
- Lehman, V.W. 1969.** Forgotten legions, sheep in the Rio Grande Plains of Texas. *Texas Western Press. U.S.A.: Univ. of Texas at El Paso.* 226 pp.
- Maltsberger, W.A. 1989.** Prickly pear cactus - an unsung blessing of the Rio Grande Plains. pp. 19-30. *In: C.W. Hanselka and J.C. Paschal (eds.) Developing Prickly Pear as a Forage, Fruit, and Vegetable Resource.* Proc. of Conference July 14, 1989. Kingsville, Tex. *Tex. Agr. Ext. Serv. College Station.*
- Mayeux, H.S., Jr. and H. B. Johnson. 1989.** Absorption and translocation of picloram by Lindheimer pricklypear (*Opuntia lindheimeri*). *Weed Sci.* 37:161-166.
- Newman, J.A., A.J. Parsons, and A. Harvey. 1992.** Not all sheep prefer clover: diet selection revisited. *J. Agr. Sci. Cambridge.* 119:275-283.
- Newman, J.A., P.D. Penning, A.J. Parsons, A. Harvey, and R.J. Orr. 1994.** Fasting affects intake behaviour and diet preference of grazing sheep. *Anim. Behav.* 47:185-193.
- NRC. 1981.** Nutrient Requirements of Goats: Angora, Dairy, and Meat Goats in Temperate and Tropical Countries. National Academy Press, Wash. D.C.
- Nunez-Hernandez, G., J.L. Holecchek, D. Arthun, A. Tembo, J.D. Wallace, M.L. Galyean, M. Cardenas, R. Valdez. 1992.** Evaluation of fecal indicators for assessing energy and nitrogen status of cattle and goats. *J. Range Manage.* 45:143-147.
- Parsons, A.J., J.A. Newman, P.D. Penning, A. Harvey, and R.J. Orr. 1994.** Diet preference of sheep: effect of recent diet, physiological state and species abundance. *J. Anim. Ecol.* 63:465-478.
- Provenza, F.D. 1994.** Ontogeny and social transmission of food selection in domesticated ruminants. *In press In: P. Valsecchi and B.G. Galef (eds.) Ontogeny and social transmission of food preferences in mammals: Basic and Applied Research.* Harwood Acad. Press, London.
- Provenza, F.D. 1995.** Postingestive feedback as an elementary determinant of food preferences and intake in ruminants. *J. Range Manage.* 48:2-17.
- Provenza, F.D., C.B. Scott, T.S. Phy, and J.J. Lynch. 1996.** Preference of sheep for foods varying in flavors and nutrients. *J. Anim. Sci.* 74:2355-2361.
- Ramos, A. and T. Tennesen. 1993.** A note on the effect of dietary variety on food intake of cattle. *Anim. Prod.* 57:323-325.
- Retamal, N., J.M. Duran, and J. Fernandez. 1987.** Seasonal variations of chemical composition of prickly pear (*Opuntia ficus-indica* (L.) Miller). *J. Sci. Food Agr.* 38:303-311.
- SAS. 1994.** JMP User's Guide, Version 3.1. SAS Institute Inc., N.C.
- Taylor, C.A., M.M. Kothmann, L.B. Merrill, and D. Elledge. 1980.** Diet selection by cattle under high-intensity low-frequency, short duration, and Merrill grazing systems. *J. Range Manage.* 6:428-434.
- Teles, F.F.F., J.W. Stull, W.H. Brown, and F.M. Whitney. 1984.** Amino and organic acids of the prickly pear cactus (*Opuntia ficus-indica* L.). *J. Sci. Food Agr.* 35:421-425.
- Turpin, H.W., and G.A. Gill. 1928.** Insurance against drought. *So. Africa Dept. Agr. Bull.* 36:32.
- Ueckert, D.N. 1997.** Pricklypear ecology. *Proc. of Brush Sculptors Symposium.* pp. 35-38. *Tex Agri. Exp. Sta. and Tex Agr. Ext. Ser. San Angelo.*
- Ueckert, D.N., J.L. Petersen, R.L. Potter, J.D. Whipple and M.W. Wagner. 1988.** Managing pricklypear with herbicides and fire. *Texas Agr. Exp. Sta. Prog. Rep.* Pr-4570.
- Ueckert, D.N., C.W. Livingston, Jr., J.E. Huston, C.S. Menzies, R.K. Dusek, J.L. Petersen, and B.K. Lawrence. 1990.** Range and sheep management for reducing pear-mouth and other pricklypear-related health problems in sheep flocks. *Sheep and Goat, Wool and Mohair, Res. Report.* *Tex Agr. Exp. Sta., San Angelo, Tex.*
- Villalba, J.J. and F.D. Provenza. 1997a.** Preference for wheat straw by lambs conditioned with intraruminal infusions of starch. *Br. J. Nutr.* 77:287-297.
- Villalba, J.J. and F.D. Provenza. 1997b.** Preference for flavoured wheat straw by lambs conditioned with intraruminal infusions of acetate and propionate. *J. Anim. Sci.* 75:2905-2914.
- Villalba, J.J. and F.D. Provenza. 1997c.** Preference for flavoured foods by lambs conditioned with intraruminal administration of nitrogen. *Br. J. Nutr.* 78:545-561.
- Villalba, J.J. and F.D. Provenza. 1999.** Effects of food structure and nutritional quality and animal nutritional state on intake behaviour and food preferences of sheep. *Appl. Anim. Behav. Sci.* 63:145-163.

Intensive-early stocking for yearling cattle in the Northern Great Plains

E. E. GRINGS, R. K. HEITSCHMIDT, R. E. SHORT, AND M. R. HAFERKAMP

Authors are Research Animal Scientist, Supervisory Rangeland Scientist, Research Physiologist, and Rangeland Scientist, USDA-ARS, Fort Keogh Livestock and Range Research Laboratory, Miles City, Mont. 59301.

Abstract

A 3-year study was conducted to evaluate grazing strategies for production of growing cattle during summer on Northern Great Plains rangeland. Crossbred yearling steers (N = 123 per year, avg initial weight = 275 kg) were allotted to 1 of 2 treatments replicated in 3 pastures. Treatments were season-long grazing of pastures at recommended stocking rates assuming a 4-month grazing period or intensive-early grazing of pastures stocked at the same rate assuming only a 2-month grazing season. Precipitation in 1993 was 169% of normal resulting in greater forage quality than in other years and no differences were observed in weight gains between treatments during 1993. In 1994 and 1995, steers in the intensive-early stocked pastures gained less weight during the 2 months of grazing than did those in the season-long stocked pastures; however, gain per hectare was greater in the intensive-early stocked pastures. Intensive-early stocking with growing steers may be a viable means to overcome limited forage quality during late summer in the Northern Great Plains and to maximize forage utilization in years of abundant forage.

Key Words: grazing management, beef cattle, protein supplementation

Growing season precipitation in the Northern Great Plains occurs mainly during May and June. Drier, hotter conditions in late summer result in lowered forage quality and quantity with an associated decreased rate of gain of steers grazing these forages (Heitschmidt et al. 1993). By monitoring daily weight of grazing steers, Currie et al. (1989) found gains to decline in late July to early August, and some steers lost weight during late summer, indicating that keeping steers on rangeland after this time could be counterproductive.

Decreased gains during late summer may be avoided by removing steers from rangeland before the decrease in forage quality. Intensive-early stocking strategies that employ high stocking rates

Resumen

Se condujo un estudio de tres años para evaluar las estrategias de apacentamiento para la producción de ganado en crecimiento durante el verano, el estudio se realizó en el pastizal de las Grandes Planicies del Norte. Novillos un año de cruza de razas (N = 123 por año, peso inicial promedio = 275 kg) se asignaron a 1 de 2 tratamientos repetidos en tres potreros. Los tratamientos fueron: 1) apacentamiento del pastizal durante estaciones largas con la carga animal recomendada, asumiendo un periodo de apacentamiento de 4 meses y 2) apacentamiento intensivo temprano de los pastizales con la misma carga animal asumiendo un periodo de apacentamiento de solo 2 meses. La precipitación en 1993 fue 169% de la precipitación normal resultando una mayor calidad de forraje que en otros años, por lo que no se observaron diferencias en las ganancias de peso entre los tratamientos. En 1994 y 1995 los novillos en el tratamiento de apacentamiento intensivo y temprano ganaron menos peso durante los dos meses de apacentamiento que los novillos en el tratamiento de apacentamiento de estación larga, sin embargo, la ganancia por hectárea fue mayor en el tratamiento de apacentamiento intensivo y temprano. El apacentamiento intensivo con novillos en crecimiento puede ser un medio viable para sobreponer la calidad limitada del forraje a fines del verano en las Grandes Planicies del Norte y para maximizar la utilización del forraje en años en que este es abundante.

but remove cattle from range in mid-summer have been used in the central and southern Great Plains to effectively utilize early season forage for the production of growing cattle (McCollum et al. 1990, Olson et al. 1993, Smith and Owensby 1978). Economic analyses of intensive-early stocking strategies in Oklahoma (Bernardo and McCollum 1987) indicate that these systems require high rates of gain early in the growing season. Heitschmidt et al. (1993) found that gains over 1 kg/day can be expected for steers on Northern Great Plains rangelands in early summer, indicating good potential for intensive-early stocking strategies. The objective of this study was to evaluate intensive-early stocking compared with season-long stocking for the production of growing cattle grazing Northern Great Plains rangelands.

Methods

The study was conducted at the Fort Keogh Livestock and Range Research Laboratory near Miles City, Mont. (46°22'N 105°5'W). Climate is continental and semi-arid with vegetation

The authors express appreciation to Norm Bellows, Richard Bonine, JoAnne Gresens, Byron Hould, Caralea Leidholt, Susan Reil, and Brooke Shipp for assistance with this research.

This paper is a contribution from the U.S. Department of Agriculture, Agricultural Research Service and the Montana Agricultural Experiment Station, Miles City, Mont.

U.S. Department of Agriculture, Agricultural Research Service, Northern Plains Area, is an equal opportunity/affirmative action employer, and all agency services are available without discrimination.

Manuscript accepted 9 May 01.

dominated by western wheatgrass [*Pascopyrum smithii* (Rydb.) Love], threadleaf sedge [*Carex filifolia* Nutt.], needle and thread [*Stipa comata* Trin. and Rupr.], blue grama [*Bouteloua gracilis* (H.B.K.)], and downy [*Bromus tectorum* L.] and Japanese bromes [*B. japonicus* Thunb.]. Average annual rainfall in the area is 338 mm with 60% received during the 150-day, mid-April to mid-September growing season.

During each of 3 years, 123 crossbred yearling steers of British-type breeding (avg initial weight = 275 kg) were allotted to 1 of 2 treatments replicated in 3 pastures (6 pastures total) in a completely random design. Treatments were season-long stocking with pastures stocked at the recommended rate assuming a 4-month grazing period and intensive-early stocking with pastures stocked with about twice the number of steers for a shorter period of time. The timing of grazing varied among years due to forage conditions (Table 1). Pasture size varied from 36 to 90 hectares. Stocking rate was based on SCS (1983) guidelines for range sites in good condition. Hectares available per steer averaged 4.9 for season-long and 1.9 for intensive-early stocked pastures. Animal numbers per pasture were assigned based on range site composition, therefore, number of hectares per steer for the season-long-stocked treatment did not equal twice that of intensive-early stocked pastures. Pastures were assigned the same treatment each year, allowing evaluation of any short-term carryover effects of grazing management on pasture quality and animal performance.

Before the study, steers were implanted with a 200-day estradiol implant. Steers were weighed initially and then about every 14 days on a non-shrunk basis. Decisions concerning removal of cattle from intensive-early stocked pastures were based on biweekly weight changes and visual estimates of forage quality and utilization. Steers were removed from intensive-early stocked pastures when weight gains began to diverge from those of steers in season-long stocked pastures and when cool-season forages became dormant. During 1993, forage quality and quantity were visibly above average and cattle remained on intensive-early stocked pastures until 17 September.

Standing crop was estimated each year before grazing, after removal of intensive-early stocked steers and after remaining steers were removed from pastures. Two sites per pasture were chosen, representing an average of 48.5% of the pasture area

Table 1. Dates of the beginning and ending of the grazing periods for season-long (SS) and intensive-early stocked (IES) pastures.

Year	Start of grazing	IES cattle removed	SS cattle removed
1993	19 May	17 Sep.	4 Oct.
1994	17 May	15 Jul.	8 Sep.
1995	15 May	4 Aug.	26 Sep.

with a range from 26.2 to 73.1%. Three total range sites were sampled as not all pastures were comprised of the same range sites. Botanical composition of each site was visually estimated by the dry weight rank method (t'Mannetje and Haydock 1963) and is presented in Table 2. For standing crop, 4 non-random refer-

(Robertson and Van Soest 1977), and in vitro organic matter digestibility (IVOMD; Tilley and Terry 1963).

Analysis of variance of weight gain data was conducted with a model that included treatment, year, and pasture within treatment (SAS 1989). Treatment means were tested with the pasture within treatment

Table 2. Botanical composition of 3 range sites found within pastures used for intensive-early or season-long stocking of pastures.

Species group	Range site		
	Silty clay	Claypan	Silty-Shallow
	------(%)-----		
<i>Pascopyrum smithii</i>	35.9	63.0	18.3
<i>Stipa comata</i>	25.2	1.3	26.5
Other cool-season grasses	1.3	2.7	5.2
Warm-season grasses	12.7	17.0	18.3
Annual bromes	9.2	8.8	3.7
<i>Carex filifolia</i>	3.3	0.0	23.5
Forbs	12.4	7.2	4.5

ence plots (0.25 m²) per range site were chosen based on a range of biomass densities from least to most abundant. Additionally, 10 random plots per site per pasture were estimated. The 4 reference plots and every fifth random plot were clipped for calibration of the estimates. Herbage was clipped to the ground, sorted by grass and forbs, dried at 55°C for 48 hours, and weighed. The non-random reference plots were not included in standing crop estimates for the pasture. Samples were composited by site within grazing treatment and saved for chemical analysis. Chemical analyses on herbage included dry matter, ash (AOAC 1990), crude protein (Hach 1987), neutral detergent fiber

mean square as the error term. Year effects were tested with the residual error term. Standing crop was evaluated with a model including year, treatment, and the interaction which were tested with pasture within treatment as the error term. The model also included sampling time, year x sampling time, treatment x sampling time, and year x treatment x sampling time which were tested using the residual mean square as the error term. The model for forage quality included year and time of sampling (pre-grazing, mid-grazing, and end of grazing). Due to compositing of samples for chemical analysis, the residual error was used to test effects on chemical analysis of forage.

Table 3. Forage standing crop for 2 range sites within pastures used for intensive-early stocking (IES) and season-long stocking (SS), SEM = 32.6.

Item	Treatment		Year		
	IES	SS	1993	1994	1995
	------(kg/ha)-----				
Initial pre-grazing ¹	1,406	1,576			
Pre-grazing	1,425	1,803	1,491	1,807	1,544
Mid-grazing	1,483	1,814	1,804	1,711	1,431
Post-grazing	1,418	1,904	1,636	1,722	1,625
Average	1,442	1,840	1,644 ^{a2}	1,747 ^a	1,533 ^b

¹May 1993.

²Means by year with differing superscripts differ, P < 0.05.

Fig. 1. Temperature and precipitation throughout 1993 to 1995 compared to a 115 year average.

Results and Discussion

Environmental Conditions

Precipitation during May through August 1993 was about 169% of normal, with rain falling throughout the grazing period (Fig. 1). July 1993 precipitation was 400% above normal. Precipitation in 1994 was 44% of normal, with all months being below normal. Precipitation in 1995 was close (104%) to the average for the area, with a fairly typical monthly pattern.

Seasonal Changes in Herbage Quantity and Herbage

At the initial pre-grazing sample in 1993, available forage did not differ between treatments (Table 3). The increase in forage availability between 1993 and 1994 may be related to carry-over of biomass from 1993 into 1994. Quantity of forage was less in 1995 than it had been the previous 2 years. No interactions ($P > 0.10$) of grazing treatment with year or sampling time on forage availability were observed.

As forage quantity did not differ between treatments at any time, we hypothesize that pastures could have been stocked at a heavier rate with little detriment to cattle performance. However, care should be taken to not overstock pastures with an intensive-early stocking system. Olson et al. (1993) compared season-long

to intensive-early stocking in the Central Great Plains at either 2- or 3-times the number of animals in the intensive-early stocked pastures for 9-years and found vegetation shifted to more warm-season grasses with the heavier intensive-early stocking. Willms and Jefferson (1993) also suggested shifts to warm-season grasses will occur with heavy early grazing in the Northern Great Plains.

Forage quality declined throughout the summer as evidenced by a consistent decline in crude protein between pre-graz-

ing samples and those collected later in the season (Table 4). Crude protein did not differ between mid- and post-grazing samples. Greater forage crude protein was observed in 1993 than in other years and is related to the greater amounts of precipitation and cooler temperatures observed in 1993. Forage IVOMD did not differ among years for the pre-grazing sample, but was greater for mid- and post-grazing samples in 1993 than in other years. Mid- and post-grazing IVOMD were lowest in 1995.

The only forage quality measure to be affected by grazing treatment was neutral detergent fiber. These values were higher ($P < 0.05$) for samples collected from intensive-early stocked (81.1%) than season-long (79.2%) treatments. This could be the result of increased grazing intensity in the intensive-early stocked pastures.

Grazing Management

At the end of the early grazing period, cattle grazing intensive-early stocked pastures weighed about 10 kg less than the cattle grazing season-long stocked pastures (Table 5). In 1993, steers were lighter at the beginning of grazing than in other years, but were heavier by the end of both grazing periods. This was related primarily to the increased length of grazing in 1993.

There was a year x treatment interaction ($P < 0.05$) for average daily gain during the early grazing period as no differences were observed in gains between the treatments during 1993 (Table 6). This occurred even though the intensive-early stocked pastures were grazed for 4 months rather than the proposed 2 months (Table 1). The increased length of grazing greatly

Table 4. Forage quality of pastures used during the summer with intensive-early stocking (IES) or season-long stocking (SS) and sampled before grazing, at the time steers were removed from IES pastures, and at the end of SS grazing.

Item	Time of sampling			SEM
	Before grazing ¹	IES steers removed	Post-SS grazing	
Crude protein ¹	-----(% OM)-----			
1993 ^{A2}	9.7	7.8	7.3	0.19
1994 ^B	8.1	5.4	4.9	0.17
1995 ^B	7.8	5.2	5.2	0.17
Neutral detergent fiber				
1993	77.0 ^{aA}	81.6 ^{bA}	82.1 ^{bA}	0.79
1994	78.6 ^{aA}	82.9 ^{bA}	82.4 ^{bA}	0.72
1995	73.7 ^{aB}	78.9 ^{bB}	84.5 ^{cB}	0.73
IVOMD				
1993	61.4 ^a	58.9 ^{bA}	54.8 ^{cA}	0.67
1994	60.4 ^a	51.7 ^{bB}	50.6 ^{bB}	0.61
1995	59.6 ^a	48.2 ^{bC}	45.9 ^{cC}	0.62

¹There was a main effect of sampling time with pre-grazing differing from mid- and post-grazing samples, $P < 0.05$.

²Means within year with differing lowercase superscripts differ by sampling time. Means within sampling time with differing uppercase superscripts differ by year, $P < 0.05$.

Table 5. Weight changes of yearling steers grazing Northern Great Plains rangeland in summer and intensive-early-stocked (IES), season-long stocked (SS).

	Treatment		Year			SEM
	IES	SS	1993	1994	1995	
	------(kg)-----					
Initial weight	276	275	268 ^{A1}	278 ^B	280 ^B	0.87
Weight, after IES	391	401	432 ^A	370 ^B	386 ^C	1.16
Weight, at end of SS grazing	-	429	451 ^A	408 ^B	426 ^C	2.11

¹Year means with differing superscripts differ, $P < 0.01$.

increased the gain per hectare (Table 6) for this treatment in 1993 (treatment x year interaction) and indicates a potential advantage to the intensive-early stocking system. It was possible to take advantage of a season of high forage production for additional weight gains in steers. In 1994 and 1995, steers in the intensive-early stocked pastures gained less weight per day during the 2 months of grazing than did those grazing season-long; however, gain per hectare was greater in the intensive-early stocked pastures. The decreased gain per steer but increased gain per hectare is typical of intensive-early stocked grazing systems (Smith and Owensby 1978, McCollum et al. 1990). Olson et al. (1993) did not observe this response on shortgrass range in Kansas and suggested that this may be related to a slower decline in forage quality on those ranges. In the current study, forage quality had substantially declined in 1994 and 1995 by the time intensive-early stocking cattle were removed from pastures and associated gains of season-long stocking steers were reduced in the second half of the grazing season.

High rates of gain early in the grazing

season (1.3 kg/day) are reflective of the high forage quality available at this time of the year. Average daily gain over the entire grazing season for the season-long stocked steers was 1.19, 1.07, and 1.11 kg/day in 1993, 1994, and 1995, respectively. Average daily gain throughout the season-long grazing period was greater ($P < 0.05$) for 1993 (1.2 kg/day) than for 1994 and 1995 (1.1 kg/day). This was related to the increased available forage crude protein and IVOMD observed in 1993 compared with other years.

Implications

Gain per hectare was improved with the use of intensive-early stocking for yearling steers; therefore, the use of this strategy for growing cattle may be a viable means to overcome limited forage quality during late summer in the Northern Great Plains and to maximize utilization of the rangeland resource in years of abundant forage. Additional long-term research is required to define optimal stocking rates for this environment.

Table 6. Average daily gain and gain per hectare for steers grazing intensive-early stocked (IES) or season-long stocked (SS) pastures.

	IES	SS	SEM
	------(kg/day)-----		0.01
ADG, during IES period			
1993	1.22 ^{A1}	1.24 ^A	
1994	1.29 ^{aB}	1.48 ^{bB}	
1995	1.25 ^{aA}	1.38 ^{bC}	
ADG after IES period			0.02
1993	-	1.11 ^A	
1994	-	0.59 ^B	
1995	-	0.66 ^B	
Gain per hectare	------(kg gain/ha)-----		0.69
1993	82.8 ^{aA}	39.8 ^{bA}	
1994	43.2 ^{aB}	26.8 ^{bB}	
1995	52.8 ^{aC}	30.0 ^{bB}	

¹Means with differing lowercase superscripts differ by treatment within year, $P < 0.05$. Means with differing uppercase superscripts differ by year within treatment, $P < 0.05$.

Literature Cited

- AOAC. 1990. Official methods of analysis. 16th ed. Assoc. Official Anal. Chem., Washington, D.C.
- Bernardo, D.J. and F.T. McCollum. 1987. An economic analysis of intensive-early stocking, season-long stocking and prescribed burning programs for stocker cattle operations in central Oklahoma. Okla. Agric. Exp. Sta. Anim. Sci. Res. Rep. MP-119 238-242.
- Currie, P.O., J.D. Volesky, D.C. Adams, and B.W. Knapp. 1989. Growth patterns of yearling steers determined from daily live weights. J. Range Manage. 42:393-396.
- Hach. 1987. Feed analysis manual. Hach Co., Ames, Iowa.
- Heitschmidt, R.K., J.D. Volesky, M.R. Haferkamp, and P.O. Currie. 1993. Steer performance on native and modified Northern Great Plains rangeland. J. Range Manage. 46:529-533.
- McCollum, F.T., R.L. Gillen, D.M. Engle, and G.W. Horn. 1990. Stocker cattle performance and vegetation response to intensive-early stocking of Cross Timbers rangeland. J. Range Manage. 43:99-103.
- Olson, K.C., J.R. Brethour, and J.L. Launchbaugh. 1993. Shortgrass range vegetation and steer growth response to intensive-early stocking. J. Range Manage. 46:127-132.
- Robertson, J.B. and P.J. Van Soest. 1977. Dietary fiber estimation in concentrate feed-stuffs. J. Anim. Sci. 45 (Suppl. 1):254 (Abstr.).
- SAS. 1989. SAS users guide: Basics. SAS Institute, Cary, N.C.
- SCS. 1983. Technical guide, Section II-E-8. 10-14" Precipitation zone. Eastern Sedimentary Plains. Mont.
- Smith, E.F. and C.E. Owensby. 1978. Intensive-early stocking and season-long stocking of Kansas Flint Hills range. J. Range Manage. 31:14-17.
- Tilley, J.M.A. and R.A. Terry. 1963. A two-stage technique for the in vitro digestion of forage crops. J. Brit. Grassl. Soc. 18:104-111.
- t'Mannetje, L. and K.P. Haydock. 1963. The dry-weight-rank method for the botanical analysis of pasture. J. Br. Grassl. Soc. 18:268-275.
- Willms, W.D. and P.G. Jefferson. 1993. Production characteristics of the mixed prairie: constraints and potential. Can. J. Anim. Sci. 73:765-778.

Evaluating the ecological relevance of habitat maps for wild herbivores

MARC E. STALMANS, ED T.F. WITKOWSKI, AND KEVIN BALKWILL

Authors are respectively Ecologist, Head of the Restoration and Conservation Biology Research Group and Curator of the C.E. Moss Herbarium, Department of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag 3, Wits 2050, Republic of South Africa. Present address of the first author is Mpumalanga Parks Board, PO Box 1990, 1200 Nelspruit, Republic of South Africa.

Abstract

Informed management of large herbivores depends largely on how well habitat availability and suitability are understood. The aims of the study were to quantify and map the distribution of sour and mixed grasslands in the 48,000 ha Songimvelo Game Reserve, Mpumalanga, South Africa. Mixed grassland retains its forage quality and hence its ability to sustain animal production for longer in the year than sour grassland. An unsupervised classification technique was applied to a LANDSAT 5 TM image acquired in 1993. The probability that each resulting cluster represented either sour or mixed grassland was calculated based on the proportional allocation of 428 sample plots. The 2 resulting probability maps were combined into a single image by selecting the class image that contained the maximum posterior probability and assigning that class to the output pixel. The accuracy of the vegetation map was assessed by ground-truthing with an independent set of 85 plots. This yielded a correct classification of 84.8% for the sour and 76.9% for the mixed plots. The mixed grasslands covered only 31.0% of the area but accounted for 66.1% of the game stocking. Water is widely distributed and is not a limiting factor to habitat selection. Based on a GIS analysis, the qualitative difference between mixed and sour grasslands overrides quantitative differences in forage availability, fire history and human disturbance in influencing herbivore distribution. The integration of field data and satellite imagery into a GIS system thus offers a powerful tool for the objective quantification and mapping of available habitat.

Key Words: wildlife, GIS, remote sensing, LANDSAT, ground-truthing

The informed management of large herbivores in conservation areas depends largely on how well habitat availability and suitability are understood. The Songimvelo Game Reserve (henceforth SGR) is spatially very diverse in terms of its average annual rainfall, underlying geological substrate, elevation, slope, and aspect (Barnes 1998). This results in a very diverse vegetation pattern with marked differences in habitat suitability for herbi-

Resumen

El manejo actualizado de los grandes herbívoros depende en gran parte de que tan bien son entendidos la disponibilidad y lo apropiado del hábitat. Los objetivos de este estudio fueron cuantificar y mapear la distribución de los pastizales mixtos y ásperos en las 48,000 ha de la reserva de fauna Songimvelo en Mpumalanga, South Africa. Los pastizales mixtos conservan su calidad, y de aquí su habilidad para mantener la producción animal durante un mayor periodo de tiempo durante el año que los pastizales ásperos. Una técnica de clasificación no supervisada se aplicó a una imagen LANDSAT 5 TM adquirida en 1993. La probabilidad de que cada conglomerado resultante represente el pastizal mixto o el áspero se calculó en base a la asignación proporcional de 428 parcelas de muestra. Los 2 mapas de probabilidades resultantes se combinaron en una sola imagen seleccionando la clase de imagen que contenía la probabilidad máxima posterior y asignando esa clase a la salida de pixel. La certeza del mapa de vegetación se evaluó mediante un reconocimiento terrestre con un juego independiente de 85 parcelas. Esto produjo una clasificación correcta en 84.4% de las parcelas de pastizal ásperos y en 76.9% de las parcelas de pastizal mixto. El pastizal mixto cubría solo el 31% del área, pero sostenía el 66.1% de la carga animal de fauna. El agua esta ampliamente distribuida y no es un factor limitante en la selección del hábitat. Basado en un análisis de Sistemas de Información geográfica (GIS) las diferencias cualitativas entre los pastizales mixtos y los ásperos anulan las diferencias cuantitativas en la disponibilidad de forraje, la historia de fuego y el disturbio humano en influenciar la distribución de los herbívoros. La integración de datos de campo e imagen de satélite en un sistema de GIS ofrece una herramienta poderosa para el objetivo de cuantificación y mapeo del hábitat disponible.

vores (Stalmans et al. 1999). This diverse vegetation can be generalised into 2 herbivore habitats, 'sourveld' and 'mixed veld' (Stalmans et al. 1999) based on forage quality characteristics.

Within the South African ecological context, 'sourveld' refers to range in which the forage plants become unacceptable and less nutritious to large herbivores on reaching maturity. Sourveld consequently is utilised only during spring and summer (Trollope et al. 1990). 'Sweetveld' in contrast retains its acceptability and nutritive value after maturity and is used throughout most of the year. In essence, herbivores feeding on sourveld lose body weight during the dry winter season due to a decline in forage quality below the level for efficient digestion, whereas in sweetveld, for-

Funding and logistical support were provided by the Mpumalanga Parks Board. Authors wish to acknowledge the support by Wilna Heymans who collected the independent data set used for the validation of the satellite map. Magda Rall, Annelize Steyn and other management staff assisted with the collection of vegetation, fire and game monitoring data. Dr Y. Bai and 2 anonymous reviewers provided useful comments and recommendations.

Manuscript accepted 12 Apr. 2001.

age quality never declines such that animals cannot maintain growth (Ellery et al. 1995). 'Mixed veld' is intermediate between sourveld and sweetveld. Prior to this study, little quantitative information existed on the spatial extent and distribution of sour and mixed range across the reserve. This quantification is necessary in order to determine appropriate stocking levels of game. The range of game species present, their numbers and their distribution determine the potential for tourism development which is required in the face of the great socio-economic needs experienced by rural communities bordering the SGR (Heinsohn et al. 1992).

Remote sensing is a useful tool for inventory and evaluation of wildlife habitat because of its multispectral and multi-temporal capabilities at different spatial scales (Quattrochi and Pelletier 1991). Processed remotely sensed data may be used as input to a Geographic Information System (GIS) and together with ancillary data be used for environmental modelling and analysis (Wilkinson 1996). Wildlife habitat maps derived from remote sensing need to be evaluated for accuracy and ecological relevancy before they are used for management purposes. Accuracy assessment relies on independent reference data, not used during the process of classification (Fairbanks and Thompson 1996).

The aim of the study was to evaluate the ecological relevance of habitat maps derived from multispectral remote sensing by first comparing the spatial distribution of the spectrally-derived habitats to the distribution obtained through field sampling and by secondly evaluating the actual herbivore distribution in relation to the spectrally-identified habitats.

Materials and Methods

Study Area

The Songimvelo Game Reserve (SGR) is located in the southeastern part of Mpumalanga on the South African-Swaziland border (25°45' to 26°06'S and 30°46' to 31°16'E) and is approximately 48,000 ha in extent (Fig. 1). The terrain is generally rugged with elevation ranging from 600 m above sea level along the Komati River in the south to over 1,900 m in the north and northeast. The geology is very diverse and ranges from alluvium and mafic and ultramafic lavas in the Komati Valley, to felsic lavas, conglomerates, shales, sandstones and quartzites at higher elevations.

Rainfall is concentrated between

Fig. 1. Locality map of the Songimvelo Game Reserve in southern Africa.

November and March, and varies from less than 800 mm per year in the south-west to over 1,400 mm in the north-east (Gamble 1988). Mean minimum monthly temperatures are 5.4°C and 8°C in July and mean maximum temperatures are 22°C and 34°C in January for the highland and lowland areas respectively (Stalmans et al. 1999). The generally acid and arenaceous geological substrates in the north-east, combined with a higher rainfall, result in leached acidic soils. In contrast, relatively nutrient-rich soils are found in the Komati Valley.

The SGR is characterised by a long and diverse history of small-scale cropping and livestock in the more fertile lowlands (Van der Merwe and Retief 1995). Since its inception in 1986, 20 species of large herbivores have been re-introduced within the 31,700 ha game-fenced portion of the reserve.

The vegetation of the higher-lying regions of the SGR belongs to the grassland biome. The lower-lying Komati Valley falls within the savanna biome (Rutherford and Westfall 1986). Three of Acocks (1975) vegetation types occur in the SGR. These are veld types 8 (North Eastern Mountain Sourveld) and 63 (Piet Retief Sourveld) which correspond to the North-eastern Mountain Grassland of the grassland biome as defined by Low and Rebelo (1996). Veld type 9 (Lowveld Sour Bushveld) corresponds to the Sour Lowveld Bushveld of the savanna biome. The forest biome is represented in the SGR by numerous isolated patches of for-

est, mostly at higher elevation and along drainage lines (Stalmans et al. 1999).

Conceptual approach

Three basic steps were followed. First, a classification into habitats was produced based on spectral differences in the vegetation. Field data were used to assign classification results into habitats with distinct differences in forage quality. Secondly, the accuracy of the resultant habitat map was assessed using a set of independent field data. Lastly, the ecological relevance of the map produced was evaluated using actual herbivore distribution patterns.

Vegetation field data

Reference data on the spatial spread of the sour and mixed range were collected for use in developing the wildlife habitat map from remote sensing imagery. A total of 428 sample plots of 30 X 30 m were subjectively located across the Songimvelo Game Reserve (SGR) during the period 1993–1995. Cover and height classes for individual woody and grass species within the 30 X 30 m plots were estimated using the semi-quantitative measures of the Braun-Blanquet approach (Mueller-Dombois and Ellenberg 1974) and structural measurements of Edwards (1983). Records of environmental data included elevation (by means of an altimeter (± 20 m) and the 1:50 000 topocadastral maps), geology (according to 1:250 000 geological survey maps (Geological Survey 1986) and locally at a finer scale through personal observations), landscape position (Land

Type Survey Staff 1989), aspect (whether predominantly N, E, S or W), slope steepness (class estimate), soil texture (using the sausage method (National Working Group for Vegetation Ecology 1986)) and rockiness (estimated as a percentage of the ground cover). The sampling adequately covered the different combinations of environmental factors (Stalmans et al. 1999), in particular elevation and geology which are known to be major determinants of plant community composition and distribution in this montane setting (Deall and Theron 1990). Grazing pressure within each plot was rated according to 3 broad subjective classes: none to light, medium, and heavy.

Ordination and classification of the data set resulted in the delimitation of 18 plant communities identifiable in the field (Stalmans et al. 1999). These 18 communities were combined into 3 main vegetation units: mixed communities, forest and thicket communities, and sour communities. Mixed and sour communities are distinguished using criteria developed by Ellery et al. (1995) regarding the proportion of 'sour' (unpalatable), 'sweet' (palatable) and 'mixed' species. Forest and thicket communities are dominated by woody species with a closed canopy cover.

Manipulation of satellite imagery

Landsat Thematic Mapper quarter scene WRS 168-3-078, acquired on 8 January 1993, was used. The image was radiometrically corrected. Geometric corrections were applied in both the along-scan and across-scan directions using ground control points. Pixel size is 30 X 30 m. Bands 3, 4, and 5 were selected. Bands 3 (red) and 4 (near infrared) have been shown to give a good measure of vegetation density, especially as it relates to leaf area, whereas band 5 (middle infrared) provides a good measure of canopy closure (Rey-Benayas and Pope 1995). This combination of bands has been used successfully in rangeland (Mackay and Zietsman 1996) and forest studies (Fuller et al. 1998).

A hybrid approach was adopted for the classification of the LANDSAT data. Unsupervised classification allocates each pixel to a certain class based on its spectral characteristics only. In contrast, supervised classification of the imagery requires pre-defined training sites to assign each pixel of the image to a certain class. The drawback to the supervised approach is that it is often difficult to locate and define homogenous training sites for all plant communities of interest. The considerable

pixel to pixel variation generally results in many pixels being misclassified (Tueller 1989). Unsupervised classification approaches have worked better in rangelands. The drawback of the unsupervised classification is that subjectivity in the interpretation of the resulting classes is unavoidable.

In this instance, no *a priori* assumptions were made regarding the information content of the LANDSAT image or of the classification clusters. Instead, the emphasis was on the interpretation of the classification results and the improvement of the classification by incorporating ancillary data (Hutchinson 1982, Medler and Yool 1997). An adequate spatial spread of the ground data was considered key to a successful interpretation of the different classification clusters, in particular where it is known that clusters could be the result of differential spectral response linked to slope and aspect characteristics (Quattrochi and Pelletier 1991). The available sample of 428 vegetation plots adequately covered the different elevation, aspect and geology combinations on the Songimvelo Game Reserve (SGR) (Stalmans et al. 1999) and thus enabled the combination of 2 or more different clusters (based on spectral characteristics) into a single vegetation unit (based on field data).

As a first step, the composite image of the 3 bands was subjected to an unsupervised classification using a histogram peak technique of cluster analysis in the IDRISI Geographical Information System (Eastman 1992). Based on its spectral characteristics, each pixel is assigned to a particular cluster or class. This resulted in 46 classes or clusters, each consisting of multiple individual polygons. Twenty-one clusters each covered less than 100 ha (or 0.2% of the SGR) scattered across the area. In view of the very small spatial extent of these scattered fragments, these 21 clusters were discarded and the original composite image was again classified with a maximum limit of 25 clusters to ensure that each remaining cluster covered at least 100 ha. In terms of managing the reserve, very small areas cannot realistically be managed differently than the surrounding matrix.

The available field data were used in an objective manner to determine the probability of the classification results representing certain communities. The 428 sample plots were each assigned to one of the 3 vegetation units, namely sour grasslands, mixed grasslands, or forests and thickets. Each point was buffered to cover a window of 3 rows X 3 columns of pixels from the LANDSAT image. This trans-

lates into a physical dimension of 90 X 90 m which takes into account inaccuracies inherent to the Global Positioning System (henceforth GPS) positioning (see Fuller et al. 1998 for a similar approach). Habitat type assignments for pixels in the cluster image were compared to that of the buffered sample points. A crosstabulation of the cluster image with the buffered image was made. The resulting matrix was used to assign probabilities for each cluster to represent respectively mixed or sour vegetation based on the percentage mixed and sour sample plots occurring in each cluster. These probabilities were used to produce 2 probability images; one for the mixed and one for the sour vegetation unit. These 2 probability images were combined into a single image by selecting the class image that contains the maximum posterior probability, and assigning that class to the output pixel.

Only 43 of the vegetation plots (10% of the total sample) represented forests and thickets. Their GPS position was likely to be less accurate because of the thick canopy cover, which when combined with the generally narrow linear distribution of these formations, renders the above approach less meaningful. An alternative approach was therefore followed. Six known and clearly identifiable forest patches were digitized from 1:10,000 scale orthophotos. The classification clusters corresponding best to these patches were identified. All other clusters with the same identity were consolidated across the whole image into a forest/thicket unit. The forest/thicket unit was superimposed on the mixed/sour habitat map.

The habitat map obtained was further refined by assigning any mixed vegetation pixels occurring above 1,300 m elevation to the sour range. Based on their composition, none of the 112 sample plots situated above 1,300 m elevation represented mixed vegetation. Secondly, a median 3 X 3 pixel filter was applied to remove random noise and unwanted speckle (Fuller et al. 1998). Lastly, the known extent of the non-native pine (*Pinus* spp.) plantations occurring within the boundaries of the SGR was superimposed on the map resulting in a final map with 4 habitat units.

Ground-truthing of the satellite-derived map

Three measurements of error were used to assess the accuracy of the habitat map derived from the satellite imagery. Errors of omission occur when the satellite map fails to recognise the actual habitat class of an independent sample plot. Errors of

commission result when the satellite map misclassifies the sampling plot from the independent data set. A Kappa Index of Agreement (KIA), both for all classes and on a per category basis, constitutes the third measure of error. The KIA ranges from 0.0 indicating no correlation to 1.0 indicating perfect correlation (Eastman 1992).

A data set collected during 1989 prior to, and independently from the present study was used to assess the accuracy of the habitat map. Grasslayer composition of 85 plots of 25 X 100 m, subjectively located across the Songimvelo Game Reserve (SGR), was assessed by means of 100 points per plot using the nearest-rooted plant criterion (Mentis 1984). These plots were assigned to the mixed and sour vegetation units based on species composition. A crosstabulation was performed between the assigned plots and the satellite-derived image. Habitat categories from the plots were compared with those of the satellite map. A tabulation was kept of the number of cells in each category combination. No tabulations were made for cells marked with a 0 on the ground-truth map. Omission, commission and KIA were calculated from the crosstabulation results.

Ecological significance of the satellite-derived map

Overall stocking densities for the Songimvelo Game Reserve (SGR) (1815 kg km⁻² during 1994 and 3288 kg km⁻² during 1999) fall well below the estimated grazing capacity for this part of the country (5,000 kg km⁻² or higher) (Barnes 1990). Given these overall low stocking densities on the reserve and large contiguous areas of different habitats being available to game, the spatial distribution of large herbivores should reflect the spatial distribution of mixed and sour grasslands. This would particularly apply during winter when forage resources are most limiting both in terms of quality and quantity (Voeten and Prins 1999).

Two helicopter game counts were conducted during the winter months of August 1994 and September 1999 respectively as herbivores were more easily visible due to the lower leaf cover (as the vast majority of savanna trees are deciduous). Counts were conducted by means of a Bell Jetranger helicopter seating a pilot, navigator and 2 observers in the back recording game within 300 m wide parallel strips. The helicopter was maintained at a constant height of 53 m above the ground. Airspeed was maintained at around 96 km hour⁻¹ (60 knots). Each count was conducted

within a period of 3 days. Extensive field experience from the pilot and observers indicates that no large-scale movement of game occurs within such a limited time period. Breaks during the counting were made along natural boundaries across which little or no short-term movement of game is expected. Double-counting of individual animals or herds is avoided by herding animals from the counting strip deeper into strips already counted. A GPS co-ordinate was recorded for each game sighting. Viljoen and Retief (1994) found the measured errors between actual and recorded localities using GPS technology for game counts to be well within the requirements for ecological work of this kind. Each GPS point was compared with the habitat map to establish whether the sighting fell within mixed or sour range. A value in kg km⁻² was calculated for each point based on the species and number of animals involved in each sighting.

The underlying assumption in distinguishing between mixed and sour habitats is that nutritional value represents the overriding factor determining herbivore distribution. Three other important factors however could influence herbivore distribution across the landscape. These are water availability, feed availability and fire history. Another complicating factor in the SGR is the presence of a number of human settlements within the game-fenced area. It is critical to ascertain that the assessment of the value of the mixed and sour habitats delimited on the satellite map is not biased through 1 of these factors.

Distance to the nearest watering point is known to be important in determining herbivore use intensity (Thrash et al. 1995). With the GIS a distance analysis was performed from all known perennial streams and rivers in order to establish whether any parts of the SGR might be unavailable to water-dependent species such as impala (*Aepyceros melampus* Lichtenstein) (Young 1970).

A crude index of grass quantity available in the sour and mixed habitats was calculated as follows during the survey of the 428 vegetation plots. The class value for the grass cover estimate (1 = sparse, 2 = open, or 3 = closed) (structural terminology and categories follow Edwards (1983)) in each sample plot was multiplied by the square root of the midpoint of the 3 following height classes (1 = < 0.5 m, 2 = 0.5 to 1.0 m, 3 = 1.0 to 2.0 m). Trollope and Potgieter (1986) used a similar approach to measuring standing phytomass.

Many African ungulates are attracted to recently burnt grassland (Wilsey 1996). The extent of areas burnt during the 12 months preceding the 1994 and 1999 winter helicopter counts was determined for the mixed and sour habitats. Fires have been mapped since 1987 in the Songimvelo Game Reserve (SGR) and the data have been consolidated in the GIS. A crosstabulation of burnt and unburnt areas was performed with the GPS positions of the game to assess relative and absolute stocking densities.

Illegal hunting and snaring are not considered to have a major effect around the settlements within the SGR. However, competition from livestock, habitat modification through cultivation and exclusion through protective fencing around croplands could negatively influence wild herbivores. A distance analysis was performed from the GPS positions of the settlements. An overlay of the buffered image was made with the habitat map. The resulting distance-habitat map was crosstabulated with the GPS positions of the game.

Throughout the assessment of the ecological significance of the satellite-derived map, a Chi-square goodness-of-fit analysis (Zar 1984) was used to evaluate differences between the observed crosstabulation results and the expected patterns of occurrence based on proportional habitat availability.

Results and Discussion

Habitat units

Twenty-five out of the 428 sample plots represented wetland and non-native communities dominated by planted pine or closed-canopy stands of self-seeded Black wattle (*Acacia mearnsii* De Wild.) and were not considered further. Of the remainder, 43 plots represented forests or thickets. No single plot was classified as sweet range requiring more than 30% of the total cover to consist of 'sweet' species and less than 20% cover by 'sour' species (Ellery et al. 1995). A total of 224 plots were classified as sour range with 'sour' species contributing more than 60% of the cover of the plot and 'sweet' species contributing less than 20% cover. The remaining 136 plots were by definition mixed range by not conforming to either the sweet or sour criteria. The grazing intensities recorded in the field indicate a dramatic and significant difference in usage of the mixed and sour vegetation units ($\chi^2 = 101.64$, $\chi^2_{0.05,1} = 3.481$, $P < 0.001$).

Fig. 2. Satellite-derived range map of the Songimvelo Game Reserve. Note mixed range in the south-western lower-lying Komati River valley and sour range in the north-eastern high mountains.

Whereas 57.3% of the mixed plots were assessed as being medium to heavily grazed, only 7.6% of the sour plots were similarly rated. This indicates that the split into sour and mixed range based on floristic composition criteria translates into an ecologically meaningful difference to herbivores.

Habitat map

Crosstabulation of the 25 classification clusters with the vegetation plots generally resulted in a high individual probability for each of the clusters to represent either sour or mixed range. More than half of the surface area of the Songimvelo Game Reserve (SGR) has a cluster probability above 80%. For 92.2% of the total area, the cluster probability is above 65%. Only 2 clusters have less than a 65% probability factor of representing only sour or only mixed vegetation. These 2 clusters only make up 7.8% of the total area. Their spatial distribution is of interest. The 2 clusters are spread in a horseshoe marking the transition from the low-lying Komati Valley to the higher mountains to the north and east (Fig. 2). The *Themeda triandra* Forssk. (Rooigras)–*Cymbopogon* spp. short Grassland community which is a transitional community intermediate between typical mixed woodland communities and sour grassland communities was identified for this zone (Stalmans et al. 1999). The low probability scores for these clusters probably reflect the heterogeneous and intermediate nature of the vegetation in this particular area.

The final habitat map clearly depicts the

mainly mixed vegetation in the low-lying Komati Valley and Msoi Valley (Fig. 2). The higher-lying mountains to the north and east are mainly covered by sour vegetation. The forest and thickets also occur mostly at higher elevation as small pockets and linear formations in drainage lines. Pine plantations are located in the north-east. The mixed vegetation is the smallest of the 3 main units covering 8,504 ha or 17.3% of the SGR, followed by the thickets and forests (10,119 ha or 20.6%). The sour habitat occupies 29,684 ha which represent 60.4% of the game reserve.

Ground-truthing of satellite-derived map

The habitat map conforms in broad terms to the understanding of the vegetation as obtained through ordination and classification of the 428 sample plots (Stalmans et al. 1999). Mixed communities occur mostly in the Komati Valley and sour communities at higher elevation.

The independent sample of 85 plots used for the validation consisted of 52 mixed and 33 sour plots. The unsupervised

procedure correctly classified 76.9% of the mixed and 84.8% of the sour sample plots. The Kappa coefficient (KIA) was 0.59. The overall percentage correct classification was 80% (obtained by dividing the sum of the diagonal entries in the error matrix by the total number of sample plots) (Table 1).

A good correspondence between the 6 digitized forest patches and the satellite-derived forest patches was obtained. The overall correct classification for the 6 patches was 78.4%. The KIA was 0.74. The satellite map overestimated the actual forest cover by 13.6%. The forest/thicket coverage was simply used to identify those parts of the SGR not dominated by grasslands which were the focus of the present study.

Classification accuracy reported by other researchers mapping landcover (Brondizio et al. 1996, Fuller et al. 1998, Hodgson et al. 1988, Lunetta and Balogh 1999), forest cover (Congalton et al. 1993) and grassland cover (Lauver and Whistler 1993) ranged from 69 to 94%. The accuracy figures of 78 to 80% achieved for the mixed/sour vegetation and forest patches on the SGR are thus considered to be satisfactory for an operational product of this kind.

Ecological significance of the habitat map

During 1994 a total of 22,800 ha was covered by the helicopter survey whereas during 1999 the whole game-fenced area of 31,700 ha was flown. A total of 705 GPS coordinates of wild herbivores were recorded for the 1994 count and 865 for the 1999 count. The associated animal biomass per GPS locality ranges from 10 kg (1 klipspringer (*Oreotragus oreotragus* Zimmermann)) to 16,560 kg (a herd of 36 eland (*Taurotragus oryx* Pallas)). Elephant (*Loxodonta africana* Blumenbach) constituted 11.4% of the total metabolic mass of wild herbivores present on the Songimvelo Game Reserve (SGR) in 1999. They generally move around in 1 or 2 herds and large daily movements across the land-

Table 1 Error matrix resulting from the crosstabulation of the 85 independent sample plots with the habitat map of the Songimvelo Game Reserve obtained through unsupervised classification of LANDSAT Thematic Mapper quarter scene WRS 168-3-078.

Independent data set	Satellite-derived habitat map			
	Mixed range	Sour range	Row total	Commission error (%)
Mixed range	40	12	52	23.1
Sour range	5	28	33	15.2
Column total	45	40	85	
Omission error (%)	11.1	30.0		

scape have been observed in the field. Elephant were not considered further for this study as a single GPS observation could dramatically bias the evaluation of habitat selection.

The results from the crosstabulation clearly indicate the proportionally greater selection of the mixed compared to the sour vegetation (Fig. 3). Although only representing 31.0% (range 26.4 to 35.7%) of the available habitat, the mixed vegetation holds 66.1% (range 60.4 to 71.9%) of the game. In contrast, 54% (range 50.4 to 57.7%) of the surveyed area consisted of sour vegetation that held only 26.5% (range 22.9 to 30.1%) of the game. This differential pattern in stocking rate according to range type remained similar for the 1994 and 1999 surveys. The forests and thickets represented 14.9% (range 13.9 to 15.8%) of the available habitat but contributed only 7.3% (range 5.2 to 9.5%) to the game stocking. The possibility exists that game numbers were undercounted for forests and thickets because of the difficulty of observing animals under the canopy. Field observations however suggest that few herbivores are found in this vegetation formation and particularly not in the dense and moist forests.

In terms of absolute values, the mixed portion of the landscape had an average stocking density 4 times higher than the sour portion (Table 2). This difference reflects the general stocking densities of 10^3 to 10^4 kg km⁻² for medium and high

Table 2 Stocking densities during winter in the different habitats of the Songimvelo Game Reserve.

Habitat	Stocking density		
	1994	1999	Weighted mean ¹
	----- (kg km ⁻²) -----		
Mixed	3415	2989	3198
Sour	771	684	717
Forest/thicket	629	784	724
Weighted mean ¹	1694	1309	1470

¹ weighted to take into account different extent of habitat and differences in area surveyed during 1994 and 1999 respectively.

soil nutrient status dystrophic savannas with a rainfall of approximately 1,000 mm as compared to only 10^2 to 10^3 kg km⁻² for low soil nutrient status savannas reported by East (1984). As mentioned in the description of the SGR, the lower-lying Komati Valley receives a much lower rainfall and is characterised by more fertile substrates compared to the higher-

Fig. 3. Mean relative habitat availability and stocking densities in the Songimvelo Game Reserve for the 1994 and 1999 game counts. Note the proportionally greater stocking of the mixed range.

lying north-easterly parts.

Differences in stocking rates between 1994 and 1999 cannot be directly compared. They are more a consequence of the differences in flight areas covered than a biologically significant change in animal numbers. The total recorded wild herbivore biomass, excluding elephant, was 391,367 kg in 1994 and 412,471 kg in 1999. The 1999 figure is 5.4% higher but is spread across an area 30% larger than 1994 resulting in an apparent drop of 23% in stocking rates (Table 2). During the intervening years, game numbers were controlled and a total of 272,478 kg was removed, mostly through live capture and relocation to other conservation areas. The higher total biomass figure recorded during 1999 therefore reflects the larger area surveyed and not an increase in wildlife numbers.

The overall stocking rate for the Songimvelo Game Reserve (SGR) is low compared to the agricultural guidelines for this part of the country (Barnes 1990). In view of the overall conservative stocking rates one can assume a fair degree of choice being available to the herbivores regarding area selection. The other factors that could influence herbivore distribution are the availability of water, availability of forage, fire history and human disturbance. No artificial waterpoints are provided in the SGR. The perennial Komati River bisects the game-fenced area.

Numerous other perennial rivers and streams occur. Fully 98.9% of the SGR is located within 2 km from perennial water. No part is situated further than 3 km from perennial water. The average radius of range utilisation around watering points in winter in the Kruger National Park has been documented as respectively 3.5 km for impala, 11.25 km for zebra (*Equus burchellii* Gray) and 11.5 km for blue wildebeest (*Connochaetus taurinus* Burchell) (Young 1970). Water is therefore not considered a major constraint to, or determinant of herbivore distribution in the SGR.

The crude index of grass quantity based on the 3 cover and 3 height classes has a possible range from 1 to 5.2. Based on the actual recorded values a mean of 2.9 (SD 1.02) was obtained for the mixed habitat (n = 136 sample plots) and 3.3 (SD 0.83) for the sour habitat (n = 224 plots). A larger quantity of grass is thus generally available in the sour habitat. This difference is however not significant ($\chi^2 = 0.03$, $\chi^2_{0.05,1} = 3.481$, $0.75 < P < 0.90$). The greater standard deviation for the mixed range reflects the figure of 57.3% of the plots assessed as being medium to heavily grazed, compared to only 7.6% of the sour plots being grazed. The mixed range consists of short-ly grazed areas as well as little grazed areas, whereas the sour range is generally uniformly non-utilised. In the field, the availability of grass, particularly in winter, is clearly more limited on the mixed areas.

Table 3. Stocking densities during winter in the different habitats of the Songimvelo Game Reserve in relation to fire history and distance from human settlements.

		Stocking density		
		1994	1999	Weighted mean
		----- (kg km ⁻²) -----		
Habitat and fire history				
Mixed	unburnt	3537	2858	3207
	burnt	49	3979	3100
Sour				
	unburnt	882	653	736
	burnt	366	886	624
Habitat and distance from settlements				
Mixed				
	< 4 km	1758	1073	1398
	> 4 km	3896	3571	3732
Sour				
	< 4 km	424	606	536
	> 4 km	1256	790	970

Taking into account the lower stocking densities on the sour habitat, herbivore distribution is clearly not primarily governed by the absolute quantitative availability of feed.

The difference in order of magnitude of stocking density was maintained for mixed and sour habitats regardless of burning history (Table 3). Overall, mixed range in the SGR is stocked at a rate 4 to 5 times higher than sour range whether burnt or unburnt. This difference is significant ($\chi^2 = 18120.6$, $\chi^2_{0.05,1} = 3.481$, $P < 0.001$). Differences were observed between individual years. The burnt areas were stocked at a lower density during 1994 within each habitat. The inverse pattern, with higher stocking densities on burnt areas, was observed during 1999. Objective evaluation of this pattern was complicated by the relatively small extent of the burnt areas. The burnt portion covered only 279 ha (3.4%) of the total mixed habitat surveyed in 1994 and only 970 ha (11.7%) of the mixed habitat in 1999. Burnt areas covered 2451 ha (21.6%) and 2407 ha (13.4%) of the sour habitat respectively in 1994 and 1999. Chance events and daily movements of herbivores could be an important factor in the evaluation of the relatively small burnt areas. Field observations (Unpublished data, M.E. Stalmans) certainly indicate a greater use of burnt areas at a smaller spatial scale and for a limited period of time. In summary, at a large spatial scale and a temporal scale of one year, the fundamental difference in the nature of the mixed and sour habitat overrides fire history.

Some 30 human settlements occur mostly in the southern and eastern boundary

areas of the game-fenced portion of the SGR. Each settlement is occupied by a single and sometimes extended family which practices subsistence agriculture and receives remittances from family members employed outside the Songimvelo Game Reserve (SGR). Mean herd size in 1992 was 27 head of cattle (range 0 to 126) (Heinsohn et al. 1992). Cultivation mainly consists of maize. Mean area of lands cultivated by a single family was 2.9 ha (range 0.4 to 9 ha). Trees and branches are cut down for building purposes and as firewood. The maximum distance in the SGR away from settlements is between 12 and 13 km. A cut-off value of 4 km was used for the habitat evaluation as 48.5% of the SGR is less than 4 km from a settlement leaving 51.5% of the area to be further than 4 km away.

The stocking density of wild ungulates on areas less than 4 km away from settlements was less than half that of areas further away for both mixed and sour habitat for both counts (Table 3). This apparent negative effect from human settlements on game stocking density tested significant ($\chi^2 = 1653.9$, $\chi^2_{0.05,1} = 3.481$, $P < 0.001$). Nevertheless, mixed areas close to settlements are still stocked at values two to three times higher than equivalent sour areas. Furthermore, the stocking density on mixed areas close to settlements still remains higher than the stocking density on sour areas further away from settlements.

Human settlements have been documented as having a negative impact on wild herbivore densities for a distance of at least 7 km in a forest environment (Eltringham 1990) and 10 km in arid envi-

ronments (Verlinden 1997). The definite negative impact within the 4 km cut-off selected for the SGR is therefore not unexpected but it does not override the fundamental difference in habitat quality between mixed and sour range.

At the landscape scale and at temporal scales of a year or more, the broad differences in habitat quality and its spatial distribution clearly outweigh the effects of any short-term, localised management action or human disturbance. Senft et al. (1987) hypothesised that in the absence of overriding constraints, foraging behaviour by large herbivores should produce a landscape stocking rate that is a linear function of landscape productivity. The mixed range, although limited in extent, is critical to wild herbivores in the SGR.

The habitat make-up of the SGR as derived from remote sensing and as confirmed by ground data, forms the base upon which further studies can be undertaken regarding individual herbivore species preference, performance and stocking.

Conclusions

The broad habitat map, which was derived from the satellite imagery, identified mixed and sour range units differing in terms of composition and palatability. Broad herbivore distribution patterns were well correlated with the spatial distribution of these habitat units derived from remote sensing. At the landscape scale, the habitat quality in terms of grass layer composition and palatability overrides its quantitative availability and its smaller-scale fire history. Because of its ubiquitous nature, water distribution is not a significant factor in the Songimvelo Game Reserve (SGR). Although stocking densities of wild ungulates are lower close to human settlements, the overall high ratio in stocking densities between mixed and sour habitat is maintained. These findings, applying to both the 1994 and 1999 game surveys, suggest the fundamental differences in forage quality between range types persist across seasons. Anecdotal field evidence from intervening years supports this assumption.

The integration of field data and satellite imagery into a GIS system for analysis offers a powerful tool for the objective quantification and mapping of the spatial distribution of available habitat. The resulting image is ecologically relevant and of practical value to the manager and ecologist dealing with this heterogeneous system. As such this approach could be

applied to other nature reserves and to the growing number of game farms in southern Africa and elsewhere.

Literature Cited

- Acocks, J.P.H. 1975.** Veld types of South Africa. Mem. Bot. Surv. So. Afr. 40:1–128.
- Barnes, D.L. 1990.** A survey of grazed and ungrazed grasslands in the south-eastern Transvaal highveld. 1. Palatability composition and grazing capacity. J. Grassl. Soc. So. Afr. 7:217–222.
- Barnes, K.N. (ed.). 1998.** The important bird areas of southern Africa. Avian Demography Unit, BirdLife South Africa, Johannesburg, So. Afr.
- Brondizio, E., E. Moran, P. Mausel, and Y. Wu. 1996.** Land cover in the Amazon estuary: Linking of the thematic mapper with botanical and historical data. Photogramm. Eng. Remote Sens. 62:921–929.
- Congalton, R.G., K. Green, and J. Tepley. 1993.** Mapping old growth forests on National Forests and Park Lands in the Pacific Northwest from remotely sensed data. Photogramm. Eng. Remote Sens. 59:529–535.
- Deall, G.B. and G.K. Theron. 1990.** Ordinations as a tool for substantiating and interpreting floristic classifications: A case study. Bothalia 20:223–227.
- East, R. 1984.** Rainfall, soil nutrient status and biomass of large African savanna mammals. Afr. J. Ecol. 22:245–270.
- Eastman, J.R. 1992.** IDRISI. Clark University Graduate School of Geography, Worcester, Mass.
- Edwards, D. 1983.** A broad-scale structural classification of vegetation for practical purposes. Bothalia 14: 705–712.
- Ellery, W.N., R.J. Scholes, and M.C. Scholes. 1995.** The distribution of sweetveld and sourveld in South Africa's grassland biome in relation to environmental factors. Afr. J. Range For. Sci. 12:38–45.
- Eltringham, S.K. 1990.** Wildlife carrying capacities in relation to human settlement. Koedoe 33:87–97.
- Fairbanks, D.H.K. and M.W. Thompson. 1996.** Assessing land-cover map accuracy for the South African Land-Cover database. So. Afr. J. Sci. 92:465–470.
- Fuller, R.M., G.B. Groom, S. Mugisha, P. Ipuet, D. Pomeroy, A. Katende, R. Bailey, and R. Ogutu-Ohwayo. 1998.** The integration of field survey and remote sensing for biodiversity assessment: a case study in the tropical forests and wetlands of Sango Bay, Uganda. Biol. Conserv. 86:379–391.
- Gamble, F. 1988.** Climate of the Transvaal Escarpment, p. 1–4. In: A.A. Ferrar, G. Isaacs and J.R. Stacey (eds.), Environmental conservation features of the Transvaal Escarpment. Occasional Rep. 31. CSIR, Pretoria.
- Geological Survey. 1986.** Geology map 1:250,000 geological series: 2430 Barberton. Government Printer, Pretoria.
- Heinsohn, R-D., S.J. Woodburne, and S.E. Alexander. 1992.** Demographic, socio-economic and attitudinal surveys of affected communities in and around Songimvelo Game Reserve. A.C.E.R. (Africa) Tech. Rep. to Dept. Development Aid, Pretoria.
- Hodgson, M.E., J.R. Jensen, H.E. Mackey, and M.C. Coulter. 1988.** Monitoring wood stork foraging habitat using remote sensing and geographic information systems. Photogramm. Eng. Remote Sens. 54:1601–1607.
- Hutchinson, C.F. 1982.** Techniques for combining Landsat and ancillary data for digital classification improvement. Photogramm. Eng. & Remote Sens. 48:123–130.
- Land Type Survey Staff. 1989.** Land types of the map 2530 Barberton. Memoirs of the Agric. Natur. Resources of So. Afr. 13, Pretoria.
- Lauver, C.L. and J.L. Whistler. 1993.** A hierarchical classification of Landsat TM imagery to identify natural grassland areas and rare species habitat. Photogramm. Eng. Remote Sens. 59:627–634.
- Low, A.B. and A.G. Rebelo. (eds.) 1996.** Vegetation of South Africa, Lesotho and Swaziland. Dept. Environ. Affairs and Tourism, Pretoria.
- Lunetta, R.S. and M.E. Balogh. 1999.** Application of multi-temporal Landsat 5 TM imagery for wetland identification. Photogramm. Eng. Remote Sens. 65:1303–1310.
- Mackay, C.H. and H.L. Zietsman. 1996.** Assessing and monitoring rangeland condition in extensive pastoral regions using satellite remote sensing and GIS techniques: An application to the Ceres Karoo region of South Africa. Afr. J. Range For. Sci. 13:100–112.
- Medler, M.J. and S.R. Yool. 1997.** Improving thematic mapper based classification of wildfire induced vegetation mortality. Geocarto Int. 12:49–58.
- Mentis, M.T. 1984.** Monitoring in South African grasslands. South African Nat. Sci. Programmes Rep. 91, CSIR, Pretoria.
- Mueller-Dombois, D. and H. Ellenberg. 1974.** Aims and methods of vegetation ecology. John Wiley & Sons, New York.
- National working group for vegetation ecology. 1986.** Soil classification according to the binomial classification system. Tech. Commun. 3, Pretoria.
- Quattrochi, D.A. and R.E. Pelletier. 1991.** Remote sensing for analysis of landscapes: An introduction. p. 52–76. In: M.G. Turner and R.H. Gardner (eds.), Quantitative methods in landscape ecology. Springer-Verlag, New York.
- Rey-Benayas, J.M. and K.O. Pope. 1995.** Landscape ecology and diversity patterns in the seasonal tropics from Landsat TM imagery. Ecol. Appl. 5: 386–394.
- Rutherford, M.C., and R.H. Westfall. 1986.** Biomes of southern Africa - An objective categorisation. Mem. Bot. Surv. So. Afr. 54:1–98.
- Senft, R.L., M.B. Coughenour, D.W. Bailey, L.R. Rittenhouse, O.E. Sala, and D.M. Swift. 1987.** Large herbivore foraging and ecological hierarchies. BioSci. 37:789–799.
- Stalmans, M., E.R. Robinson, and K. Balkwill. 1999.** Ordination and classification of vegetation of Songimvelo Game Reserve in the Barberton Mountainland, South Africa as a basis for the assessment of wildlife habitat distribution and quality. Bothalia 29:305–325.
- Thrash, I., G.K. Theron, and J. du P. Bothma. 1995.** Dry season herbivore densities around drinking troughs in the Kruger National Park. J. Arid Environ. 29:213–219.
- Trollope, W.S.W. and A.L.F. Potgieter. 1986.** Estimating grass fuel loads with a disc pasture meter in the Kruger National Park. J. Grassl. Soc. So. Afr. 3:148–152.
- Trollope, W.S.W., L.A. Trollope, and O.J.H. Bosch. 1990.** Veld and pasture management terminology in southern Africa. J. Grassl. Soc. So. Afr. 7:52–61.
- Tueller, P.T. 1989.** Remote sensing technology for rangeland management applications. J. Range Manage. 42:442–453.
- Van der Merwe, P.D.R. and E.F. Retief. 1995.** The Songimvelo Game Reserve inhabitants: individual data and background information. Tech. Rep. Dept. of Constitutional Development, Pretoria, So. Afr.
- Verlinden, A. 1997.** Human settlements and wildlife distribution in the southern Kalahari of Botswana. Biol. Conserv. 82:129–136.
- Viljoen, P.C. and P.F. Retief. 1994.** The use of the Global Positioning System for real-time data collecting during aerial surveys in the Kruger National Park. Koedoe 37:149–154.
- Voeten, M.M. and H.H.T. Prins. 1999.** Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania. Oecologia 120:287–294.
- Wilkinson, G.G. 1996.** A review of current issues in the integration of GIS and remote sensing. Int. J. Geographical Information Systems 10:85–101.
- Wilsey, B.J. 1996.** Variation in use of green flushes following burns among African ungulate species: the importance of body size. Afr. J. Ecol. 34:32–38.
- Young, E. 1970.** Water as faktor in die ekologie van wild in die Nasionale Krugerwildtuin. Ph.D. Thesis, Univ. Pretoria, So. Afr.
- Zar, J.H. 1984.** Biostatistical analysis. Prentice-Hall, N.J.

Elk management strategies and profitability of beef cattle ranches

WENDY L. F. TORSTENSON, MICHAEL W. TESS, AND JAMES E. KNIGHT

Authors are Research Associate, Professor, and Wildlife Extension Specialist, Department of Animal and Range Sciences, Montana State University, Bozeman, Mont. 59717-2900.

Abstract

Computer simulation was used to determine the effects of wild elk (*Cervus elaphus*) on available forage, cattle herd size, and ranch gross margin in southwestern Montana beef cow-calf production systems. Data collected from 5 southwestern Montana ranches were used to develop input parameters for bio-economic models of elk forage harvest and beef production. Input parameters described ranch resources, animal inventories, and animal management. Cattle herd size ranged from 241 to 1147 head. Elk numbers varied by season within ranch and ranged from 49 to 421 head. Ranches were simulated as currently managed with elk present and with 10, 20, 30, and 100% of the elk removed. Simulated management scenarios were replicated 10 times. Data from each ranch were analyzed by one-way analysis of variance. Cattle herd size, gross margin, and available forage significantly ($P < 0.05$) increased when all elk were removed; however, the magnitude of these effects differed among ranches. Removal of all elk permitted cattle herd size to increase from 7 to 32% across ranches. Annual costs of elk on the 5 ranches (i.e., increase in gross margin from elk removal) ranged from \$5,949 to \$21,152. On an AUM basis, elk costs ranged from \$8.55 to \$14.51. Three management alternatives were evaluated for their potential to recover elk costs: Montana's Block Management Program, coordinated exchange of forage use, and leasing of hunting access. For each ranch, at least one of these management strategies could recover all estimated costs of providing elk habitat. Elk can significantly reduce profits for cow-calf ranches in southwestern Montana. Elk impacts on beef enterprise profits are closely associated with efficiency of resource use by cattle—i.e., ranches with lower unit costs of production lose more gross margin by providing forage for elk compared to ranches with higher production costs.

Key Words: range economics

Beef cattle and elk (*Cervus elaphus*) are important parts of the economy and heritage of the Rocky Mountain West. As native wild ungulates, elk are important components of healthy ecosystems. Elk and cattle use similar habitats and prefer similar diets for much of the year. Because private lands, primarily livestock ranches, provide an important part of annual elk habitat, cattle-elk interactions are important to public resource managers and live-

Resumen

Simulación por computadora fue usada para determinar los efectos del alce silvestre (*Cervus elaphus*) en forraje disponible, tamaño del hato de ganado, y margen bruto del rancho en sistemas de producción vaca- becerro en el suroeste de Montana. Los datos recolectados de 5 ranchos del suroeste de Montana fueron usados para desarrollar parámetros de entrada para modelos bio-económicos del consumo de forraje del alce y la producción de ganado de carne. Los parámetros de entrada describieron los recursos del rancho, inventario y manejo de animales. El tamaño del hato de ganado varió de 241 a 1147 cabezas. El número de alces varió por temporada en el rancho y fluctuó entre 49 a 421 cabezas. Los ranchos fueron simulados tanto como si el alce estuviera presente como si este hubiera sido retirado de los mismos. Escenarios de administración simulados fueron repetidos 10 veces. Los datos fueron analizados por procedimientos de mínimos cuadrados, contabilizando los efectos del alce. El tamaño del hato de ganado, el margen bruto, y el forraje disponible incrementó significativamente ($P < 0.05$) cuando los alces fueron retirados; aunque la magnitud de estos efectos fue diferente entre ranchos. El retirar todos los alces permitió que el tamaño del hato de ganado se incrementara de 7 a 32% entre los diferentes ranchos. Los costos anuales del alce en los 5 ranchos (e.g., incremento en el margen bruto por el retiro del alce) variaron de US\$ 5,949 a US\$ 21,152. Sobre la base de unidades animal por mes (UAM), los costos del alce variaron de US\$ 8.55 a US\$ 14.51. Tres alternativas de manejo fueron evaluadas por su potencial para recuperar los costos del alce: programa de administración por bloque de Montana, intercambio coordinado de uso de forraje, y renta por acceso a la caza del alce. Para cada rancho, al menos una de estas estrategias podría recuperar todos los costos estimados de proveer un hábitat para el alce. El alce puede reducir significativamente las ganancias de ranchos vaca- becerro en el suroeste de Montana. Los efectos del alce en empresas de ganado de carne están asociados con la eficiencia del uso de los recursos por el ganado (e.g., ranchos con bajos costos unitarios de producción pierden mas margen bruto al proveer forraje para el alce, comparados con ranchos con altos costos de producción).

stock producers (Adams 1982, Skovlin 1982, Alt et al. 1992, Henderson and O'Herrin 1992).

Interactions between cattle and elk sharing habitats are complex and determined by many factors (Smith 1961, Vavra et al. 1989). These factors include similarity of feeding strategies, and spatial, temporal and dietary overlap (Mackie 1970; Edge and Marcum 1990, Vavra 1992, Sheehy and Vavra 1996). For competi-

Research was funded in part by USDA-NRICGP.
Journal Series No. 2001-39, Montana Agricultural Experiment Station.
Manuscript accepted 20 Jul. 01.

tion for forage to occur, both cattle and elk must be consuming the same forage species in the same area and the forage species must be in short supply (Murie 1951, Gordan 1968, Wagner 1969, Holechek 1980, Vavra et al 1989, Vavra 1992, Edge and Marcum 1990).

Given the goals of environmental and economic sustainability, when elk and cattle share the same habitats, numbers of both species may need to be reduced in order to prevent damage to the range resource. Assuming cattle prices are above breakeven prices and other sources of income are held constant, a reduction in cattle numbers will reduce ranch profit. For beef producers on private land, most strategies to preserve ranch income involve minimizing competition between elk and cattle and (or) deriving supplemental income from elk. The relative economic benefits of these alternatives have not been studied.

The objectives of our research were to: 1) evaluate the effects of elk populations on profitability of beef cattle enterprises, and 2) compare alternative elk/cattle management strategies for their effects on ranch profitability.

Materials and Methods

Five ranches located in southwestern Montana cooperated in the study. Livestock, wildlife, and management data collected from each ranch were used to develop input parameters for 2 computer simulation models. The first model predicted forage harvest by elk based on number, age, sex, reproduction and season of use. The second model simulated cattle performance and profit for the ranch.

Ranch and Cattle Data

Five ranches were selected as representatives of southwestern Montana. Criteria for selection were that the ranch was a beef cow-calf operation with: a) private land representing a large portion of the resource base, b) revenues from the sale of cattle constituting its primary source of income, and c) migratory and (or) resident elk using the ranch for at least part of the year. Advice on suitable ranches was received from Montana Fish, Wildlife & Parks (FWP) biologists and Montana State University Extension personnel.

Inventories and descriptions of forage resources and cattle grazing strategies were obtained from each ranch. Cattle data included: herd size, genetic composition, replacement strategies, breeding seasons,

health management, nutritional management, marketing practices, and performance measures for reproductive rate, mortality, and growth. Feeding management data included amounts and type of forage, dates when cattle were moved on and off range, along with how each management group was treated (Table 1).

Elk data collection

Estimates of the number of elk on each ranch were obtained from FWP biologists and ranch managers. Yearly flight data (FWP) for elk numbers were used to categorize elk herds into bulls, cows, and calves. Most flights occurred after the hunting season and near the end of winter after a large portion of elk mortality had occurred. Calves were assumed to be 50% male. Taber et al. (1982) constructed static life tables (defined by Begon et al. 1990) based on field studies of Rocky Mountain elk. We adapted their reproductive percentages to determine age distributions within sex. Amount of time and type of activity elk spent on the ranches was determined from interviews with FWP biologists and ranch managers.

Dietary overlap (percentage of elk diet, by season, that would be potentially consumed by cattle if available) was determined from literature reports based on vegetation types that we judged to be relevant to the habitats found on the 5 ranches (Murie 1951, Stevens 1966, Gordon 1968, Mackie 1970, Nelson 1982, Peek 1982, Kasworm et al. 1984). Similarly, spatial overlap (percentage of habitat used by elk, by season, that was used by cattle sometime during the year) was estimated based on literature reports (Smith 1961, Mackie 1970, Skovlin 1982, Witmer and deCalesta 1983, Hart et al. 1991, Yeo et al. 1993) and by interviews with ranch managers and local FWP biologists.

Elk Forage Consumption Model

In an effort to quantify dietary overlap between elk and cattle, many researchers have compared forage intake by elk to the standard AUM. Intuitive reasoning has formed the basis for many estimates of AUM equivalents (Holechek 1980). Several estimates have been based simply on body weight (Murie 1951, Stoddart and Smith 1955, Loomis et al. 1989, Lacey et al. 1993). Calculations based on weight alone risk errors due to differences in gender, animal physiological state, and spatial and dietary overlap (Holechek 1980, Nelson and Leege 1982).

An AUM is a useful, but imprecise method of measuring forage intake (SRM 1989). A more precise measure of what an animal eats would be based on caloric intake. Because energy is usually the limiting nutrient under range conditions, animals eat to meet its energy requirements (Vavra 1992), and intake is expected to vary with gender and physiological state. Because the energy density of forages changes with plant maturity, dry matter intake will change with plant maturity for animals in the same physiological state.

The purpose of our elk model is to simulate forage consumption by wild elk in an effort to quantify dietary overlap between elk and domestic cattle. The model takes into account the different physiological needs of elk as related to age, sex, reproductive status, and time of year, as well as forage quality and dietary and spatial overlap of elk and cattle. The model is deterministic and relatively simple. We emphasize that the primary purpose of the model is to estimate forage removal by an existing elk herd, and not to simulate the dynamics of a herd in response to changing resources. See Appendix for further description of the model and the equations used.

Table 1. Characteristics of ranches simulated.^a

Ranch	1	2	3	4	5
Herd Size	240	368	838	900	1142
Weaning Weight, kg	262	251	257	265	235
Cow Mature Weight, kg	595	550	544	544	550
Conception Rate, %	92	93	92	92	95
Breeding Date	May 21	May 22	May 20	May 10	June 1
Breeding Season, days	75	60	90	50	90
Death Loss, %	2.5	3.0	3.0	5.0	10.0
Native Range, days	132	138	214	85	201
Domestic Pasture, days	38	46	30	136	29
Winter Feeding, days	195	181	121	144	135
Wean & Sale Date	Oct 20	Oct 20	Nov 8	Oct 25	Nov 1

^aHerd Size = number of beef cows exposed to bulls per year, including replacements; Weaning weight = average weaning weight of steers and heifers; Breeding Date = first day of breeding for mature cows, all ranches except #2 bred yearling heifers earlier (Ranch 1 = 14 d, Ranches 3 & 5 = 10 d, Ranch 4 = 30 d); Breeding Season = length of season for mature cows; Death Loss = calves lost from birth to weaning; Domestic Pasture = early spring pasture (Ranch 4) and hay aftermath (all ranches).

Beef Cow-Calf Model

The beef cow-calf model developed by Tess and Kolstad (2000a,2000b) was used to simulate cattle and ranch enterprise performance. The model simulates performance of beef cattle of varying genetic types in response to changes in forage quality and management strategies, and simulates economic performance of beef production systems in response to alternate breeding and management systems. It uses parameters input by the user describing genotypes, mating systems, nutritional characteristics of native range and stored feed, management decisions, input costs, and cattle prices. Importantly, the model simulates performance of ranches of fixed size—i.e., the grazed forage base is a fixed number of AUM. Resource and management data for the ranches used in the simulations are presented in Table 1. Input prices and cattle prices used were averages during 1996.

The beef simulation model produces several measures of system performance. Only 3 statistics will be reported here. Because the model simulates a ranch with a fixed range resource base, adding resources or changing the management of the range forage base can lead to differences in annual cattle herd carrying capacity. Hence, herd size (specifically, the number of cows exposed for breeding) provides a measure of carrying capacity. Ranch gross margin, computed as gross income minus variable costs, provides a measure of profitability for each ranch when the ranch is constrained to a fixed range resource base. This economic measure considers some expenses as fixed—for example, home raised hay, grazed forage, property taxes, and some family labor. In contrast, unit cost of production (specifically, input cost per kg of steer equivalent weight sold) provides a measure of production efficiency treating all input costs as variable and without constraints. In other words, for this measure of economic efficiency, all resources used, including raised hay and grazed forage, are priced at their rental values and are not considered to be in limited supply. See Tess and Kolstad (2000a,2000b) for further details.

Integration of Elk and Cattle Data

The elk forage model was used to determine forage harvest by elk on each ranch. Forage use by elk was equated to AUM that potentially could have been used by cattle if elk were not present and if elk were eating what the cows could access—i.e., as affected by slope, terrain, etc. It is

important to understand that our definition of a fixed forage resource base assumes that there is a fixed amount of forage produced annually that can be grazed without harming the range resource.

Using the cow-calf model, ranches were simulated as they were actually managed. To compare how these ranches could theoretically be run if elk were not present, AUM harvested by elk on the respective ranches, as determined by the elk forage model, were added into the cow-calf model for the individual ranches. Comparisons of these simulations, allowed us to determine how many additional cattle could be maintained on the ranches due to an increase in forage if elk were not present, and the effects this had on ranch gross margin. Amounts of home-raised hay and domestic pasture were also considered fixed for each ranch. Hence, adding range resources would allow each ranch to run more cattle, but also might require the purchase of additional hay for winter feeding.

Alternative Management Strategies

Several potential methods exist by which beef cattle ranchers can reduce conflict between elk and cattle and (or) recover costs associated with elk on private lands. Variability of available resources on ranches and the number of elk utilizing the ranches makes it difficult to find a single best solution to the problem.

Block Management. In Montana, the Block Management Program was devised to keep private lands open for public hunting, while paying landowners for allowing free hunter access. Through management of the number and strategic placement of hunters, more efficient hunting is expected, thereby reducing elk herd numbers (Governor's Advisory Council on Private Lands/Public Wildlife, unpublished). In addition to assisting landowners with hunter management, the program also offers benefits that reduce or eliminate the cost of having hunters on private land, and in some cases offers taxable reimbursements of up to \$8,000 (Montana Session Laws 1995).

To mimic more efficient hunting, each ranch was simulated with elk herds reduced by 10, 20, and 30%. Effects on cattle herd size and gross margins were evaluated.

Coordinated Exchange of Forage Use. Coordinated grazing of rangelands among state, federal, and private lands allows private landowners to rest pastures that have been grazed by elk during the fall, winter, and (or) spring (Frisina and Morin 1991, Alt et al. 1992). With the exchange of for-

age, landowners may not have to purchase stored forage to replace forage removed by elk. For example, members of the Wall Creek Stock Association participating in the Wall Creek Wildlife Management Area exchange of use program received an additional month of livestock grazing, resulting in an extra 826 AUM of grazing by cattle (Alt et al. 1992). A major limitation of this scenario is that there must be available state and federal lands close enough to the private landowner to make transporting cattle to these public ranges feasible. To evaluate this scenario, the fair market value of an AUM on private property was compared to the value of an AUM as simulated for each of the five ranches.

Leasing Hunting Access. Leasing private land to outfitters in Montana is a common, but sometimes controversial, practice. Hunters are willing to pay for the opportunity to hunt elk, particularly if they are assured of an un-crowded hunt. This "market" allows outfitters to lease land from ranchers at a value that increases the landowners' income.

There are several forms of fee hunting. However, for this study, we chose only the leasing of the land to an outfitter. Once land was leased to an outfitter it was assumed that no further costs associated with hunters, such as time spent managing or guiding hunters, would be incurred by the rancher. Also, the monetary value of the lease was fixed, whereas if a landowner were to lease hunting access to individual hunters, the income would be variable, dependent on the number of hunters wanting to hunt.

To determine the value of a lease on each ranch, a survey was sent to 100 outfitters in FWP hunting regions 1, 2, and 3, where elk hunting is prevalent. Survey procedures were based on previous studies (Swensson and Knight 1998, 2001). The survey consisted of a cover letter explaining the study and what was being asked of the outfitter; general maps of the individual study ranches showing county roads and habitat types; and a description of the elk herd that occupied the ranch during hunting season. The elk herd was described by percentage of bulls in various age classes, as well as number of calves per 100 cows and number of bulls per 100 cows. Outfitters were requested to estimate the market value of each lease. Six weeks after mailing the initial surveys, follow-up phone calls were made to a random 50% of the non-respondents. Reasons for not completing the survey were determined. When feasible, non-respondents were again asked to complete the survey.

Statistical Analyses

Five scenarios were simulated in determining the effects of elk on ranches. To meet our first objective, each ranch was simulated as currently managed with elk present. The simulations were repeated with elk removed from the ranch, i.e., forage resources utilized by elk were added to the AUM available for cattle. These simulations also provided insights into the merits of the exchange of forage management strategy. To evaluate the potential effects of partial reduction in the elk herds, as might be expected due to Block Management, each ranch was simulated with a 10, 20, or 30% reduction in the ranch's elk population.

Due to the stochastic nature of the beef cow-calf model (reproductive traits exhibit random variation; Tess and Kolstad 2000a), it is possible to statistically compare simulated systems. Because not all traits are modeled with random variation, simulated variation between replicates is not the same as would be measured among actual ranches; however, the variation simulated does provide a basis for evaluating differences. Hence, each ranch/scenario combination was replicated ten times.

Because variances differed among ranches, simulated data for each ranch was analyzed separately. One-way analysis of variance was conducted to evaluate treatment effects (i.e., 0, 10, 20, 30, or 100% elk removal) on ranch gross margin and cattle herd size (SAS 1992). Means were separated using Duncan's Multiple Range test.

Results of the outfitter surveys were summarized by computing simple means and standard deviations of the estimated lease values.

Results

Elk AUM Equivalents

Table 2 illustrates the performance of the elk model for animals of different sexes and physiological states, and consuming forage of different quality. To a large degree, previous estimates of AUM equivalents have been based on differences in mature weight between elk and cattle, assuming that intake of elk was proportional to cattle but not considering physiological state. Murie (1951) and Loomis et al. (1989) used values of 0.25 and 0.27 for elk calves. Coupled with their value for lactating elk cows (0.67), the values of Loomis et al. (1989) agree with the model's predictions. Arychuk (2000) distinguished yearlings (0.3), adult females (0.5) and adult males (0.7).

Table 2. Effects of variable forage energy content and physiological state of elk on animal unit value equivalents.^a

	Male		Female-N		Female-G		Female-L	
	Metabolizable energy per kilogram dry matter							
Age	2.00	1.70	2.00	1.70	2.00	1.70	2.00	2.13
Y1	0.47	0.56	0.43	0.49	N/A	N/A	N/A	N/A
Y2	0.59	0.67	0.50	0.57	0.49	0.59	1.01	0.89
M	0.63	0.79	0.51	0.63	0.53	0.65	0.96	0.87

^aY1 = yearling, Y2 = two-year old animal, and M = mature animal of five-years old or older. Female-N = non-reproductive female, Female-G = gestating female, and Female-L = lactating female, including calf.

Previous AUM equivalents for adult elk (sex not specified) include 0.4 (Murie 1951, Meresczak et al. 1981, Loomis et al. 1989, Wisdom 1992), 0.5 (Stoddart and Smith 1955, Skovlin et al. 1968, Lacey et al. 1993), 0.6 (Lacey et al. 1988), 0.65 (Vallentine 1990), and 0.75 (Telfer and Scotter 1975).

Our results demonstrate the effects that age, gender, physiological state, and forage quality can have on forage intake. By accounting for these variables and dietary overlap, our model permits more precise description of the study case. These results also point to the hazards of using single, general predictions of AUM consumed by elk, because such predictions cannot account for species differences in food habits and distribution across rangelands (Vavra 1992).

Animal Use and Ranch Resources

Numbers of elk utilizing the ranches were likely conservative (Table 3). With only one yearly flight to determine the population characteristics of a herd for the

entire year, we assumed no recruitment of bachelor bulls took place, and average recruitment through reproduction occurred.

Elk use and numbers varied across ranches. All ranches showed an influx of elk in late fall that continued to early spring (Table 4). In general, there was a decline in elk numbers during the summer as elk migrated to higher elevation habitats, typically on state and federal lands. The exception to this was Ranch 5, which provided calving grounds to 250 cow elk. Four of the 5 ranches supported both resident and migratory populations of elk.

Elk-use data presented in Table 4 represent our best estimates for the product of spatial and dietary overlap between elk and cattle by season and reflect differences due to forage species, elevation, slope, ruggedness, and distance from water (also see review by Fuller 1997). Late fall and winter showed the highest percentages of resource overlap of up to 90%, with the exception of Ranch 2. The manager of Ranch 2 felt there was only 20% overlap due to the fact that all hay

Table 3. Summary of elk herds on individual ranches.^a

Ranch	Age Class	Male	Female-N	Female-R
1	Y0	9	9	
	Y1	8	13	2
	Y2	2	7	6
	M	9	28	25
2	Y0	32	32	
	Y1	30	45	8
	Y2	5	25	22
	M	29	102	91
3	Y0	24	24	
	Y1	21	31	6
	Y2	7	18	15
	M	19	71	62
4	Y0	26	26	
	Y1	4	17	3
	Y2	3	9	9
	M	5	41	35
5	Y0	34	33	
	Y1	10	25	4
	Y2	4	14	12
	M	9	56	49

^aNumbers shown are estimated maximum populations.

Y0 = calves, Y1 = yearlings; Y2 = 2 year olds; M = 3+years

Female-N = non-reproductive female; Female-R = reproductive female.

Table 4. Summary of elk use on individual ranches.

Ranch	Period of Use	Number of Elk	Overlap ^a	AUM
1	Oct 1 -Nov 30	118	90	110
	Dec 1 - May 15	118	75	262
	May 16 - May 31	118	75	22
	June 1 - Oct 1	71	40	68
2	Oct 1 - Nov 30	199	90	186
	Dec 1 - Mar 31	347	20	156
	Apr 1 - May 30	421	40	182
	June 1 - Sept 9	331	50	328
	Sept 10 - 30	199	80	70
3	Oct 1 - Nov 30	290	90	271
	Dec 1 - Apr 15	298	85	673
	Apr 16 - Jun 20	249	40	111
	Jun 21 - Sept 9	199	50	169
	Sept 10 - 30	290	80	101
4	Oct 1 - Nov 30	178	90	157
	Dec 1 -Mar 31	178	90	333
	Apr 1 - Jun 20	49	40	27
	Jun 21 - Sept 9	100	50	83
	Sept 10 - 30	178	80	61
5	Oct 1 - Nov 30	194	90	173
	Dec 1 - Apr 15	114	85	245
	May 15 - Aug 15	250	40	168
	Sept 10 - 30	194	80	66

^aOverlap=dietary and spatial overlap between elk and cattle, %.

Table 5. Simulated ranch performance without elk removal.^a

Ranch	Herd Size	Cattle AUM	Elk w/o Overlap	Cattle used by Elk
		(\$/kg)	---	(AUM) ---
1	241	1,835	1.62	674
2	368	2,820	1.65	2,189
3	838	7,750	1.53	1,836
4	902	7,760	1.58	857
5	1,147	9,200	1.80	987

^aHerd Size = number of beef cows exposed per year, including replacements. Cattle AUM = AUM used by cattle; \$/kg = unit cost of beef production; Elk AUM w/o overlap = AUM used by elk without considering dietary and spatial overlap; Cattle AUM used by Elk = AUM that could be used by cattle if elk were not present.

Table 6. Simulated effects of elk herd reduction on beef enterprise performance.

Ranch	Percentage Reduction in Elk Numbers					SEM
	0	10	20	30	100	
	Cattle Herd Size = Cows Exposed/Year					
1	241 ^c	247 ^d	253 ^c	260 ^b	301 ^a	0.74
2	368 ^c	381 ^d	394 ^c	404 ^b	486 ^a	1.10
3	838 ^c	851 ^d	867 ^c	881 ^b	979 ^a	1.54
4	902 ^c	905 ^d	917 ^c	924 ^b	978 ^a	1.08
5	1,147 ^d	1,148 ^d	1,155 ^c	1,166 ^b	1,228 ^a	2.46
	Ranch Gross Margin, \$/year					
1	64,879 ^c	66,185 ^c	65,925 ^c	67,981 ^b	71,193 ^a	586
2	88,682 ^b	89,126 ^b	89,961 ^b	90,996 ^b	100,487 ^a	827
3	176,715 ^c	181,066 ^b	181,010 ^b	183,084 ^b	197,867 ^a	1,099
4	232,861 ^c	234,829 ^c	234,227 ^c	237,534 ^b	242,151 ^a	919
5	237,756 ^b	241,457 ^{ab}	243,019 ^a	243,536 ^a	243,705 ^a	1637

^{abcde}Means within rows with different superscripts differ (P < 0.05).

was stored in “elk-proof” sheds, and elk did not generally intermingle with cattle during winter feeding of hay. In general, summer months showed only a 40% overlap mostly due to changes in dietary preferences of elk from grasses to forbs (Murie 1951, Mackie 1970).

Table 5 summarizes ranch performance under actual management and elk numbers. Differences in production costs (\$/kg) were due to several factors. Reproductive rates were similar among ranches; however, calf mortality was high for Ranch 5, spreading production costs over less output. Due to snow cover, Ranches 1 and 2 fed hay for extended periods, increasing feed costs.

By accounting for less than complete dietary and spatial overlap (Table 4), AUM harvested by elk in competition with cattle were considerably less than might be predicted otherwise (Vavra et al. 1989, Kingery et al. 1996). This highlights the importance of dietary overlap in quantifying potential competition between livestock and wildlife.

Forage Resources Gained From Elk Removal

Differences among ranches in gross margin reflect differences in herd size as well as differences in unit costs of production (Table 6). Recovering all forage resources used by elk (i.e., 100% elk removal) increased cattle carrying capacity and gross margin for each ranch (P < 0.05); however, responses were unique for each ranch. The ratio of added AUM to added cows ranged from 7.7 to 9.4, indicating how ranches differed in their dependence on range resources. Because of their short grazing seasons, Ranches 1 and 2 added more cows per AUM than Ranch 3, which was able to graze for nearly two months longer. Ranches 4 and 5 were intermediate.

The value of added AUM (added gross margin divided by added AUM) also differed among ranches; however, standard errors were large. Because this statistic was deemed important to the interpretation of results, we repeated the simulations for the base scenario, and the scenario assuming total removal of elk. This time we replicated each scenario 200 times. Estimated values of an added AUM ranged from \$8.55 to \$14.51 (Table 7). Differences were related to, but not totally explained by differences in grazing season. Ranches that grazed longer and fed less hay were generally more efficient (i.e., lower production costs, \$/kg) and recovered more gross margin per added

Table 7. Simulated added AUM value after removal of all elk.

Ranch	Added AUM Value ^a
1	\$11.95
2	\$11.87
3	\$14.51
4	\$13.73
5	\$8.55

^aAdded AUM value = Added ranch gross margin divided by added AUM, based on 200 replicates.

AUM. The exception was Ranch 5, where unit cost of production was high primarily due to high calf mortality. In a survey conducted by Lacey et al. (1993) landowners in southwestern Montana reported average annual losses to big game of 511 AUM (214 due to elk) and 7.5 metric tons of hay, valued at \$6,066—i.e., \$11.87/AUM.

Block Management

Incentives for ranchers to participate in the Montana Block Management Program include hunter management, monetary compensation, and potentially some reduction in elk numbers. According to Montana Session Laws (1995) ranches participating in the Block Management Program are entitled to some benefits, including a monetary benefit of up to \$8,000, depending on the type of habitat provided for wildlife, species and number of wildlife present, and access provided to adjacent private and public lands. We simulated 10, 20, and 30% reductions in elk numbers to evaluate economic effects on each ranch.

Responses to reduction in elk numbers (Table 6) were essentially linear because we assumed no change in elk sex or age structure, only population size. However, slopes of the responses were not the same across ranches, which reflect differences among ranches in elk population structure, as well as differences in dietary overlap. Ranches 1, 2, 3, and 4 were able to increase cattle numbers ($P < 0.05$) by reducing elk by 10%, and all ranches experienced significant increases in cattle numbers when elk were reduced by 20%. Only Ranch 3 increased gross margin ($P < 0.05$) with a 10% reduction in elk numbers. Ranch 2 was unable to increase gross margin with even a 30% reduction in elk numbers.

These results suggest that elk herd reduction is likely to be of only minor benefit to ranches participating in Block Management. However, expenses associated with elk were less than \$8,000 on Ranches 1 and 5, suggesting these ranches could potentially recover all elk costs through participation in the Block Management Program, even without a reduction in elk numbers.

Outfitter Lease

Sixteen of the 100 mail surveys were returned. Five surveys were removed from the data because they were not completed properly. Follow-up phone calls made to a random half of non-respondents indicated that many of the outfitters felt unqualified to value a lease on private land because their business was limited to public land. Follow-up calls increased the number of useable surveys back to 16.

Based on their comments, outfitters gave conservative estimates for the value of a 1-year lease on the individual ranches for elk hunting (Table 8). Some respondents noted that leases would be worth more if deer hunting were included and if leases were of longer duration than just 1 year. All respondents agreed that it was very difficult to gauge an accurate price quote for a ranch without actually having been on the ranch during a hunting season to see the behavioral patterns and population characteristics of the elk herd. Also, aesthetics, reputation, and rapport between client and outfitter are difficult to measure yet can have a large influence on the price an outfitter is able to get for a hunt (Knight et al. 1995), which in turn influences the value of the lease.

Mean values assigned by the outfitters were all below the simulated costs of providing elk habitat on private land; yet there was a wide range of estimates for each lease. Each ranch was valued by at least one outfitter above elk costs. Though not accounted for in the simulations, Ranches 3, 4, and 5 did receive some annual income from elk hunting. For example, Ranch 3 leased hunting access for \$25,000/yr, which is less than the maximum value assigned by the outfitter surveys but more than our estimated expenses associated with elk.

Exchange of Forage Use

In theory, exchange of forage use with a state or federal resource management agency should fairly recover all expenses associated with elk, except possibly repair costs for fences and other improvements (note, that in Montana FWP provides some ranchers with panels to protect haystacks from wildlife). This assumes that added AUM allotted to ranches on

public land are equal to or greater than the AUM consumed by elk on private land. Table 5 shows our estimates of the number of AUM needed for an equitable exchange of use.

The fair market value of an AUM lease is the price a person would expect to pay if he/she leased land for the purpose of grazing cattle. Average rates for a “cow-calf pair” in Montana were \$13.90 and \$15.60, in 1996 and 2000, respectively (NASS 2001). Reported lease rates do not account for differences in cattle mature size; hence, they are not easily compared to AUM values reported here. On average, 30% of a private grazing lease represents landlord services such as fence maintenance, water access, etc. (Torell and Fowler 1992, LaFrance and Watts 1995), which were not varied in our simulations. Following such adjustment, average Montana lease rates would be \$9.73 and \$10.92 for 1996 and 2000, respectively. Our estimates of the value of an AUM recovered from elk use for the 5 ranches are above and below these values (Table 7). Interestingly, these results suggest that it may be more advantageous for some ranchers to accept fair market value of AUM eaten by elk rather than accept a direct exchange of forage use. On the other hand, ranches that show returns per AUM higher than lease values may be better off exchanging use with a public agency, if available.

The main focus of exchange of use in this study was on the monetary value of such an alternative management scheme. Where feasible, a coordinated exchange of use has other beneficial elements than just recouping costs associated with elk. As noted by Alt et al. (1992) and Frisina and Morin (1991), a cooperative grazing system actually increased available AUM by improving forage on the range. This had a secondary effect of keeping elk on wildlife management areas for a longer period of time before elk migrated to private ranges in search of food. Potential benefits of grazing on subsequent forage nutritional quality may be due to removal of old growth and delayed senescence, though studies have shown mixed results (Anderson and Scherzinger 1975, Severson and Urness 1994, Hobbs et al. 1996a, Wambolt et al. 1997). Increased

Table 8. Lease value of ranches for elk hunting based on outfitter survey.

Ranch	1	2	3	4	5
Mean	\$2,919	\$3,900	\$10,375	\$7,175	\$2,953
Maximum	\$6,700	\$15,000	\$30,000	\$17,700	\$7,500
Standard deviation	\$2,288	\$3,850	\$7,386	\$5,129	\$2,520

landowner tolerance of elk, while increasing cattle and elk numbers able to use the land (Frisina and Morin 1991) are other advantages to exchanging use of forage.

Discussion

Simulation is a tool to examine scenarios that are beyond the scope of experimentation. It is used to address questions that are too expensive or too time consuming to address with experimentation. Often these questions take the form of: "How would the system respond if _____?" The assumptions made and the boundaries of the models used define what inferences can be made from the studies. Our work represents an attempt to integrate a large amount of published research into a systems framework, and make a science-based application to a real-life issue; in this case estimating costs of providing wildlife habitat on private land, and evaluating methods to recoup these costs.

The accuracy of our predicted costs could be improved by more precise measures of elk population parameters, including diet composition. However, it should be noted that the type of data available to us in this study is the type of data available to resource managers, policy makers, and ranchers. Ranch managers know the number and classes of livestock. On the other hand, data on wild ungulates are "generally obtained from state wildlife agencies or collected in cooperation with such agencies" (Cooperrider and Bailey 1984). To account for imprecision in elk population parameters, using results presented in Tables 5 and 6 one could decrease or increase the number of elk to bracket a range of costs. Similar tactics could be employed if our methods were used to study different ranches.

Our model to predict forage harvest by elk has not been validated from energy metabolism studies with elk. We expect the precision of our estimates to be lower than expected from validated models of domestic animal metabolism; yet, better than simple predictions made from an "average elk," or using some average definition of animal unit equivalency. Importantly, our approach accounts for differences among elk populations in sex ratios and age distributions. Compared to domestic animals, there are few scientific studies of energy metabolism in elk. Clearly our ability to model digestion and metabolism of elk would be improved if more studies were completed with elk. Our approach was to use equations specific for elk when available. However, for

many equations we assumed that relationships for elk were similar to domestic cattle, scaling the equations for differences in mature size and output rates. Many aspects of energy metabolism are similar among ruminants of different species (e.g., sheep and cattle, ARC 1980). Several previous studies have applied relationships from cattle studies to wild ungulates (e.g., Moen 1973, 1978, 1983, Nelson and Legee 1982, Hudson and White 1985).

Our approach in this study was to allocate all forage to cattle and elk, defining the forage resource as the amount of forage that could be harvested without damaging the range resource. In other words, to manage a range resource responsibly, we assumed that forage harvest must be limited to a certain degree of use – the degree of use currently experienced by each ranch. Hence, under this assumption, forage consumed by elk (accounting for dietary overlap) reduced forage available to cattle. An increase in elk herd size would lead to a reduction in cattle herd size, and conversely an increase in cattle herd size would require a reduction in the number of elk. Hobbs et al. (1996a,1996b) showed that elk grazing led to decreased forage intake, and reduced weight gains for cattle. Some responses demonstrated threshold effects—i.e., if sufficient forage was available to cattle after elk grazing, then cattle showed little response to elk grazing. Our assumptions and the results of Hobbs et al. (1996a,1996b) are both consistent with accepted definitions of competition, i.e., for competition for forage to occur, both cattle and elk must be consuming the same forage species in the same area and the forage species must be in short supply (Vavra 1992).

Simulating ranches as if no elk existed was used as a tool to quantify the economic impact elk had on beef cattle enterprises. We emphasize, however, that it is seldom possible or legal to remove all elk from a ranch (Youmans 1992). In our experience, very few ranchers desire to remove all elk (or other wildlife) from their properties. Further, an increasing number of people outside of agriculture recognize the importance of livestock operations in providing/conserving wildlife habitat. Alternatives for managing elk, i.e., strategies to maintain herd sizes at reasonable levels and (or) recoup income lost or foregone by providing habitat, are vital to the sustainability of many ranches.

Implications

Our results show that providing elk habitat on private land does represent an

economic cost to ranches. Importantly, our results also suggest that Montana ranches represented by our sample can recover most if not all of these costs, and in some cases actually profit from elk by implementing various elk management strategies. Our study focused on expenses associated with forage use. Elk may also be responsible for damage to fences and other facilities. Lacey et al. (1993) reported that annual non-feed expenses associated with wildlife were \$401 per ranch.

Feed costs generally represent one of the largest expenses for beef cattle producers. Grazed forage is often a more economical feed source than harvested or purchased feed. Our results suggest that the more dependent ranches are on rangeland, and the more efficiently they produce beef (i.e., lower unit cost of production, \$/kg), the more these ranches have to lose from providing elk habitat. More efficient ranches stand to benefit most from exchange of use programs, while ranches that are less efficient should benefit most from direct compensation. The greatest benefits from the Montana Block Management program appear to come from improved hunter management and compensation for access and habitat rather than from reduction in elk numbers.

Our survey of outfitters suggests that leasing of hunting access may be a viable method to recoup costs for some ranches. Commercial recreation values associated with elk provide incentives for ranches to provide elk habitat (Anderson and Hill 1995). Multiple factors determine the market values of recreational leases. However, market incentives may not address needs associated with non-game species or opportunities for low income people (Burger and Teer 1981, Jordan and Workman 1989), nor longer term management objectives related to biodiversity (Freese and Trauger 2000, Gowdy 2000).

The ranches studied illustrate that solutions to wildlife-livestock issues are situation specific. A single, universal recommendation is not likely to be acceptable. We considered only 3 options for recovering costs associated with elk utilizing private ranges. Other options may play important roles in solutions to wildlife-livestock problems (e.g., conservation easements, different types of leases, owner-managed recreational enterprises, etc.) (Knight 1996a,1996b, 1996c). Wildlife-livestock interactions are complex and dynamic. Improved understanding of these systems and cooperative approaches are needed to identify sustainable and equitable solutions (Swensson and Knight 1998).

Appendix: Description of Elk Forage Consumption Model

The model is based on a 1-day time step. Metabolizable energy (ME) requirements for maintenance (MEM, Mcal) are predicted from current animal weight (WT) and adjusted for season to reflect energy expenditures for travel (Nelson and Legee 1982, Jiang and Hudson 1993).

$$MEM = \frac{BM(WT^{0.75})}{KM} \quad (1)$$

where, BM = 0.1002, 0.1094, 0.1138, 0.1072 in winter, spring, summer, and fall, respectively. Efficiency of ME use for maintenance (KM), is predicted as a function of diet energy density (ME/kg dry matter [MEDM]) following NRC (1984).

$$KM = \frac{1.37 MEDM - 1.38 MEDM^2 + 0.0105 MEDM^3 - 1.12}{MEDM} \quad (2)$$

Postweaning growth is simulated based on WT, asymptotic mature weight (AWT), and weight gain (WTG) following data presented by Murie (1951) and equations by Moen (1973) as:

$$WTG = B1(AWT - WT) \quad (3)$$

where B1 = 0.0030 for bulls and 0.0035 for cows, and AWT is assumed to be 350 and 260 kg for bulls and cows, respectively (Nelson and Legee 1982). Predictions of ME requirements for gain (MEG) are based on NRC (1984), and assume that the composition of gains for elk and cattle are similar at similar stages of maturity and similar relative rates of growth. For bulls,

$$MEG = \frac{0.0493WT^{0.75}(WTG^{1.097})ARATIO^{0.847}}{KG} \quad (4)$$

and for cows,

$$MEG = \frac{0.0686WT^{0.75}(WTG^{1.119})ARATIO^{0.869}}{KG} \quad (5)$$

where ARATIO is the ratio of mature weights for cattle and elk (e.g., 525/260 = 2.02 in this study). See below for derivation. Postweaning rates of growth for elk are expected to be slower and with lower percent fat than for domestic cattle fed concentrate diets. This prediction accounts for such differences. The efficiency of ME use for gain (KG) is computed based on NRC (1984) as:

$$KG = \frac{1.42 MEDM - 0.174 MEDM^2 + 0.0122 MEDM^3 - 1.62}{MEDM} \quad (6)$$

For pregnant females, ME requirements for gestation (MEU) is measured as uterine energy deposition (UTE) which has a 15% efficiency rate and is modeled after Ferrell et al. (1976). Gain in uterine development (UTEG) is computed by the equation:

$$UTEG = \frac{0.06973e^{DT(0.0323-0.0000275DT)}16.0}{40.0} - UTE \quad (7)$$

where, the ratio 16.0/40.0 accounts for difference in birth weight between elk and cattle, and UTE is the accumulated UTE on the day of gestation (DT). Then,

$$MEU = \frac{UTEG}{0.15} \quad (8)$$

For cows nursing a calf, it is necessary to calculate the fraction of the calf's requirements satisfied by milk, and the cow's added energy requirement to produce milk. First, we assume a 50:50 distribution of male and females calves. Second, we assume that the average nursing time is 120 days, and that calf growth is linear over this period for both sexes. During the nursing period calf ME requirements (CMEI) are:

$$CMEI = MEM + MEG \quad (9)$$

The fraction (FRACT) of MEI supplied by milk is assumed to decrease with calf age, and estimated as:

$$FRACT = 1.0 + \frac{16.0 + CWT}{WWT - 16.0} \quad (10)$$

where, CWT = current calf weight, and WWT = weaning weight (note that birth weight = 16 kg). Weaning weights are assumed to be 85.2 kg for bulls and 79.5 kg for cows (Nelson and Legee 1982). Then, CMEI supplied by forage is computed as:

$$CMEIF = CMEI(1.0 - FRACT) \quad (11)$$

The ME required by the cow to produce the milk consumed by the calf (MEL) is estimated as:

$$MEL = \frac{CMEI(FRACT)}{0.85KM} \quad (12)$$

where, 0.85 accounts for metabolizability of milk consumed by the calf (NRC 1989).

For all animals past weaning age, total ME consumed (MEI) is:

$$MEI = MEM + MEG + MEU + MEL \quad (13)$$

where MEG, MEU, or MEL could be zero, depending on animal age, sex, and physiological state. Metabolizable energy consumed was translated into animal unit months (AUM = 360 kg dry matter, SRM 1989) as:

$$AUM = \frac{MEI + CMEIF}{360(MEDM)} \quad (14)$$

The amount of forage consumed by elk that could have been consumed by cattle is then predicted as:

$$ADJAUM = AUM(OVERLAP) \quad (15)$$

where, OVERLAP is the product of spatial and dietary overlap expressed in decimal form.

For the purposes of this study we assumed that average birth and weaning dates for elk calves were June 1 and September 28, respectively (Skovlin 1982, Taber et al. 1982, Nelson and Legee 1982). To recognize that the number of elk using a ranch was not constant throughout the year, the model was constructed to simulate forage intake by elk during different periods of time specific for each ranch. For each period, inputs to the model included descriptions of the elk population, average forage quality during the period (i.e., MEDM), and OVERLAP.

Derivation of energy cost of gain for elk

From NRC (1984) the net energy of live weight gain for female cattle is:

$$NE_{GC} = 0.0686WTC^{0.75}(WTGC^{1.119}) \quad (16)$$

where, WTC = current live weight (kg) and WTGC = live weight gain (kg/d).

Dividing by WTGC, net energy per kg WTGC is:

$$NEKG_{GC} = 0.0686WTC^{0.75}(WTGC^{0.119}) \quad (17)$$

Our assumption is that the net energy for gain for elk is similar to that of cattle when gains and weights are at similar stages of maturity (i.e., fraction of mature size). Hence, if the current weight (WTE) and gain (WTGE) for elk are proportional to the ratio of mature weights for elk (AWTE) and cattle (AWTC), then:

$$WTE = WTC \left(\frac{AWTE}{AWTC} \right) \quad (18)$$

$$WTGE = WTGC \left(\frac{AWTE}{AWTC} \right) \quad (19)$$

Finally, solve for an adjustment factor (Z) that equalizes the net energy for gain for cattle and elk when gains are at similar fractions of mature weight.

$$0.0686WTC^{0.75}(WTGC^{0.119}) = 0.0686 \left(WTC \frac{AWTE}{AWTC} \right)^{0.75} \left(WTGC \frac{AWTE}{AWTC} \right)^{0.119} (Z) \quad (20)$$

$$Z = \left(\frac{AWTC}{AWTE} \right)^{0.869} \quad (21)$$

Note, that the coefficient $0.869 = 0.75 + 1.119 - 1.0$. Similarly, the coefficient for male elk is $0.847 = 0.75 + 1.097 - 1.0$.

Literature Cited

- Adams, A. W. 1982.** Migration, p. 301-321. *In*: J. W. Thomas and D. E. Toweill (eds.), *Elk of North America: ecology and management*. Stackpole Books, Harrisburg, Penn.
- Alt, K. L., M. R. Frisina, and F. J. King. 1992.** Coordinated management of elk and cattle, a perspective—Wall Creek Wildl. Manage. Area. *Rangelands* 14:12-15.
- Anderson, T. L. and P. J. Hill. 1995.** From a liability to an asset: developing markets for wildlife, p. xi-xv. *In*: T. L. Anderson and P. J. Hill (eds.), *Wildlife in the Marketplace*. Rowman and Littlefield Publishers, Inc, Lanham, Md.
- Anderson, E. W. and R. J. Scherzinger. 1975.** Improving quality of winter forage for elk by cattle grazing. *J. Range Manage.* 28:120-125.
- ARC. 1980.** The nutrient requirements of ruminant livestock. Commonwealth Agr. Bureaux, Farnham Royal, U.K.
- Arychuk, C. E. 2000.** Setting stocking rates for pastures. *The Tracker* 4:72-73.
- Begon, M., J. L. Harper, and C. R. Townsend. 1990.** Ecology, individuals, populations and communities. Blackwell Sci. Publ., Inc. Cambridge, Mass.
- Burger, G. V. and J. G. Teer. 1981.** Economic and socioeconomic issues influencing wildlife management on private land, p. 252-263. *In*: R. T. Dumke, G. V. Burger, and J. R. March (eds.), *Wildlife Management on Private Lands*. Wisconsin Wildl. Soc., Madison, Wis.
- Cooperrider, A. Y. and J. A. Bailey. 1984.** A simulation approach to forage allocation, p. 525-560. *In*: *Developing Strategies for Rangeland Management*. Westview Press, Boulder, Colo.
- Edge, W. D. and C. L. Marcum. 1990.** Elk and cattle on public lands: a new look at an old conflict. *West. Wildl.* 16(2):12-15.
- Ferrell, C. L., W. N. Garrett, N. Hinman. 1976.** Growth, development and composition of the udder and gravid uterus of beef heifers during pregnancy. *J. Anim. Sci.* 42:1477-1489.
- Freese, C. H. and D. L. Trauger. 2000.** Wildlife markets and biodiversity conservation in North America. *Wildl. Soc. Bull.* 28:42-51.
- Frisina, M. R. and G. Morin. 1991.** Grazing private and public land to improve Fleecer elk winter range. *Rangelands* 13:291-294.
- Fuller, W. L. 1997.** Elk management strategies for sustainable beef cattle enterprises. M. S. Thesis, Montana State Univ.-Bozeman, Bozeman, Mont.
- Gordon, F. A. 1968.** Range relationships of elk and cattle on elk winter range, Crow Creek, Montana. Master's Thesis, Montana State Univ., Bozeman, Mont.
- Gowdy, J. M. 2000.** Terms and concepts in ecological economics. *Wildl. Soc. Bull.* 28:26-33.
- Hart, R. H., K. W. Hepworth, M. A. Smith, and J. W. Waggoner, Jr. 1991.** Cattle grazing behavior on a foothill elk winter range in southeastern Wyoming. *J. Range Manage.* 44:262-266.
- Henderson, R. E. and A. O'Herren. 1992.** Winter ranges for elk and deer: victims of uncontrolled subdivisions? *Western Wildl.* 18(2):20-25.
- Hobbs, N. T., D. L. Baker, G. D. Bear, and D. C. Bowden. 1996a.** Ungulate grazing in sagebrush grassland: Mechanisms of resource competition. *Ecol. Appl.* 6:200-217.
- Hobbs, N. T., D. L. Baker, G. D. Bear, and D. C. Bowden. 1996b.** Ungulate grazing in sagebrush grassland: Effects of resource competition on secondary production. *Ecol. Appl.* 6:218-227.
- Holechek, J. L. 1980.** Concepts concerning forage allocation to livestock and big game. *Rangelands* 2:158-159.
- Hudson, R. J. and R. G. White. 1985.** Computer simulation of energy budgets. p. 261-290. *In*: R. J. Hudson and R. G. White (eds.), *Bioenergetics of wild herbivores*. CRC Press, Boca Raton, Fla.
- Jiang, Z. and R. J. Hudson. 1993.** Seasonal energy requirements of wapiti (*Cervus elaphus*) for maintenance and growth. *Can. J. Anim. Sci.* 74:97-102.
- Jordan, L. A. and J. P. Workman. 1989.** Economics and management of fee hunting for deer and elk in Utah. *Wildl. Soc. Bull.* 17:482-487.
- Kasworm, W. F., L. R. Irby, and H. B. Ihle Pac. 1984.** Diets on ungulates using winter ranges in northcentral Montana. *J. Range Manage.* 37:67-71.
- Kingery, J. L., J. C. Mosley, and K. C. Bordwell. 1996.** Dietary overlap among cattle and cervids in northern Idaho forests. *J. Range Manage.* 49:8-15.
- Knight, J. E. 1996a.** Minimizing controversy in wildlife and livestock grazing management. *Trans. 61st No. Amer. Wildl. and Natur. Resour. Conf.* 137-141.
- Knight, J. E. 1996b.** Noncontroversial techniques to manage rangeland resources, p. 107-111. *In*: *Sharing Common Ground on Western Rangelands*. U.S.D.A. For. Ser. Intermountain Research Section. Gen. Tech. Rep. INT-GTR-343.
- Knight, J. E. 1996c.** Conservation easements on Montana ranches. *MontGuide* 9618 AG.
- Knight, J. E., J. M. Fowler, and C. M. Morgan. 1995.** Expenses and income associated with fee hunting enterprises. *RITF Report No. 41*.
- Lacey, J. R., K. Jamtgaard, L. Riggle, and T. Hayes. 1993.** Impacts of big game on private land in south-western Montana: Landowner perceptions. *J. Range Manage.* 46:31-37.
- Lacey, J. R., S. B. Laursen, J. C. Gilchrist, R. M. Brownson, J. Anzick, and S. Doggett. 1988.** Economic and social implications of managing wildlife on private land in Montana. *Northwest Sci.* 62:1-9.
- LaFrance, J. T. and M. J. Watts. 1995.** Public grazing in the West and "Rangeland Reform '94". *Amer. J. Agr. Econ.* 77:447-461.
- Loomis, J., D. Donnelly, and C. Sorg-Swanson. 1989.** Comparing the economic value of forage on public lands for wildlife and livestock. *J. Range Manage.* 42:134-138.
- Mackie, J. R. 1970.** Range ecology and relations of mule deer, elk, and cattle in the Missouri River Breaks, Montana. *Wildl. Monogr.* 20.
- Mereszczak, I. M., W. C. Krueger, and M. Vavra. 1981.** Effects of range improvement on Roosevelt elk winter nutrition. *J. Range Manage.* 34:184-187.
- Moen, A. 1973.** *Wildlife ecology, an analytical approach*. W. H. Freeman, San Francisco, Calif.
- Moen, A. N. 1978.** Seasonal changes in heart rates, activity, metabolism, and forage intake of white-tailed deer. *J. Wildl. Manage.* 42:715-738.
- Moen, A. N., 1983.** *Agriculture and Wildlife Management*. CornerBrook Press, Lansing, N.Y.

- Montana Session Laws. 1995.** House Bill 195, p 2216-2225. *In: Laws and Resolutions of the State of Montana, Fifty-fourth Legislature.* Montana Legislative Services, Helena, Mont.
- Murie, O. J. 1951.** The Elk of North America. The Stackpole Company, Harrisburg, Penn.
- NASS. 2001.** Agricultural Prices (PAP-BB). National Agricultural Statistics Service, Agricultural Statistics Board, U.S. Department of Agriculture. <http://usda.mannlib.cornell.edu/> - accessed 4/27/01.
- Nelson, J. R. 1982.** Relationships of elk and other large herbivores, p 415-442. *In: J. W. Thomas and D. E. Toweill (eds), Elk of North America: Ecology and Management.* Stackpole Books, Harrisburg, Penn.
- Nelson, J. R. and T. A. Leege. 1982.** Nutritional requirements and food habits, p 323-367. *In: J.W. Thomas and D.E. Toweill (eds.), Elk of North America: Ecology and Management.* Stackpole Books, Harrisburg, Penn.
- NRC. 1984.** Nutrient requirements of beef cattle (6th Ed.). National Academy Press, Washington, DC.
- NRC. 1989.** Nutrient requirements of dairy cattle (6th Ed.). National Academy Press, Washington, DC.
- Peek, J. M. 1982.** Elk, p 851-861. *In: Joseph A. Chapman and George A. Feldhamer (eds), Wild Mammals of North America, Biology, Management, and Economics.* John Hopkins University Press, Baltimore, Md.
- SAS. 1992.** SAS user's guide: statistics. SAS Inst., Inc., Cary, N.C.
- Severson, K. E. and P. J. Urness. 1994.** Livestock grazing: A tool to improve wildlife habitat p. 232-249. *In: M. Vavra, W. A. Laycock, and R. D. Pieper (eds.), Ecological Implications of Livestock Herbivory in the West.* Soc. for Range Manage., Denver, Colo.
- Sheehy, D. P. and M. Vavra. 1996.** Ungulate foraging areas on seasonal rangeland in northeastern Oregon. *J Range Manage.* 49:16-23.
- Skovlin, J. M. 1982.** Habitat requirements and evaluations, p 369-413. *In: J. W. Thomas and D. E. Toweill (eds.), Elk of North America: ecology and management.* Stackpole Books, Harrisburg, Penn.
- Skovlin, J. M., P. J. Edgerton, and R. W. Harris. 1968.** The influence of cattle management on deer and elk. *Trans. N. A. Wildl. Natur. Resour. Conf.* 33:169-178.
- Smith, D. R. 1961.** Competition between cattle and game on elk winter range. *Univ. of Wyoming Agr. Exp. Sta.*
- Society for Range Management. 1989.** A glossary of terms used in range management. Denver, Colo.
- Stevens, D. R. 1966.** Range relationships of elk and livestock, Crow Creek Drainage, Montana. *J. Wildl. Manage.* 30:349-363.
- Stoddart, L. A. and A. D. Smith. 1955.** Range management. McGraw-Hill, N.Y.
- Swenson, E. J. and J. E. Knight. 1998.** Identifying Montana hunter/rancher problems and solutions. *J. Range Manage.* 51:423-428.
- Swenson, E. J. and J. E. Knight. 2001.** Hunter management strategies used by Montana ranchers. *Wildl. Soc. Bull.* 29:306-310.
- Taber, R.D., K. Raedeke, and D. A. McCaughran. 1982.** Population Characteristics, p 279-298. *In: J. W. Thomas and D. E. Toweill (eds.), Elk of North America: ecology and management.* Stackpole Books, Harrisburg, Penn.
- Tefler, E. S. and G. W. Scotter. 1975.** Potential for game farming in boreal aspen forests of western Canada. *J. Range Manage.* 28:172-181.
- Tess, M. W. and B. W. Kolstad. 2000a.** Simulation of cow-calf production systems in a range environment. I. Model development. *J. Anim. Sci.* 78:1159-1169.
- Tess, M. W. and B. W. Kolstad. 2000b.** Simulation of cow-calf production systems in a range environment. II. Model evaluation. *J. Anim. Sci.* 78:1170-1179.
- Torell, L. A. and J. M. Fowler. 1992.** Grazing fees: how much is fair? *Agr. Exp. Sta. Rept.* 666. New Mexico State Univ., Las Cruces, N.M.
- Vallentine, J. F. 1990.** Grazing management. Academic Press, Inc., San Diego, Calif.
- Vavra, M. 1992.** Livestock and big game forage relationships. *Rangelands* 14:57-59.
- Vavra, M., M. McInnis, and D. Sheehy. 1989.** Implications of dietary overlap to management of free-ranging large herbivores. *Proc. West. Sect. ASAS.* 40:489-495.
- Wagner, F. H. 1969.** Ecosystem concepts in fish and game management. p. 259-307. *In: G. M. Van Dyne (Ed.). The ecosystem concept in natural resource management.* Academic Press, New York, N.Y.
- Wambolt, C. L., M. R. Frisina, K. S. Douglass, and H. W. Sherwood. 1997.** Grazing effects on nutritional quality of bluebunch wheatgrass for elk. *J. Range Manage.* 50:503-506.
- Wisdom, M. 1992.** The Starkey Project: new technologies chase old questions about deer and elk management. *Western Wildl.* 18:32-38.
- Witmer, G. W. and D. S. deCalesta. 1983.** Habitat use by female Roosevelt elk in the Oregon coast range. *J. Wildl. Manage.* 47:933-939.
- Yeo, J. J., J. M. Peek, W. T. Wittenger, and C. T. Kvale. 1993.** Influence of rest-rotation cattle grazing on mule deer and elk habitat use in east-central Idaho. *J. Range Manage.* 46:245-250.
- Youmans, H. B. 1992.** Editor: Elk Management Plan. Montana Dept. of Fish, Wildl., and Parks, Helena, Mont.

Cull cow management and its implications for cow-calf profitability

RANDALL D. LITTLE, ALLEN R. WILLIAMS, R. CURT LACY, AND CHARLIE S. FORREST

Authors are Associate Professor, Department of Agricultural Economics, Associate Professor, Department of Animal and Dairy Sciences, Graduate Research Assistant and Extension Specialist, Department of Agricultural Economics, Mississippi State University, Mississippi State, Mississippi 39762. Dr. Little is the corresponding author. (662) 325-2884; fax: (662) 325-8777; email: little@agecon.msstate.edu

Abstract

Selling culled breeding livestock is often viewed as "just another chore." Most cull sales are made in the fall, after calves are weaned and cows are pregnancy checked and open. Since cull cow sales comprise from 15 to 30% of a cow-calf enterprise's gross revenue, perhaps they should be viewed as a potential profit center.

This paper uses enterprise budgets and sensitivity analyses to illustrate cull cow management strategies that overcome certain physical and economic factors that limit the profitability of fall cow sales. The key limiting physical factor is often poor body condition, which results from the combined effect of lactation and deteriorating forage quality. The key economic factor is a seasonal price low, generated by a large beef supply in the fall.

The results suggest potential, with adequate, low-cost feedstuffs, to increase net returns by properly managing cull breeding stock. In only 1 year during the 10-year period, 1990–1999, was selling cull cows in the fall the more profitable option. Over that time period, the net present value of spring cull sales averaged about \$30 per cow more than selling cull cows in the fall.

Key Words: seasonal price trends, net present value

Selling culled breeding livestock is often viewed as "just another chore." Most sales are made in the fall, after calves are weaned and cows are pregnancy checked and found to be open. Since cull cow sales comprise from 15 to 30 percent of a cow-calf enterprise's gross revenue, the culling activity should, perhaps, be viewed and managed as a potential profit center.

The purpose of the research reported in this paper was to determine if cull cow management strategies using cool season forages on improved pastures can overcome certain physical and economic factors limiting the profitability of fall cull sales. The key physical factor that frequently limits the profit potential of fall sales is poor body condition. Cows typically start the fall season in poor body condition because of the combined effect of the demands of lactation and the deteriorating quality of summer forages. The key economic effect is a seasonal price low, generated by large fall supplies (Fuez 1996, Spreen and Simpson 1992). While the model used reflects a production situation typical throughout much of the Southeastern U.S., the theoretical frame-

Resumen

La venta de ganado para crianza que es de baja producción (o no productivo), es una actividad que normalmente es considerada como una "tarea rutinaria mas" en el manejo del ganado. La mayor parte de las ventas de este ganado se lleva a cabo durante la época de Primavera, después que las crías han sido destetadas y las vacas han sido revisadas y comprobadas que están libres de preñez. La venta de ganado de baja producción abarca entre un 15 a 30 por ciento del ingreso bruto de las operaciones de vaca para cría, por lo que esta actividad debería ser vista como una potencial fuente de ganancia.

Esta publicación hace uso de presupuesto de operaciones y análisis de sensibilidad para ilustrar estrategias en el manejo de ganado de baja producción, que ayudan a eliminar o reducir ciertos factores físicos y económicos que limitan la alta rentabilidad en las ventas de ganado durante la Primavera. El principal factor físico limitante, es a menudo una pobre condición corporal del ganado, lo cual es el resultado del efecto combinado de pobre lactación y la deteriorada calidad del forraje. El principal factor económico es un bajo precio temporal durante la época de Primavera, generado por una alta oferta de reses durante la época de Otoño.

Los resultados del análisis presentado indican un incremento potencial en el retorno neto, dado un manejo apropiado del ganado con una adecuada alimentación, utilizando material alimenticio de bajo costo. Solamente en un año durante el periodo de 10 años (1990–1999), la opción de mayor ganancia fue vender el ganado de baja producción durante el Otoño. Durante este mismo periodo el Valor Presente Neto (VPN) de las ventas de ganado de baja producción durante la Primavera tuvo una ganancia promedio de \$30.00 mas alto por cabeza, comparadas con las ventas en Otoño.

---

work and methods are pertinent to any place quality cool season forages can be produced.

Cull Cow Grades

Cull cows are sold based on USDA slaughter grades, which can be related to body condition scores (BCS) (Table 1). The BCS is a system that uses visual appraisal to determine the degree of fat or muscle loss an animal exhibits. Body condition is scored from 1 to 9, with 9 being the fattest classification. An evaluation of fat

Table 1. Cull cow grades and characteristics.

Grade	Dressing Percent	Lean Content of Trimmings	Cow BCS
Canner	40-46	90-92	1-3
Cutter	45-49	88-90	4-5
Utility			
Boning	50-52	78-83	5-9
Breaking	52-54	76-82	6-9
Commercial	55-60	70-80	5-9

Source: Gill (1998).

deposits at various locations of the body (back, tail head, pins, hooks, ribs, and brisket) is made to estimate the potential carcass cutout quality. An animal with a score of 5 should look average without being too thin or too fat. Animals with a score of 3 or below will have little or no fat and are scored on the degree of muscle loss.

The USDA Utility and Commercial cows usually command the best prices and have the highest dressing percentage (50 to 60 percent). They typically have body condition scores of 5 or higher. Cows that grade USDA Utility or Commercial usually have enough intramuscular fat (marbling) and muscling for primals to be pulled from the carcass (particularly cuts from the rib and loin) and marketed outside of the ground meat trade. This greatly enhances the value of a carcass, which, in turn, generates premiums paid for the higher quality animals.

Cow Prices - Historical and Trends

Figure 1 illustrates the volatility slaughter cow prices exhibit over time. For the 19-year period shown, average monthly cow prices (in nominal dollars) ranged from a high of \$1.26 per kg to a low of about \$0.64 per kg. Also evident in Figure 1 is the cyclical nature of cattle prices.

Not only is price variability an important factor, but seasonal price trends (Boyles, Spreen and Simpson 1992, Torell et al. 1998) and the price differentials between grades of cull cows (Gill 1998) are also critical to effective cull cow management and marketing decisions. On average, the difference in price between USDA Utility and Cutter is about \$0.09 per kg (Fig. 2). Figure 2 also shows the seasonal price patterns inherent in slaughter cow prices. Prices normally peak in March and decline steadily through November. Torell et al. (1997) note that "flesh adds weight and that weight adds value" (p. 955-2). Thus, if possible, it may be advantageous to target marketing of cull cows in the early spring at a body

condition score of 5-6 and avoid marketing in the fall, particularly if cows are in poor body condition.

Materials and Methods

It may be profitable for producers to take advantage of favorable seasonal price trends and the premiums for animals in better body condition. The analysis reported in this paper used a partial budgeting approach in which the cull cow selling activity was treated as an independent livestock enterprise. An enterprise budget for the cull or stocker cow activity was developed (Table 2). Interest is charged on the purchase of the stocker cow over the 6-month period; the other expense items

Fig. 1. Monthly Average Utility Cow Prices in Mississippi, 1981 to 1999.

Fig. 2. Seasonal Price Patterns for Cull Cows in Mississippi, 1990 to 1999.

Table 2. Estimated Income and Expenses for Overwintering Cull Cows in Mississippi.

Item	Unit	Price (dollars)	Quantity	Amount (dollars/cow)
INCOME				
Cull cows (Utility) 80%	Kg	1.12	(499.0*80%)	446.69
Cull cows (Cutter) 20%	Kg	1.01	(453.6*20%)	91.26
Total Income			537.95	
Total Income Per Kg Sold			1.10	
DIRECT EXPENSES				
Canner/Cutter	Kg	0.86	362.9	311.76
Death Loss	%	0.01	312	3.12
Pasture Rental (fescue)	Ha	49.42	0.607	30.00
Protein Supplement	Kg	0.2425	81.65	19.80
Hay	Kg	0.0782	508	39.72
Salt/minerals	Head	4.00	1.00	4.00
Labor	Hrs.	6.50	1.50	9.75
Veterinary/health mgt.	Head	5.00	1	5.00
Mach., fuel, oil	Head	2.50	1	2.50
Marketing	Head	10.00	1	10.00
Supplies & misc.	Head	5.00	1	5.00
Interest (for 6 months)	Dol.	0.090	376.21	16.70
Total Direct Expenses				457.35
Breakeven Selling Price (weighted average, \$/Kg)				0.934
Returns above Direct Expenses				80.65
Net Returns per Kg sold				0.16

are assumed to be distributed equally over the period.

The budget presented in Table 2 was based on the assumption that cows will graze fescue from 1 November to 1 May. Cows were assumed to enter the program at 363 kg (at a body condition score of 4 or less), grading USDA Cutter or Canner. It is recognized that not all culled cows will grade so poorly, clearly there are other reasons besides poor body condition why some cows are open, but this is a major criterion in the culling decision.

An average daily gain of 0.757 kg over the 180 day feeding period was assumed. It is estimated that most cows gaining at this rate will grade USDA Utility (body condition score of 5–6) by early spring. Research has shown that about 80% of animals should reach this desired body condition (Schnell et al. 1997, Rasby et al. 2000); hence it was assumed that 80 percent of the cull cows grade Utility and the remainder grade Cutter. Cows that grade Utility were assumed to weigh 499 kg at the time of sale, while the cows grading Cutter were assumed to weigh 454 kg.

Real prices (1999 = 100) were used to eliminate the effect of inflation on prices received, so prices across years would be more directly comparable. The consumer price index was used as the deflator. The average Utility and Cutter prices (in real dollars) received for the sale of cull cows in the spring were \$1.12 and \$1.01 per kg, respectively. The producer was assumed to pay about \$0.86 per kg for Cutter grade cull cows in the fall or to value the ranch-

produced cull herd as an opportunity cost.

To facilitate comparison of fall and spring cull sales within a cow-calf operation, the net present value (NPV) of the returns for sale in the spring was calculated. Net present value is an investment analysis technique that takes into account the time value of money and the timing of cash flows (Robison and Barry 1996).

Returns were discounted for the 180 days assumed in the cull cow enterprise using a 10% annual discount rate. While a discount rate between 6 and 9% is recommended (AAEA Task Force on Commodity Costs and Returns 1998), ten percent was used to

build in an additional risk premium for extending ownership of the culled cows. A lower discount rate would slightly increase the present value of the returns from selling cull cows in the spring.

The NPV analysis includes as gross income the returns from selling 80% Utility grade and 20% Cutter grade cows in April. Average real April prices were used. All estimated expense items from the budget in Table 2 were included except the cost of cow purchase, since this reflects an attempt to portray a cow-calf producer's decision to retain ownership of cull cows, as compared to a stocker cow enterprise. Instead, an opportunity cost of holding cows was included, based on income foregone had the returns from the fall cull sale been invested at 6%. Net returns from the sale of culls in the fall and the corresponding NPV of the net returns from the sale of those cows the following spring were calculated using price data from the fall of 1989 to the spring of 1999.

Results

Using 10-year average real prices for cows and the estimated expenses of Table 2, the expected returns above direct expenses were \$80.65 per cow. Given the expenses assumed in the cull cow budget, including the 10-year average purchase price for Cutter grade cows in the fall, the break-even selling price for the cows in the spring, weighted for the percentage expected to grade Utility and Cutter, is an estimated \$0.934 per kg.

Figure 3 shows the buy-sell margins, in nominal dollars, for the past 10 years. The

Fig. 3. Buy/Sell Margins for Cull Cows in Mississippi, 1990 to 1999.

Table 3. Estimated Returns above Specified Expenses (dollars per cow) for Different Purchase and Selling Prices.

Purchase Price (\$/Kg)	Selling Price (\$/Kg)				
	\$0.79	\$0.83	\$0.88	\$0.93	\$0.97
	(\$/Cow)				
\$0.79	-43.69	-22.09	-0.49	21.11	42.71
\$0.75	-26.81	-5.21	16.39	37.99	59.59
\$0.74	-9.93	11.67	33.27	54.87	76.47
\$0.66	6.95	28.55	50.15	71.75	93.35
\$0.62	23.83	45.43	67.03	88.63	110.23
\$0.57	40.71	62.31	83.91	105.51	127.11
\$0.53	57.59	79.19	100.79	122.39	143.99

Table 4. Estimated Returns above Specified Expenses (dollars per cow) for Different Total Feed Costs (dollars per cow) and Selling Prices.

Total Feed Costs	Selling Price (\$/Kg)				
	\$0.79	\$0.83	\$0.88	\$0.93	\$0.97
	(\$/Cow)				
\$60.00	-38.38	-16.78	4.82	26.42	48.02
\$70.00	-48.60	-27.00	-5.40	16.20	37.80
\$80.00	-58.82	-37.22	-15.62	5.98	27.58
\$90.00	-69.04	-47.44	-25.84	-4.24	17.36
\$100.00	-79.27	-57.67	-36.07	-14.47	7.13
\$110.00	-89.49	-67.89	-46.29	-24.69	-3.09

margin, which was calculated by subtracting the October Cutter cow price from the April Utility cow price of the next year, averaged about \$0.20 per kg over the 10-year period, 1990-1999. The range for this margin was from \$0.07 to \$0.38 per kg. Although positive, the margins exhibit variability.

Table 3 presents the returns per cow, assuming different purchase and selling prices. Changes in weight gain and body condition are reflected in the price differentials of Table 3, as those are key determinants of the price received in the spring. The importance of adequate margins between the fall purchase price and the spring selling price is highlighted in Table 3, as returns above direct expenses per cow do not become positive until the difference between the fall and spring prices exceed \$0.08 per kg.

The sensitivity of returns per cow to changes in feed costs is presented in Table 4. Total feed costs, including pasture costs, as reflected in the budget in Table 2, were about \$90 per cow. The returns in Table 4 assume the cull cows are purchased at the 10-year average price for cutter/canner in the fall. These results illustrate the importance of low-cost feedstuffs, in addition to the adequate price differentials from fall to spring discussed previously, to a profitable stocker cow enterprise.

The net present value of spring cull sales exceeded returns from fall sales in all but one (1995) of the 10 years studied (Fig. 4). This year was when the differential between fall and spring prices was least, \$3.00 between the fall of 1995 and spring 1996, and the only time during the

study period when selling in the fall would have been more profitable. The difference between the NPV of the returns above direct expenses from spring cull sales and the sale of culls in the fall is illustrated in Figure 5. The average difference over the 10-year period was about \$30 per cow. As in Table 3, the importance of an adequate price differential between the fall and spring prices to the profitability of holding cows for sale in the spring is highlighted.

Discussion and Conclusions

The objective of this paper was to determine if cull cow management strategies can overcome certain physical and economic factors limiting the profitability of fall cull sales. The key physical factor is often poor body condition, the combined effect of lactation and deteriorating summer forage quality. The key economic effect is a seasonal price low in the fall, due to the increase in quantity supplied in those months.

The results suggest that there is considerable and relatively stable opportunity to boost returns from the sale of cull cows by improving body condition with a cost-effective feeding program and selling them in the spring. In only 1 year during the 10-year study period was selling cull cows in the fall the more profitable option. Over that time period, the net present value of spring cull sales averaged about

Fig. 4. Fall Cull Sales and the Net Present Value of Spring Cull Sales, 1989 to 1999.

Fig. 5. Difference between the Net Present Value of Spring Cull Sales and Fall Cull Sales, 1989 to 1999.

\$30 per cow more than selling cull cows in the fall. Availability of low-cost feedstuffs, whether cool season forages or some other feed, is critical to the success of a cull cow enterprise.

There are several factors to consider when deciding to hold cull cows over for sale in the spring. Producers should estimate the weight and grade of their cull cows or purchased stocker cows. Cows should have the potential to gain 90 to 135 kg on forages and supplement over the winter. Cows must be healthy, open, and have solid mouths to increase the probability of making a profit. Producers should evaluate their markets, and, if possible, put together 40 or more head per lot when selling. This provides a truckload lot, which increases the marketing options, while lowering per head marketing costs.

It is important to remember that reaching the desired grade or body condition score (BCS) helps to avoid price discounts. Cows with a BCS in excess of 6 will likely be subject to a discount for too much external fat, especially when marketed directly to the packing plant. Likewise, cows that grade USDA Utility and Commercial are typically discounted if they have too much external fat.

Producers should also be aware of discounts on carcasses that are too light. Cows yielding a carcass weighing less than 181 kg will likely be discounted \$0.33 per kg or more. Cows that grade USDA Canner are the most likely to

receive this discount. The best way to avoid such discounts is to not market cows with a BCS of 4 or less.

The research reported here assumed the primary feed source was cool season forages on improved pasture, which implies a temperate winter climate. Consequently, the expenses shown in Table 2 reflect a grazing operation. A cull cow management program, however, can be effective with hay and/or cheap alternative feeds available in some years and at some locations. These could include crop residues, corn gluten feed (wet or dry), broiler litter, whole cottonseed, soybean hulls, rice bran, corn or sorghum silage, and haylage, to name a few. Given a feeding regime, then, the key question centers on the typical seasonal price trends. Are they sufficient to generate returns that exceed the cost of overwintering cull cows?

The results suggest potential to increase cow-calf enterprise profitability by properly managing culled breeding stock. However, there may be barriers that prevent successful addition of the cull cow enterprise into the farm or ranch plan. For example, the resource base, including space and time, on a given operation may be inadequate to support cull cows in addition to the remaining herd. Or the relative profitability of the cull cow enterprise may not be sufficiently competitive to displace other enterprises, stocker cattle, for example, for use of the operation's limited resources. Thus, individual managers

should consider how the cull cow enterprise fits into the whole farm or ranch plan before deciding to feed cull cows through the winter.

Literature Cited

- AAEA Task Force on Commodity Costs and Returns. 1998. Commodity Costs and Returns Estimation Handbook. Ames, Iowa: Amer. Agr. Econ. Assoc.
- Boyles, S. Undated. Feeding Cull Cows. Ohio State Univ. Ext.n Serv. <http://www2.ag.ohio-state.edu/~beef/library/cull.html> (Date of last access: 15 May, 2001)
- Gill, R. 1998. Marketing Cull Cows – Understanding What Determines Value. <http://agnews.tamu.edu/drought/drght-pak98/drght11.html> (Date of last access: 15 May, 2001)
- Fueze, D.M. 1996. Feeding and Marketing Cull Cows. Research Report 96-2. Managing for Today's Cattle Market and Beyond. South Dakota State Univ. <http://ag.arizona.edu/AREC/WEMC/TodaysCattlePub.html> (Date of last access: 15 May, 2001)
- Rasby, R., R. Selley, and T. Klopfenstein. 2000. Grazing Crop Residue. Nebraska Coop. Ext. EC 98-278-B.
- Robison, L.J. and P.J. Barry. 1996. Present Value Models and Investment Analysis. Northport, Ala: The Academic Page.
- Schnell, T.D., K.E. Belk, J.D. Tatum, R.K. Miller, and G.C. Smith. 1997. Performance, Carcass, and Palatability Traits for Cull Cows Fed High Energy Diets for 0, 14, 28, 42, or 56 Days. J. Anim. Sci. 75:1195-1202.
- Spreeen, T.H. and J. Simpson. 1992. Seasonality of Cow Prices. 41st Annual Florida Beef Cattle Short Course Proc.. Dept. of Ani. Sci., Univ. of Florida, Gainesville, Fla. <http://gnv.ifas.ufl.edu/~animal/short92/SPREEN.HTM> (Date of last access: 15 May, 2001)
- Torell, R., B. Bruce, and G. Myer. 1997. What is a Cow Worth? Nevada Cattlemen's Assoc. Spec. Publ. 97-1:CL955-1.
- Torell, R., B. Bruce, B. Kvasnicka, and T. Ringkob. 1998. Marketing Alternatives of "B" Maturity Cattle. Univ. of Nevada Coop. Exten. Fact Sheet 98-17.

Perspectives on water flow and the interpretation of FLIR images

S. L. LARSON, L. L. LARSON, AND P. A. LARSON

Authors are NASA EPSCoR Postdoctoral Research Associate, Department of Physics, Montana State University, Bozeman, Mont. 59717; Professor, Department of Rangeland Resources, Oregon State University, Corvallis, Ore. 97331; Forester, La Grande, Ore. 97850.

Abstract

Airborne infrared thermal radiography has been proposed as a tool which may be used to monitor the water temperature along the network of streams and rivers which compose a watershed. The proponents of this method correlate vegetative shadows on a stream channel with reduced infrared radiation (IR) reception in the radiographic data to suggest that the water temperature is reduced in such areas.

Two methods are employed to demonstrate that this interpretation of the data is in error. First, the fundamental principles of thermodynamics are employed to show that if the stream is in fact flowing, the water affected by any cooling process cannot remain in the vicinity where it was cooled. Second, temperature data taken from a stream channel are used to show that the water flowing in the channel is essentially unaffected by the patterns of vegetative shade on the surface of the channel.

Resumen

La radiografía térmica infrarroja transmitida por aire ha sido propuesta como una herramienta la cual puede ser utilizada para monitorear la temperatura del agua a lo largo de la red de corrientes y ríos que componen una cuenca hidrológica. Los proponentes de este método correlacionan las sombras vegetativas sobre el canal de la corriente con una recepción reducida de radiación infrarroja (IR) en los datos radiográficos para sugerir que la temperatura del agua es reducida en tales áreas.

Se emplearon dos métodos para demostrar que esta interpretación de los datos esta equivocada. Primero, los principios fundamentales de la termodinámica son empleados para mostrar que si la corriente esta fluyendo, el agua afectada por cualquier proceso de enfriamiento no puede permanecer en la vecindad de donde fue enfriada. Segundo, datos de temperatura tomados de un canal de corriente son usados para mostrar que el agua fluyendo en el canal esencialmente no es afectada por los patrones de sombra vegetativa sobre la superficie del canal.

Key Words: Water flow, stream temperature, FLIR imaging

Current efforts to combat reductions in salmon populations in the Columbia River Basin have led to the development of a wide variety of water management plans in the composite watersheds which seek to address issues relating to the water quality in fish habitats. At the heart of many of these plans is a desire to control the temperature of the streams in a watershed, since elevated water column temperature is the single most common water-quality violation for streams in the Pacific Northwestern states (Clean Water Act 303(d) listings for Washington, Oregon and Idaho). In each case, water temperature management must be addressed through the Total Maximum Daily Load (TMDL) provision of the Clean Water Act.

To monitor the stream temperatures in many watersheds, FLIR (Forward Looking Infrared Radiometer) imagery is being employed as a method of monitoring and directly measuring temperatures on a stream. A sample FLIR image, a paired aerial photograph taken at the same time, and the estimated water temperatures implied by the FLIR image are shown in Figure 1 (Oregon Department of Environmental Quality (1999a)). Proponents of FLIR monitoring suggest that the correlation between the white light shadows in the aerial photograph and the change in infrared signature in the FLIR data demonstrates the cooling effect of shade on the stream.

This paper considers the time it takes a body of water to cool, and explores how the signature of resulting temperature change should manifest itself in a wide area monitoring system, such as FLIR. This is shown in 2 ways: first, through a theoretical analysis based on fundamental principles of thermodynamics, and second, through collection of column temperature data directly in the water of an area similar to that shown in Figure 1.

The paper is organized in 7 parts, as follows. The effect of the flow rate on the water is analyzed to show that the coolest 'temperatures' in the FLIR images should not correspond exactly with the shaded regions in the companion aerial photograph. Examples of using the theoretical results are given, and data taken directly from a partially shaded stream is presented to show the error in the interpretation of the FLIR images. Finally, speculations are offered as to the cause in the misinterpretation of the FLIR data, and summary and conclusions are presented. An appendix presents a rigorous derivation of the mathematical results presented in the paper.

The Effect of Water Flow on Temperature Profiles

If water is to be cooled in any thermodynamic system (e.g., in a stream in a watershed), one must first determine how much heat energy must be dissipated to obtain the desired temperature, and

Fig. 1. An example of FLIR data and the accompanying temperature scale interpretation from the Oregon Department of Environmental Quality. The claim is that the mixed water column in the shade of the shoreline vegetation is cooler than water in open sunlight, evidenced by the correlation between shadows in the aerial photograph and a drop in the infrared signal of the FLIR data in the same region. On the scale of the photograph, this change occurs over several meters (e.g., near the lower ellipse, the temperature is shown as $T_i = 19^\circ\text{C}$ in the open water, but at the center of the ellipse is $T_f = 17^\circ\text{C}$).

secondly one must account for the transfer of this heat out of the system (i.e., out of the water). These quantities can be determined using standard, basic principles from thermodynamics (see, for example, Serway (1997), or Halliday and Resnick (1988)).

To conduct this analysis, one needs to use 2 quantities together: the total heat energy to be removed, Q , and the rate of heat flow, H . For a given change in temperature, $\Delta T = T_f - T_i$, the amount of heat which must be removed from the system is given by

$$Q = c m \Delta T = c m (T_f - T_i) \quad (1)$$

where Q is the heat energy, c is the specific heat of the material, m is the mass of the material, and T_f and T_i are the final and initial temperatures of the system. The transfer of heat energy out of a system cannot occur instantaneously; it takes a finite amount of time and depends on the thermal conductivity of the surrounding environment. The heat energy is conducted away from the system and dumped into some thermal reservoir which is at constant temperature, T_r . The rate, H , at which heat can be conducted out of a system and deposited in the reservoir is given by

$$H = \frac{Q}{\Delta t} = k A \frac{(T_i - T_r)}{d} \quad (2)$$

where Q is the total heat energy (computed from Eq. 1) which must be conducted away, Δt is the time it takes the heat to

flow away, k is the thermal conductivity of the medium connecting the system to the reservoir where the heat is dissipated, A is the surface area at the interface between the system and the conducting medium, d is the distance over which the heat must be conducted, T_i is the temperature of the system being cooled (or heated), and T_r is the temperature of the thermal reservoir where the heat is being dissipated. Note that when $T_i > T_r$, heat energy flows out of the system (e.g., out of a body of water and into a thermal reservoir, with $H > 0$). When $T_i < T_r$, heat energy flows into the system (e.g., into a body of water from the thermal reservoir, with $H < 0$).

By substituting the expression for Q from Eq. (1) into Eq. (2), one can use algebra to solve for the time, Δt , it would take to dissipate the heat energy in the water, yielding

$$\Delta t = \frac{m c d (T_f - T_i)}{k A (T_i - T_r)} \quad (3)$$

The time, Δt , is the key element in determining how the flow of the water should affect the thermal profile of the stream. The speed v with which the water flows over a given horizontal distance is related to the time by

$$v = \frac{\ell}{\Delta t} \Rightarrow \Delta t = \frac{\ell}{v} \quad (4)$$

Substituting this into Eq. (3), and solving for ℓ yields

$$\ell = \frac{v m c d (T_f - T_i)}{k A (T_i - T_r)} \quad (5)$$

For the application of interest (the transfer of heat energy in a stream), it is useful to cast this result in terms of parameters which describe the physical characteristics of the stream by eliminating the mass m in Eq. (5). The mass can be expressed in terms of the density of water, ρ , and the volume of the stream being considered, $V = hA$, where h is the depth of the stream channel. With these 2 quantities, the mass can be written as

$$m = \rho V = \rho h A \quad (6)$$

Substituting this into Eq. (5), one arrives at the final expression for the distance ℓ :

$$\ell = c \rho \frac{v h d (T_f - T_i)}{k (T_i - T_r)} \quad (7)$$

This is the distance over which a body of water of depth h will cool from a temperature T_i to a temperature T_f if it is connected to a thermal reservoir (heat dump) at temperature T_r . The connection is made through a conducting body with a depth d and a thermal conductivity k . Since cooling processes are being considered, the value for computed from Eq. (7) will always be negative (since $T_f < T_i$ and $T_i > T_r$); the absolute value should be taken to give a proper, measurable distance.

An Example of Water Cooling

Let us consider the implications of the result presented in Eq. (7). Consider a stream, described by the physical param-

Table 1: Example Physical Stream Parameters

Quantity	Symbol	Value
Depth	h	0.5 m
Flow Rate	v	0.25 m/s
Initial water temperature	T_i	21° C
Final water temperature	T_f	20° C
Conduction depth	d	1 m
Thermal conductivity (granite)	k	2.5 W/(m°C)
Thermal reservoir temperature	T_r	15° C
Density of water	ρ	1000 kg/m ³
Heat capacity of water	c	4190 J/(kg°C)

ters given in Table 1. Since fine sediments are considered to be detrimental in salmonid habitats, the streambed is assumed to be coarse granitic substrate.

Using these numbers to evaluate Eq. (7), water which is cooled solely by interaction with the streambed requires a distance of ℓ 35 km to cool the stream by 1° C.

Another possible thermal reservoir where heat could be deposited is the atmosphere. If the atmosphere is cooler than the water, heat energy will flow from the stream surface and dissipate into the air. The methods outlined here may again be used to estimate the distance the water will traverse before the atmosphere could cool it by a single degree Centigrade. Assume that the air reservoir maintains a constant temperature of $T_r = 15^\circ\text{C}$, and is separated from the stream by a $d = 1$ m thick conducting zone. Air is a relatively poor thermal conductor, with a thermal conductivity of $k = 0.026\text{ W/(m}^\circ\text{C)}$. Using these numbers, water cooled solely by interaction with the atmosphere over a distance of 10 m would cool only by $2.98 \times 10^{-6}^\circ\text{C}$; small fractional changes in temperature such as this are all but undetectable using field equipment.

Implications for FLIR Data Analysis

The implications of this result have important consequences for the interpretation of FLIR data. As indicated in Figure 1, the current analysis procedures using FLIR data exactly correlate the shadows in an aerial photograph with regions of supposed cooler stream temperatures. In Figure 1, the data scale would imply that stream temperatures drop by an amount $\Delta T \sim 1^\circ\text{C}$ to 2°C over the course of approximately 2 meters (the distance between open sunlight and fully shaded areas). Based on the analysis presented above, this cannot be the case, since the fact that the water flows implies that the cooler temperatures should lie some dis-

tance ℓ downstream from the cooling influences.

To reconcile these differences, actual water column temperatures were measured on a stream, to better understand what differences should be observed between the sunlit and shaded areas.

Data was collected over 2 clear days with no clouds, during late summer when the solar angle was $\sim 54^\circ$ at noon standard time. Ten data-logging thermistors (Onset Computer Corp., Pocasset, Mass.) were distributed along a partially shaded stream channel, as shown in Figure 2. The thermistors were spaced 3 meters apart, and suspended 25 cm below the water's surface, to measure the temperature of the mixed water column. Standard thermister protocol was followed with thermister validation occurring at 2 known temperatures; stowaway temperature loggers have a

manufacturer specified accuracy of $\pm 0.2^\circ\text{C}$ and recorded temperatures at 1 hour intervals. The approximate flow rate of the water was 0.3 m/s and was estimated using a pygmy flow meter. Over the course of the day, the Sun tracked across the sky, and the pattern of shade on the stream changed. Thermistors which began the experiment in sunlight move into shade, and vice versa, over the course of time. The data from the thermistors is presented in Table 2.

As an example, data from Table 2 is plotted in Figure 3. For clarity, only the readouts from 2 of the 10 thermistors are plotted, with indicators marking the approximate times when each was shaded. The temperature readout from each of the thermistors closely follows the other, showing no correlation with illumination by the Sun. In particular, thermister #6 was illuminated for 6 continuous hours, and showed no drastic increase in the water temperature.

Observations and Conclusions

The theoretical analysis presented at the start of this paper, and the data presented in successive sections clearly show that the interpretation of the FLIR data for measuring stream temperatures is in error.

Fig. 2. The site for the experiment was along a stream channel running east west. The stream is shaded by a closed canopy for 1 km above the site and throughout the area where the temperature data was taken (canopy cover on the north side of the channel has been omitted from the figure for clarity). Ten thermistors were placed in 25 cm of water, every 3 m along both sides of the stream (marked by "x" at each location in the figure). The instruments recorded the temperature of the water once each hour. The daily motion of the Sun from east to west through the southern sky is indicated. As the position of the Sun changes, the pattern of shade and illumination on the stream channel changes, moving individual thermistors from light to shade.

Table 2. Thermister Temperature Data, °C. The cells of the table are shaded if the thermister was in shaded water at the time of the temperature measurement, and are unshaded if the thermister was in sunlit water at the time of the temperature measurement. The last row of the table, %Sun, indicates what percentage of time during the experiment each thermister was in full sunlit water. All temperatures given in °C.

Time	Thermister ID Number									
	#1	#2	#3	#4	#5	#6	#7	#8	#9	#10
5:34	10.0	10.0	9.9	9.9	9.9	9.8	9.9	9.9	9.9	9.9
6:34	9.4	9.4	9.6	9.6	9.6	9.4	9.6	9.6	9.6	9.6
7:34	9.4	9.4	9.2	9.2	9.3	9.2	9.3	9.2	9.3	9.2
8:34	8.9	8.9	9.0	9.0	9.0	8.9	9.0	9.0	9.0	9.0
9:34	8.9	8.9	8.9	8.9	8.9	8.7	8.9	8.9	8.9	8.9
10:34	8.9	8.9	8.9	9.0	9.0	8.9	9.2	9.2	8.9	9.0
11:34	8.9	8.9	9.0	9.0	9.2	9.2	9.3	9.3	9.0	9.3
12:34	9.4	9.4	9.3	9.3	9.4	9.3	9.4	9.6	9.3	9.6
13:34	9.4	9.4	9.4	9.4	9.6	9.4	9.6	9.8	9.4	9.8
14:34	9.4	9.4	9.3	9.3	9.3	9.3	9.4	9.6	9.3	9.4
15:34	9.4	9.4	9.2	9.2	9.3	9.2	9.3	9.3	9.3	9.3
16:34	8.9	8.9	9.0	9.2	9.0	9.0	9.2	9.2	9.2	9.2
17:34	8.9	8.9	8.9	8.9	8.9	8.7	8.9	8.9	8.9	8.9
% Sun	50%	67%	42%	17%	33%	50%	42%	58%	58%	50%

The most likely source of this error is that the data processing of the FLIR images has not accounted for all sources of infrared radiation, which should include: emitted radiation from the water, reflected radiation from the water (the reflected radiation could originate from several sources, be it direct radiation from the Sun, or reflected IR irradiance from the sky), and ambient sources of filtered radiation in the atmosphere and surrounding landscape scattering into the camera.

A possible argument against the results presented here is related to the question of what temperature FLIR data supposedly measures: the global temperature of the body of water, or the surface temperature of the water (Oregon Department of Environmental Quality (1999b)).

If FLIR data is a direct measure of the global water temperature, then the analysis presented here firmly demonstrates that the temperature interpretation (e.g., in Figure 1) is in error.

If FLIR data measures only the surface temperature of the water, then there are only 3 ways in which to interpret FLIR data as a monitor of water quality.

(1) The first possible interpretation is that the surface temperature of the water has nothing to do with the temperature of the water at depth. If this were the case, then FLIR data would be useless for monitoring water quality, and the technique should be abandoned.

(2) The second possibility is that the surface temperature of the water is relat-

ed to the temperature at depth, but is not the same. If this were the case, then changes in surface temperature should mimic changes in temperature at below the surface (e.g., if the surface cools, the sub-surface water should also cool). As

the analysis and data presented in this paper show, stream temperature does not change on short scales below the surface. As such, the suggestion of surface temperature changes on short scales by FLIR data is in no way correlated to the temperature below the surface, indicating an error in the FLIR interpretation.

(3) The last possibility is that surface temperature is exactly the same as the sub-surface temperature. If this is the case, monitoring the surface temperature is exactly the same as monitoring the temperature at depth. Again, the analysis and data presented in this work has shown that temperatures do not change on short scales, and the interpretation of the FLIR data is incorrect.

The use of airborne surveys of a watershed is a powerful technique for monitoring water quality. However, more robust methods will need to be developed if aerial imaging (in any spectrum) is to be used for monitoring water temperature. These techniques should be evaluated and tested against direct measurements of temperature in the streams themselves if they are going to be used to enforce regulatory policy.

Full Sunlight vs. Intermittent Shade

Fig. 3. A graph of the temperature readouts from 2 individual thermisters in the stream channel, showing the negligible effect of shade on the temperature. Solid lines between vertical triangles (Δ) indicate times when thermister #4 was shaded. Dotted lines between inverted triangles indicate times when thermister #6 was shaded.

APPENDIX: Robust Mathematical Treatment and Building Intuition

The results presented in the body of this paper will tend to *underestimate* the effect of the cooling. This can be understood by considering the heat transfer described by Eq. (2). According to this equation, when the temperature difference between the system being cooled and the temperature of the thermal reservoir is large, then the rate at which heat energy is conducted is large as well. As the temperatures approach equilibrium, the flow of heat energy decreases, extending the time it will take for the system to cool completely to a state of equilibrium.

In the analysis previously presented (in the section 'The Effect of Water Flow on Temperature Profiles'), the rate of heat flow is always assumed to be *maximal*, at the rate the heat is transferred when the systems are first placed in thermal contact and cooling begins. A more robust estimate of the cooling distance can be derived by accounting for the change in water temperature over the course of the cooling process. This can be accomplished by taking differential forms of Eqs. (1) and (2), then integrating over the time the water is cooled.

Eq. (1) can be rewritten in differential form by writing the small amount of heat, dQ , required to create a small change in temperature, dT , to yield

$$dQ = mc dT \quad (A1)$$

Similarly, the rate of heat flow can be written as the time-rate of change in the heat energy, yielding

$$H = \frac{dQ}{dt} = kA \frac{(T - T_r)}{d} \quad (A2)$$

which depends on the instantaneous temperature, T , of the body of water. Using Eq. (A1) to express the differential quantity of heat in Eq. (A2) produces a first order differential equation for the time rate of change of the temperature:

$$mc \frac{dT}{dt} = \frac{kA}{d} (T - T_r) \quad (A3)$$

This equation is separable, giving

$$\frac{mc d}{kA} \frac{dT}{(T - T_r)} = dt \quad (A4)$$

which can be integrated over the entire cooling time:

$$\frac{mc d}{kA} \int_{T_i}^{T_f} \frac{dT}{(T - T_r)} = \int_{t_i}^{t_f} dt \quad (A5)$$

The integrals are of a standard form and may be performed analytically, yielding an expression for the cooling time, Δt :

$$\Delta t = \frac{mc d}{kA} \ln \left[\frac{T_f - T_r}{T_i - T_r} \right] \quad (A6)$$

As before, this expression for the time may be converted into an expression for the cooling distance ℓ by using the definition of the speed the water flows, $v = \ell/\Delta t$, to give

$$\ell = \frac{vmcd}{kA} \ln \left[\frac{T_f - T_r}{T_i - T_r} \right] \quad (A7)$$

Again, replacing the mass yields $m = \rho V = \rho hA$ yields

$$\ell = c\rho \frac{vh d}{k} \ln \left[\frac{T_f - T_r}{T_i - T_r} \right] \quad (A8)$$

As in the body of this paper, cooling processes are being considered, so the value for distance computed from Eq. (A8) will always be negative (since $T_f < T_i$, making the argument of the logarithm some fraction between 0 and 1); the absolute value should be taken to give a proper, measurable distance.

The structure of the temperatures in this equation appears subtly different from that shown in Eq. (7). This can be rectified by massaging the form of the logarithm in Eq. (A8). Begin by adding and subtracting the initial temperature, T_i , to the numerator:

$$\frac{T_f - T_r}{T_i - T_r} = \frac{T_f - T_i + T_i - T_r}{T_i - T_r} = \frac{T_f - T_i}{T_i - T_r} + 1 \quad (A9)$$

This allows the final form of the cooling distance to be expressed as

$$\ell = c\rho \frac{vh d}{k} \ln \left[\frac{T_f - T_i}{T_i - T_r} + 1 \right] \quad (A10)$$

which has the same temperature structure as Eq. (7).

The result presented in Eq. (A10) is compared to that of Eq. (7) in Figure 4. As

Cooling Distances

Fig. 4. Comparison of the cooling distances predicted by Eq. (7) and Eq. (A10), as a function of the quantity $u = (T_f - T_i)/(T_i - T_r)$. The u -axis covers only negative u values, showing that only cooling processes are being considered (see text for details). As can be seen, the simple description offered by Eq. (7) underestimates the cooling distance for all possible cooling scenarios.

can be seen, for all possible cooling scenarios, Eq. (7) underestimates the cooling distance. When is it valid to use Eq. (7) and not Eq. (A10)? If one identifies the parameter $u = (T_f - T_i)/(T_i - T_r)$, then the logarithm in Eq. (A10) may be expanded in a Taylor series

$$\ln(1+u) = u - \frac{u^2}{2} + \frac{u^3}{3} - \frac{u^4}{4} + \dots$$

$$-1 < u \leq +1 \quad (\text{A11})$$

If $|u| \ll 1$ (implying either a small required change in water temperature, a large temperature differential with the thermal reservoir, or both), then the logarithm is well approximated by the first term in the Taylor series, which yields Eq. (7). This relationship is apparent in Figure 3, which shows the 2 functions roughly equal at small values of u .

The analysis presented here assumes that the water remains well mixed and of homogeneous temperature. If this condition is relaxed, then the analysis becomes much more difficult because of the presence of thermal gradients across the depth of the water. In this case, the analysis of the temperature evolution is governed by the one-dimensional heat diffusion equation,

$$\frac{\partial T}{\partial t} = \frac{k}{\rho c} \frac{\partial^2 T}{\partial x^2} \quad (\text{A12})$$

Understanding the implications of basic thermodynamic calculations, such as the ones presented in this paper, can be greatly enhanced by developing an intuitive sense of what the equations and results actually mean. Intuitive sense can be developed in 2 ways: by considering extreme limits, and through proportional reasoning.

As an example of an extreme limit to this calculation, one could consider that critics of water temperature regulation might remark that one should refrigerate the streams to meet temperature marks that regulatory agencies have specified for healthy stream environments. Initially, the idea of cooling a stream by technological means appears ludicrous, but the idea is one which can be explored within the context of this analysis to illuminate the difficulty of actually cooling a body of water. Because of its high specific heat, heat energy is not easily dissipated from a body of water. To demonstrate this, consider the following hypothetical situation, which demonstrates the difficulty of cooling

water. Imagine refrigeration units could be installed in the streambed. This system would connect the water to a cooling reservoir at temperature $T_r = 0^\circ \text{C}$ through a metal which conducts heat very effectively (for example, copper which has a thermal conductivity of $k = 401 \text{ W/(m } ^\circ\text{C))}$. In this purely idealized situation, the requisite distance to cool a stream (only 1/2 meter deep) by 1°C would be $\ell = 62 \text{ m}$.

When confronted by a result such as Eq. (7), it is often useful to expand the formula into an expression which depends only on the physical parameters which describe the system under consideration, in this case a stream in a watershed. This process allows one to understand in very simple terms, what will affect the transfer of heat energy in the system using proportional reasoning.

To simplify our understanding of the implications of Eq. (7), let us make the following identifications:

$$\Delta T_w = T_f - T_i \quad \text{change in water temperature}$$

$$\Delta T_o = T_f - T_r \quad \text{initial difference between water temperature and thermal reservoir}$$

With these identifications, Eq. (7) may be rewritten as:

$$\ell = c\rho \frac{vhd}{k} \frac{\Delta T_w}{\Delta T_o} \quad (7)$$

The specific heat of water, c , and the density of water, ρ , are constants which cannot be changed, leaving only 6 parameters which might vary between any given stream. It is a simple matter to consider what will increase and decrease the time (or in this case, the distance ℓ) required to

transfer heat energy out of a system using proportional reasoning.

For *direct proportionality*, an increase in parameter value increases the distance over which the stream cools, and a decrease in value decreases the distance. For *inverse proportionality*, an increase in parameter value *decreases* the distance over which cooling occurs, while smaller values increase the cooling distance. For each of the 6 parameters in Eq. (7), their effects are summarized in Table 3.

Literature Cited

- Halliday, D. and R. Resnick. 1988. Fundamentals of Physics, Extended Third Edition. John Wiley & Sons, New York.
- Oregon Department of Environmental Quality. 1999a. Upper Grande Ronde River sub-basin temperature total maximum daily load (TMDL). Portland, Ore.
- Oregon Department of Environmental Quality. 1999b. Tualatin basin temperature total maximum daily load (TMDL). Portland, Ore.
- Serway, R. 1997. Physics for Scientists and Engineers with Modern Physics, Fourth Edition. Saunders College Publishing, New York.

Table 3. Effect of Change in Parameters on Cooling Distance

Parameter	Change	Effect on ℓ
v	increase flow speed	increase
	decrease flow speed	decrease
h	increase water depth	increase
	decrease water depth	decrease
d	increase conduction layer	increase
	decrease conduction layer	decrease
k	increase thermal conduction	decrease
	decrease thermal conduction	increase
ΔT_w	increase temperature change	increase
	decrease temperature change	decrease
ΔT_o	increase thermal gradient	decrease
	decrease thermal gradient	increase

Cull cow management and its implications for cow-calf profitability

RANDALL D. LITTLE, ALLEN R. WILLIAMS, R. CURT LACY, AND CHARLIE S. FORREST

Authors are Associate Professor, Department of Agricultural Economics, Associate Professor, Department of Animal and Dairy Sciences, Graduate Research Assistant and Extension Specialist, Department of Agricultural Economics, Mississippi State University, Mississippi State, Mississippi 39762. Dr. Little is the corresponding author. (662) 325-2884; fax: (662) 325-8777; email: little@agecon.msstate.edu

Abstract

Selling culled breeding livestock is often viewed as "just another chore." Most cull sales are made in the fall, after calves are weaned and cows are pregnancy checked and open. Since cull cow sales comprise from 15 to 30% of a cow-calf enterprise's gross revenue, perhaps they should be viewed as a potential profit center.

This paper uses enterprise budgets and sensitivity analyses to illustrate cull cow management strategies that overcome certain physical and economic factors that limit the profitability of fall cow sales. The key limiting physical factor is often poor body condition, which results from the combined effect of lactation and deteriorating forage quality. The key economic factor is a seasonal price low, generated by a large beef supply in the fall.

The results suggest potential, with adequate, low-cost feedstuffs, to increase net returns by properly managing cull breeding stock. In only 1 year during the 10-year period, 1990–1999, was selling cull cows in the fall the more profitable option. Over that time period, the net present value of spring cull sales averaged about \$30 per cow more than selling cull cows in the fall.

Key Words: seasonal price trends, net present value

Selling culled breeding livestock is often viewed as "just another chore." Most sales are made in the fall, after calves are weaned and cows are pregnancy checked and found to be open. Since cull cow sales comprise from 15 to 30 percent of a cow-calf enterprise's gross revenue, the culling activity should, perhaps, be viewed and managed as a potential profit center.

The purpose of the research reported in this paper was to determine if cull cow management strategies using cool season forages on improved pastures can overcome certain physical and economic factors limiting the profitability of fall cull sales. The key physical factor that frequently limits the profit potential of fall sales is poor body condition. Cows typically start the fall season in poor body condition because of the combined effect of the demands of lactation and the deteriorating quality of summer forages. The key economic effect is a seasonal price low, generated by large fall supplies (Fuez 1996, Spreen and Simpson 1992). While the model used reflects a production situation typical throughout much of the Southeastern U.S., the theoretical frame-

Resumen

La venta de ganado para crianza que es de baja producción (o no productivo), es una actividad que normalmente es considerada como una "tarea rutinaria mas" en el manejo del ganado. La mayor parte de las ventas de este ganado se lleva a cabo durante la época de Primavera, después que las crías han sido destetadas y las vacas han sido revisadas y comprobadas que están libres de preñez. La venta de ganado de baja producción abarca entre un 15 a 30 por ciento del ingreso bruto de las operaciones de vaca para cría, por lo que esta actividad debería ser vista como una potencial fuente de ganancia.

Esta publicación hace uso de presupuesto de operaciones y análisis de sensibilidad para ilustrar estrategias en el manejo de ganado de baja producción, que ayudan a eliminar o reducir ciertos factores físicos y económicos que limitan la alta rentabilidad en las ventas de ganado durante la Primavera. El principal factor físico limitante, es a menudo una pobre condición corporal del ganado, lo cual es el resultado del efecto combinado de pobre lactación y la deteriorada calidad del forraje. El principal factor económico es un bajo precio temporal durante la época de Primavera, generado por una alta oferta de reses durante la época de Otoño.

Los resultados del análisis presentado indican un incremento potencial en el retorno neto, dado un manejo apropiado del ganado con una adecuada alimentación, utilizando material alimenticio de bajo costo. Solamente en un año durante el periodo de 10 años (1990–1999), la opción de mayor ganancia fue vender el ganado de baja producción durante el Otoño. Durante este mismo periodo el Valor Presente Neto (VPN) de las ventas de ganado de baja producción durante la Primavera tuvo una ganancia promedio de \$30.00 mas alto por cabeza, comparadas con las ventas en Otoño.

---

work and methods are pertinent to any place quality cool season forages can be produced.

Cull Cow Grades

Cull cows are sold based on USDA slaughter grades, which can be related to body condition scores (BCS) (Table 1). The BCS is a system that uses visual appraisal to determine the degree of fat or muscle loss an animal exhibits. Body condition is scored from 1 to 9, with 9 being the fattest classification. An evaluation of fat

Table 1. Cull cow grades and characteristics.

Grade	Dressing Percent	Lean Content of Trimmings	Cow BCS
Canner	40-46	90-92	1-3
Cutter	45-49	88-90	4-5
Utility			
Boning	50-52	78-83	5-9
Breaking	52-54	76-82	6-9
Commercial	55-60	70-80	5-9

Source: Gill (1998).

deposits at various locations of the body (back, tail head, pins, hooks, ribs, and brisket) is made to estimate the potential carcass cutout quality. An animal with a score of 5 should look average without being too thin or too fat. Animals with a score of 3 or below will have little or no fat and are scored on the degree of muscle loss.

The USDA Utility and Commercial cows usually command the best prices and have the highest dressing percentage (50 to 60 percent). They typically have body condition scores of 5 or higher. Cows that grade USDA Utility or Commercial usually have enough intramuscular fat (marbling) and muscling for primals to be pulled from the carcass (particularly cuts from the rib and loin) and marketed outside of the ground meat trade. This greatly enhances the value of a carcass, which, in turn, generates premiums paid for the higher quality animals.

Cow Prices - Historical and Trends

Figure 1 illustrates the volatility slaughter cow prices exhibit over time. For the 19-year period shown, average monthly cow prices (in nominal dollars) ranged from a high of \$1.26 per kg to a low of about \$0.64 per kg. Also evident in Figure 1 is the cyclical nature of cattle prices.

Not only is price variability an important factor, but seasonal price trends (Boyles, Spreen and Simpson 1992, Torell et al. 1998) and the price differentials between grades of cull cows (Gill 1998) are also critical to effective cull cow management and marketing decisions. On average, the difference in price between USDA Utility and Cutter is about \$0.09 per kg (Fig. 2). Figure 2 also shows the seasonal price patterns inherent in slaughter cow prices. Prices normally peak in March and decline steadily through November. Torell et al. (1997) note that "flesh adds weight and that weight adds value" (p. 955-2). Thus, if possible, it may be advantageous to target marketing of cull cows in the early spring at a body

condition score of 5-6 and avoid marketing in the fall, particularly if cows are in poor body condition.

Materials and Methods

It may be profitable for producers to take advantage of favorable seasonal price trends and the premiums for animals in better body condition. The analysis reported in this paper used a partial budgeting approach in which the cull cow selling activity was treated as an independent livestock enterprise. An enterprise budget for the cull or stocker cow activity was developed (Table 2). Interest is charged on the purchase of the stocker cow over the 6-month period; the other expense items

Fig. 1. Monthly Average Utility Cow Prices in Mississippi, 1981 to 1999.

Fig. 2. Seasonal Price Patterns for Cull Cows in Mississippi, 1990 to 1999.

Table 2. Estimated Income and Expenses for Overwintering Cull Cows in Mississippi.

Item	Unit	Price (dollars)	Quantity	Amount (dollars/cow)
INCOME				
Cull cows (Utility) 80%	Kg	1.12	(499.0*80%)	446.69
Cull cows (Cutter) 20%	Kg	1.01	(453.6*20%)	91.26
Total Income			537.95	
Total Income Per Kg Sold			1.10	
DIRECT EXPENSES				
Canner/Cutter	Kg	0.86	362.9	311.76
Death Loss	%	0.01	312	3.12
Pasture Rental (fescue)	Ha	49.42	0.607	30.00
Protein Supplement	Kg	0.2425	81.65	19.80
Hay	Kg	0.0782	508	39.72
Salt/minerals	Head	4.00	1.00	4.00
Labor	Hrs.	6.50	1.50	9.75
Veterinary/health mgt.	Head	5.00	1	5.00
Mach., fuel, oil	Head	2.50	1	2.50
Marketing	Head	10.00	1	10.00
Supplies & misc.	Head	5.00	1	5.00
Interest (for 6 months)	Dol.	0.090	376.21	16.70
Total Direct Expenses				457.35
Breakeven Selling Price (weighted average, \$/Kg)				0.934
Returns above Direct Expenses				80.65
Net Returns per Kg sold				0.16

are assumed to be distributed equally over the period.

The budget presented in Table 2 was based on the assumption that cows will graze fescue from 1 November to 1 May. Cows were assumed to enter the program at 363 kg (at a body condition score of 4 or less), grading USDA Cutter or Canner. It is recognized that not all culled cows will grade so poorly, clearly there are other reasons besides poor body condition why some cows are open, but this is a major criterion in the culling decision.

An average daily gain of 0.757 kg over the 180 day feeding period was assumed. It is estimated that most cows gaining at this rate will grade USDA Utility (body condition score of 5–6) by early spring. Research has shown that about 80% of animals should reach this desired body condition (Schnell et al. 1997, Rasby et al. 2000); hence it was assumed that 80 percent of the cull cows grade Utility and the remainder grade Cutter. Cows that grade Utility were assumed to weigh 499 kg at the time of sale, while the cows grading Cutter were assumed to weigh 454 kg.

Real prices (1999 = 100) were used to eliminate the effect of inflation on prices received, so prices across years would be more directly comparable. The consumer price index was used as the deflator. The average Utility and Cutter prices (in real dollars) received for the sale of cull cows in the spring were \$1.12 and \$1.01 per kg, respectively. The producer was assumed to pay about \$0.86 per kg for Cutter grade cull cows in the fall or to value the ranch-

produced cull herd as an opportunity cost.

To facilitate comparison of fall and spring cull sales within a cow-calf operation, the net present value (NPV) of the returns for sale in the spring was calculated. Net present value is an investment analysis technique that takes into account the time value of money and the timing of cash flows (Robison and Barry 1996).

Returns were discounted for the 180 days assumed in the cull cow enterprise using a 10% annual discount rate. While a discount rate between 6 and 9% is recommended (AAEA Task Force on Commodity Costs and Returns 1998), ten percent was used to

build in an additional risk premium for extending ownership of the culled cows. A lower discount rate would slightly increase the present value of the returns from selling cull cows in the spring.

The NPV analysis includes as gross income the returns from selling 80% Utility grade and 20% Cutter grade cows in April. Average real April prices were used. All estimated expense items from the budget in Table 2 were included except the cost of cow purchase, since this reflects an attempt to portray a cow-calf producer's decision to retain ownership of cull cows, as compared to a stocker cow enterprise. Instead, an opportunity cost of holding cows was included, based on income foregone had the returns from the fall cull sale been invested at 6%. Net returns from the sale of culls in the fall and the corresponding NPV of the net returns from the sale of those cows the following spring were calculated using price data from the fall of 1989 to the spring of 1999.

Results

Using 10-year average real prices for cows and the estimated expenses of Table 2, the expected returns above direct expenses were \$80.65 per cow. Given the expenses assumed in the cull cow budget, including the 10-year average purchase price for Cutter grade cows in the fall, the break-even selling price for the cows in the spring, weighted for the percentage expected to grade Utility and Cutter, is an estimated \$0.934 per kg.

Figure 3 shows the buy-sell margins, in nominal dollars, for the past 10 years. The

Fig. 3. Buy/Sell Margins for Cull Cows in Mississippi, 1990 to 1999.

Table 3. Estimated Returns above Specified Expenses (dollars per cow) for Different Purchase and Selling Prices.

Purchase Price (\$/Kg)	Selling Price (\$/Kg)				
	\$0.79	\$0.83	\$0.88	\$0.93	\$0.97
	(\$/Cow)				
\$0.79	-43.69	-22.09	-0.49	21.11	42.71
\$0.75	-26.81	-5.21	16.39	37.99	59.59
\$0.74	-9.93	11.67	33.27	54.87	76.47
\$0.66	6.95	28.55	50.15	71.75	93.35
\$0.62	23.83	45.43	67.03	88.63	110.23
\$0.57	40.71	62.31	83.91	105.51	127.11
\$0.53	57.59	79.19	100.79	122.39	143.99

Table 4. Estimated Returns above Specified Expenses (dollars per cow) for Different Total Feed Costs (dollars per cow) and Selling Prices.

Total Feed Costs	Selling Price (\$/Kg)				
	\$0.79	\$0.83	\$0.88	\$0.93	\$0.97
	(\$/Cow)				
\$60.00	-38.38	-16.78	4.82	26.42	48.02
\$70.00	-48.60	-27.00	-5.40	16.20	37.80
\$80.00	-58.82	-37.22	-15.62	5.98	27.58
\$90.00	-69.04	-47.44	-25.84	-4.24	17.36
\$100.00	-79.27	-57.67	-36.07	-14.47	7.13
\$110.00	-89.49	-67.89	-46.29	-24.69	-3.09

margin, which was calculated by subtracting the October Cutter cow price from the April Utility cow price of the next year, averaged about \$0.20 per kg over the 10-year period, 1990-1999. The range for this margin was from \$0.07 to \$0.38 per kg. Although positive, the margins exhibit variability.

Table 3 presents the returns per cow, assuming different purchase and selling prices. Changes in weight gain and body condition are reflected in the price differentials of Table 3, as those are key determinants of the price received in the spring. The importance of adequate margins between the fall purchase price and the spring selling price is highlighted in Table 3, as returns above direct expenses per cow do not become positive until the difference between the fall and spring prices exceed \$0.08 per kg.

The sensitivity of returns per cow to changes in feed costs is presented in Table 4. Total feed costs, including pasture costs, as reflected in the budget in Table 2, were about \$90 per cow. The returns in Table 4 assume the cull cows are purchased at the 10-year average price for cutter/canner in the fall. These results illustrate the importance of low-cost feed-stuffs, in addition to the adequate price differentials from fall to spring discussed previously, to a profitable stocker cow enterprise.

The net present value of spring cull sales exceeded returns from fall sales in all but one (1995) of the 10 years studied (Fig. 4). This year was when the differential between fall and spring prices was least, \$3.00 between the fall of 1995 and spring 1996, and the only time during the

study period when selling in the fall would have been more profitable. The difference between the NPV of the returns above direct expenses from spring cull sales and the sale of culls in the fall is illustrated in Figure 5. The average difference over the 10-year period was about \$30 per cow. As in Table 3, the importance of an adequate price differential between the fall and spring prices to the profitability of holding cows for sale in the spring is highlighted.

Discussion and Conclusions

The objective of this paper was to determine if cull cow management strategies can overcome certain physical and economic factors limiting the profitability of fall cull sales. The key physical factor is often poor body condition, the combined effect of lactation and deteriorating summer forage quality. The key economic effect is a seasonal price low in the fall, due to the increase in quantity supplied in those months.

The results suggest that there is considerable and relatively stable opportunity to boost returns from the sale of cull cows by improving body condition with a cost-effective feeding program and selling them in the spring. In only 1 year during the 10-year study period was selling cull cows in the fall the more profitable option. Over that time period, the net present value of spring cull sales averaged about

Fig. 4. Fall Cull Sales and the Net Present Value of Spring Cull Sales, 1989 to 1999.

Fig. 5. Difference between the Net Present Value of Spring Cull Sales and Fall Cull Sales, 1989 to 1999.

\$30 per cow more than selling cull cows in the fall. Availability of low-cost feedstuffs, whether cool season forages or some other feed, is critical to the success of a cull cow enterprise.

There are several factors to consider when deciding to hold cull cows over for sale in the spring. Producers should estimate the weight and grade of their cull cows or purchased stocker cows. Cows should have the potential to gain 90 to 135 kg on forages and supplement over the winter. Cows must be healthy, open, and have solid mouths to increase the probability of making a profit. Producers should evaluate their markets, and, if possible, put together 40 or more head per lot when selling. This provides a truckload lot, which increases the marketing options, while lowering per head marketing costs.

It is important to remember that reaching the desired grade or body condition score (BCS) helps to avoid price discounts. Cows with a BCS in excess of 6 will likely be subject to a discount for too much external fat, especially when marketed directly to the packing plant. Likewise, cows that grade USDA Utility and Commercial are typically discounted if they have too much external fat.

Producers should also be aware of discounts on carcasses that are too light. Cows yielding a carcass weighing less than 181 kg will likely be discounted \$0.33 per kg or more. Cows that grade USDA Canner are the most likely to

receive this discount. The best way to avoid such discounts is to not market cows with a BCS of 4 or less.

The research reported here assumed the primary feed source was cool season forages on improved pasture, which implies a temperate winter climate. Consequently, the expenses shown in Table 2 reflect a grazing operation. A cull cow management program, however, can be effective with hay and/or cheap alternative feeds available in some years and at some locations. These could include crop residues, corn gluten feed (wet or dry), broiler litter, whole cottonseed, soybean hulls, rice bran, corn or sorghum silage, and haylage, to name a few. Given a feeding regime, then, the key question centers on the typical seasonal price trends. Are they sufficient to generate returns that exceed the cost of overwintering cull cows?

The results suggest potential to increase cow-calf enterprise profitability by properly managing culled breeding stock. However, there may be barriers that prevent successful addition of the cull cow enterprise into the farm or ranch plan. For example, the resource base, including space and time, on a given operation may be inadequate to support cull cows in addition to the remaining herd. Or the relative profitability of the cull cow enterprise may not be sufficiently competitive to displace other enterprises, stocker cattle, for example, for use of the operation's limited resources. Thus, individual managers

should consider how the cull cow enterprise fits into the whole farm or ranch plan before deciding to feed cull cows through the winter.

Literature Cited

- AAEA Task Force on Commodity Costs and Returns. 1998. Commodity Costs and Returns Estimation Handbook. Ames, Iowa: Amer. Agr. Econ. Assoc.
- Boyles, S. Undated. Feeding Cull Cows. Ohio State Univ. Ext.n Serv. <http://www2.ag.ohio-state.edu/~beef/library/cull.html> (Date of last access: 15 May, 2001)
- Gill, R. 1998. Marketing Cull Cows – Understanding What Determines Value. <http://agnews.tamu.edu/drought/drght-pak98/drght11.html> (Date of last access: 15 May, 2001)
- Fuez, D.M. 1996. Feeding and Marketing Cull Cows. Research Report 96-2. Managing for Today's Cattle Market and Beyond. South Dakota State Univ. <http://ag.arizona.edu/AREC/WEMC/TodaysCattlePub.html> (Date of last access: 15 May, 2001)
- Rasby, R., R. Selley, and T. Klopfenstein. 2000. Grazing Crop Residue. Nebraska Coop. Ext. EC 98-278-B.
- Robison, L.J. and P.J. Barry. 1996. Present Value Models and Investment Analysis. Northport, Ala: The Academic Page.
- Schnell, T.D., K.E. Belk, J.D. Tatum, R.K. Miller, and G.C. Smith. 1997. Performance, Carcass, and Palatability Traits for Cull Cows Fed High Energy Diets for 0, 14, 28, 42, or 56 Days. J. Anim. Sci. 75:1195-1202.
- Spreen, T.H. and J. Simpson. 1992. Seasonality of Cow Prices. 41st Annual Florida Beef Cattle Short Course Proc.. Dept. of Ani. Sci., Univ. of Florida, Gainesville, Fla. <http://gnv.ifas.ufl.edu/~animal/short92/SPREN.HTM> (Date of last access: 15 May, 2001)
- Torell, R., B. Bruce, and G. Myer. 1997. What is a Cow Worth? Nevada Cattlemen's Assoc. Spec. Publ. 97-1:CL955-1.
- Torell, R., B. Bruce, B. Kvasnicka, and T. Ringkob. 1998. Marketing Alternatives of "B" Maturity Cattle. Univ. of Nevada Coop. Exten. Fact Sheet 98-17.

Elk management strategies and profitability of beef cattle ranches

WENDY L. F. TORSTENSON, MICHAEL W. TESS, AND JAMES E. KNIGHT

Authors are Research Associate, Professor, and Wildlife Extension Specialist, Department of Animal and Range Sciences, Montana State University, Bozeman, Mont. 59717-2900.

Abstract

Computer simulation was used to determine the effects of wild elk (*Cervus elaphus*) on available forage, cattle herd size, and ranch gross margin in southwestern Montana beef cow-calf production systems. Data collected from 5 southwestern Montana ranches were used to develop input parameters for bio-economic models of elk forage harvest and beef production. Input parameters described ranch resources, animal inventories, and animal management. Cattle herd size ranged from 241 to 1147 head. Elk numbers varied by season within ranch and ranged from 49 to 421 head. Ranches were simulated as currently managed with elk present and with 10, 20, 30, and 100% of the elk removed. Simulated management scenarios were replicated 10 times. Data from each ranch were analyzed by one-way analysis of variance. Cattle herd size, gross margin, and available forage significantly ($P < 0.05$) increased when all elk were removed; however, the magnitude of these effects differed among ranches. Removal of all elk permitted cattle herd size to increase from 7 to 32% across ranches. Annual costs of elk on the 5 ranches (i.e., increase in gross margin from elk removal) ranged from \$5,949 to \$21,152. On an AUM basis, elk costs ranged from \$8.55 to \$14.51. Three management alternatives were evaluated for their potential to recover elk costs: Montana's Block Management Program, coordinated exchange of forage use, and leasing of hunting access. For each ranch, at least one of these management strategies could recover all estimated costs of providing elk habitat. Elk can significantly reduce profits for cow-calf ranches in southwestern Montana. Elk impacts on beef enterprise profits are closely associated with efficiency of resource use by cattle—i.e., ranches with lower unit costs of production lose more gross margin by providing forage for elk compared to ranches with higher production costs.

Key Words: range economics

Beef cattle and elk (*Cervus elaphus*) are important parts of the economy and heritage of the Rocky Mountain West. As native wild ungulates, elk are important components of healthy ecosystems. Elk and cattle use similar habitats and prefer similar diets for much of the year. Because private lands, primarily livestock ranches, provide an important part of annual elk habitat, cattle-elk interactions are important to public resource managers and live-

Resumen

Simulación por computadora fue usada para determinar los efectos del alce silvestre (*Cervus elaphus*) en forraje disponible, tamaño del hato de ganado, y margen bruto del rancho en sistemas de producción vaca- becerro en el suroeste de Montana. Los datos recolectados de 5 ranchos del suroeste de Montana fueron usados para desarrollar parámetros de entrada para modelos bio-económicos del consumo de forraje del alce y la producción de ganado de carne. Los parámetros de entrada describieron los recursos del rancho, inventario y manejo de animales. El tamaño del hato de ganado varió de 241 a 1147 cabezas. El número de alces varió por temporada en el rancho y fluctuó entre 49 a 421 cabezas. Los ranchos fueron simulados tanto como si el alce estuviera presente como si este hubiera sido retirado de los mismos. Escenarios de administración simulados fueron repetidos 10 veces. Los datos fueron analizados por procedimientos de mínimos cuadrados, contabilizando los efectos del alce. El tamaño del hato de ganado, el margen bruto, y el forraje disponible incrementó significativamente ($P < 0.05$) cuando los alces fueron retirados; aunque la magnitud de estos efectos fue diferente entre ranchos. El retirar todos los alces permitió que el tamaño del hato de ganado se incrementara de 7 a 32% entre los diferentes ranchos. Los costos anuales del alce en los 5 ranchos (e.g., incremento en el margen bruto por el retiro del alce) variaron de US\$ 5,949 a US\$ 21,152. Sobre la base de unidades animal por mes (UAM), los costos del alce variaron de US\$ 8.55 a US\$ 14.51. Tres alternativas de manejo fueron evaluadas por su potencial para recuperar los costos del alce: programa de administración por bloque de Montana, intercambio coordinado de uso de forraje, y renta por acceso a la caza del alce. Para cada rancho, al menos una de estas estrategias podría recuperar todos los costos estimados de proveer un hábitat para el alce. El alce puede reducir significativamente las ganancias de ranchos vaca- becerro en el suroeste de Montana. Los efectos del alce en empresas de ganado de carne están asociados con la eficiencia del uso de los recursos por el ganado (e.g., ranchos con bajos costos unitarios de producción pierden mas margen bruto al proveer forraje para el alce, comparados con ranchos con altos costos de producción).

stock producers (Adams 1982, Skovlin 1982, Alt et al. 1992, Henderson and O'Herrin 1992).

Interactions between cattle and elk sharing habitats are complex and determined by many factors (Smith 1961, Vavra et al. 1989). These factors include similarity of feeding strategies, and spatial, temporal and dietary overlap (Mackie 1970; Edge and Marcum 1990, Vavra 1992, Sheehy and Vavra 1996). For competi-

Research was funded in part by USDA-NRICGP.
Journal Series No. 2001-39, Montana Agricultural Experiment Station.
Manuscript accepted 20 Jul. 01.

tion for forage to occur, both cattle and elk must be consuming the same forage species in the same area and the forage species must be in short supply (Murie 1951, Gordan 1968, Wagner 1969, Holechek 1980, Vavra et al 1989, Vavra 1992, Edge and Marcum 1990).

Given the goals of environmental and economic sustainability, when elk and cattle share the same habitats, numbers of both species may need to be reduced in order to prevent damage to the range resource. Assuming cattle prices are above breakeven prices and other sources of income are held constant, a reduction in cattle numbers will reduce ranch profit. For beef producers on private land, most strategies to preserve ranch income involve minimizing competition between elk and cattle and (or) deriving supplemental income from elk. The relative economic benefits of these alternatives have not been studied.

The objectives of our research were to: 1) evaluate the effects of elk populations on profitability of beef cattle enterprises, and 2) compare alternative elk/cattle management strategies for their effects on ranch profitability.

Materials and Methods

Five ranches located in southwestern Montana cooperated in the study. Livestock, wildlife, and management data collected from each ranch were used to develop input parameters for 2 computer simulation models. The first model predicted forage harvest by elk based on number, age, sex, reproduction and season of use. The second model simulated cattle performance and profit for the ranch.

Ranch and Cattle Data

Five ranches were selected as representatives of southwestern Montana. Criteria for selection were that the ranch was a beef cow-calf operation with: a) private land representing a large portion of the resource base, b) revenues from the sale of cattle constituting its primary source of income, and c) migratory and (or) resident elk using the ranch for at least part of the year. Advice on suitable ranches was received from Montana Fish, Wildlife & Parks (FWP) biologists and Montana State University Extension personnel.

Inventories and descriptions of forage resources and cattle grazing strategies were obtained from each ranch. Cattle data included: herd size, genetic composition, replacement strategies, breeding seasons,

health management, nutritional management, marketing practices, and performance measures for reproductive rate, mortality, and growth. Feeding management data included amounts and type of forage, dates when cattle were moved on and off range, along with how each management group was treated (Table 1).

Elk data collection

Estimates of the number of elk on each ranch were obtained from FWP biologists and ranch managers. Yearly flight data (FWP) for elk numbers were used to categorize elk herds into bulls, cows, and calves. Most flights occurred after the hunting season and near the end of winter after a large portion of elk mortality had occurred. Calves were assumed to be 50% male. Taber et al. (1982) constructed static life tables (defined by Begon et al. 1990) based on field studies of Rocky Mountain elk. We adapted their reproductive percentages to determine age distributions within sex. Amount of time and type of activity elk spent on the ranches was determined from interviews with FWP biologists and ranch managers.

Dietary overlap (percentage of elk diet, by season, that would be potentially consumed by cattle if available) was determined from literature reports based on vegetation types that we judged to be relevant to the habitats found on the 5 ranches (Murie 1951, Stevens 1966, Gordon 1968, Mackie 1970, Nelson 1982, Peek 1982, Kasworm et al. 1984). Similarly, spatial overlap (percentage of habitat used by elk, by season, that was used by cattle sometime during the year) was estimated based on literature reports (Smith 1961, Mackie 1970, Skovlin 1982, Witmer and deCalesta 1983, Hart et al. 1991, Yeo et al. 1993) and by interviews with ranch managers and local FWP biologists.

Elk Forage Consumption Model

In an effort to quantify dietary overlap between elk and cattle, many researchers have compared forage intake by elk to the standard AUM. Intuitive reasoning has formed the basis for many estimates of AUM equivalents (Holechek 1980). Several estimates have been based simply on body weight (Murie 1951, Stoddart and Smith 1955, Loomis et al. 1989, Lacey et al. 1993). Calculations based on weight alone risk errors due to differences in gender, animal physiological state, and spatial and dietary overlap (Holechek 1980, Nelson and Leege 1982).

An AUM is a useful, but imprecise method of measuring forage intake (SRM 1989). A more precise measure of what an animal eats would be based on caloric intake. Because energy is usually the limiting nutrient under range conditions, animals eat to meet its energy requirements (Vavra 1992), and intake is expected to vary with gender and physiological state. Because the energy density of forages changes with plant maturity, dry matter intake will change with plant maturity for animals in the same physiological state.

The purpose of our elk model is to simulate forage consumption by wild elk in an effort to quantify dietary overlap between elk and domestic cattle. The model takes into account the different physiological needs of elk as related to age, sex, reproductive status, and time of year, as well as forage quality and dietary and spatial overlap of elk and cattle. The model is deterministic and relatively simple. We emphasize that the primary purpose of the model is to estimate forage removal by an existing elk herd, and not to simulate the dynamics of a herd in response to changing resources. See Appendix for further description of the model and the equations used.

Table 1. Characteristics of ranches simulated.^a

Ranch	1	2	3	4	5
Herd Size	240	368	838	900	1142
Weaning Weight, kg	262	251	257	265	235
Cow Mature Weight, kg	595	550	544	544	550
Conception Rate, %	92	93	92	92	95
Breeding Date	May 21	May 22	May 20	May 10	June 1
Breeding Season, days	75	60	90	50	90
Death Loss, %	2.5	3.0	3.0	5.0	10.0
Native Range, days	132	138	214	85	201
Domestic Pasture, days	38	46	30	136	29
Winter Feeding, days	195	181	121	144	135
Wean & Sale Date	Oct 20	Oct 20	Nov 8	Oct 25	Nov 1

^aHerd Size = number of beef cows exposed to bulls per year, including replacements; Weaning weight = average weaning weight of steers and heifers; Breeding Date = first day of breeding for mature cows, all ranches except #2 bred yearling heifers earlier (Ranch 1 = 14 d, Ranches 3 & 5 = 10 d, Ranch 4 = 30 d); Breeding Season = length of season for mature cows; Death Loss = calves lost from birth to weaning; Domestic Pasture = early spring pasture (Ranch 4) and hay aftermath (all ranches).

Beef Cow-Calf Model

The beef cow-calf model developed by Tess and Kolstad (2000a,2000b) was used to simulate cattle and ranch enterprise performance. The model simulates performance of beef cattle of varying genetic types in response to changes in forage quality and management strategies, and simulates economic performance of beef production systems in response to alternate breeding and management systems. It uses parameters input by the user describing genotypes, mating systems, nutritional characteristics of native range and stored feed, management decisions, input costs, and cattle prices. Importantly, the model simulates performance of ranches of fixed size—i.e., the grazed forage base is a fixed number of AUM. Resource and management data for the ranches used in the simulations are presented in Table 1. Input prices and cattle prices used were averages during 1996.

The beef simulation model produces several measures of system performance. Only 3 statistics will be reported here. Because the model simulates a ranch with a fixed range resource base, adding resources or changing the management of the range forage base can lead to differences in annual cattle herd carrying capacity. Hence, herd size (specifically, the number of cows exposed for breeding) provides a measure of carrying capacity. Ranch gross margin, computed as gross income minus variable costs, provides a measure of profitability for each ranch when the ranch is constrained to a fixed range resource base. This economic measure considers some expenses as fixed—for example, home raised hay, grazed forage, property taxes, and some family labor. In contrast, unit cost of production (specifically, input cost per kg of steer equivalent weight sold) provides a measure of production efficiency treating all input costs as variable and without constraints. In other words, for this measure of economic efficiency, all resources used, including raised hay and grazed forage, are priced at their rental values and are not considered to be in limited supply. See Tess and Kolstad (2000a,2000b) for further details.

Integration of Elk and Cattle Data

The elk forage model was used to determine forage harvest by elk on each ranch. Forage use by elk was equated to AUM that potentially could have been used by cattle if elk were not present and if elk were eating what the cows could access—i.e., as affected by slope, terrain, etc. It is

important to understand that our definition of a fixed forage resource base assumes that there is a fixed amount of forage produced annually that can be grazed without harming the range resource.

Using the cow-calf model, ranches were simulated as they were actually managed. To compare how these ranches could theoretically be run if elk were not present, AUM harvested by elk on the respective ranches, as determined by the elk forage model, were added into the cow-calf model for the individual ranches. Comparisons of these simulations, allowed us to determine how many additional cattle could be maintained on the ranches due to an increase in forage if elk were not present, and the effects this had on ranch gross margin. Amounts of home-raised hay and domestic pasture were also considered fixed for each ranch. Hence, adding range resources would allow each ranch to run more cattle, but also might require the purchase of additional hay for winter feeding.

Alternative Management Strategies

Several potential methods exist by which beef cattle ranchers can reduce conflict between elk and cattle and (or) recover costs associated with elk on private lands. Variability of available resources on ranches and the number of elk utilizing the ranches makes it difficult to find a single best solution to the problem.

Block Management. In Montana, the Block Management Program was devised to keep private lands open for public hunting, while paying landowners for allowing free hunter access. Through management of the number and strategic placement of hunters, more efficient hunting is expected, thereby reducing elk herd numbers (Governor's Advisory Council on Private Lands/Public Wildlife, unpublished). In addition to assisting landowners with hunter management, the program also offers benefits that reduce or eliminate the cost of having hunters on private land, and in some cases offers taxable reimbursements of up to \$8,000 (Montana Session Laws 1995).

To mimic more efficient hunting, each ranch was simulated with elk herds reduced by 10, 20, and 30%. Effects on cattle herd size and gross margins were evaluated.

Coordinated Exchange of Forage Use. Coordinated grazing of rangelands among state, federal, and private lands allows private landowners to rest pastures that have been grazed by elk during the fall, winter, and (or) spring (Frisina and Morin 1991, Alt et al. 1992). With the exchange of for-

age, landowners may not have to purchase stored forage to replace forage removed by elk. For example, members of the Wall Creek Stock Association participating in the Wall Creek Wildlife Management Area exchange of use program received an additional month of livestock grazing, resulting in an extra 826 AUM of grazing by cattle (Alt et al. 1992). A major limitation of this scenario is that there must be available state and federal lands close enough to the private landowner to make transporting cattle to these public ranges feasible. To evaluate this scenario, the fair market value of an AUM on private property was compared to the value of an AUM as simulated for each of the five ranches.

Leasing Hunting Access. Leasing private land to outfitters in Montana is a common, but sometimes controversial, practice. Hunters are willing to pay for the opportunity to hunt elk, particularly if they are assured of an un-crowded hunt. This "market" allows outfitters to lease land from ranchers at a value that increases the landowners' income.

There are several forms of fee hunting. However, for this study, we chose only the leasing of the land to an outfitter. Once land was leased to an outfitter it was assumed that no further costs associated with hunters, such as time spent managing or guiding hunters, would be incurred by the rancher. Also, the monetary value of the lease was fixed, whereas if a landowner were to lease hunting access to individual hunters, the income would be variable, dependent on the number of hunters wanting to hunt.

To determine the value of a lease on each ranch, a survey was sent to 100 outfitters in FWP hunting regions 1, 2, and 3, where elk hunting is prevalent. Survey procedures were based on previous studies (Swensson and Knight 1998, 2001). The survey consisted of a cover letter explaining the study and what was being asked of the outfitter; general maps of the individual study ranches showing county roads and habitat types; and a description of the elk herd that occupied the ranch during hunting season. The elk herd was described by percentage of bulls in various age classes, as well as number of calves per 100 cows and number of bulls per 100 cows. Outfitters were requested to estimate the market value of each lease. Six weeks after mailing the initial surveys, follow-up phone calls were made to a random 50% of the non-respondents. Reasons for not completing the survey were determined. When feasible, non-respondents were again asked to complete the survey.

Statistical Analyses

Five scenarios were simulated in determining the effects of elk on ranches. To meet our first objective, each ranch was simulated as currently managed with elk present. The simulations were repeated with elk removed from the ranch, i.e., forage resources utilized by elk were added to the AUM available for cattle. These simulations also provided insights into the merits of the exchange of forage management strategy. To evaluate the potential effects of partial reduction in the elk herds, as might be expected due to Block Management, each ranch was simulated with a 10, 20, or 30% reduction in the ranch's elk population.

Due to the stochastic nature of the beef cow-calf model (reproductive traits exhibit random variation; Tess and Kolstad 2000a), it is possible to statistically compare simulated systems. Because not all traits are modeled with random variation, simulated variation between replicates is not the same as would be measured among actual ranches; however, the variation simulated does provide a basis for evaluating differences. Hence, each ranch/scenario combination was replicated ten times.

Because variances differed among ranches, simulated data for each ranch was analyzed separately. One-way analysis of variance was conducted to evaluate treatment effects (i.e., 0, 10, 20, 30, or 100% elk removal) on ranch gross margin and cattle herd size (SAS 1992). Means were separated using Duncan's Multiple Range test.

Results of the outfitter surveys were summarized by computing simple means and standard deviations of the estimated lease values.

Results

Elk AUM Equivalents

Table 2 illustrates the performance of the elk model for animals of different sexes and physiological states, and consuming forage of different quality. To a large degree, previous estimates of AUM equivalents have been based on differences in mature weight between elk and cattle, assuming that intake of elk was proportional to cattle but not considering physiological state. Murie (1951) and Loomis et al. (1989) used values of 0.25 and 0.27 for elk calves. Coupled with their value for lactating elk cows (0.67), the values of Loomis et al. (1989) agree with the model's predictions. Arychuk (2000) distinguished yearlings (0.3), adult females (0.5) and adult males (0.7).

Table 2. Effects of variable forage energy content and physiological state of elk on animal unit value equivalents.^a

	Male		Female-N		Female-G		Female-L	
	Metabolizable energy per kilogram dry matter							
Age	2.00	1.70	2.00	1.70	2.00	1.70	2.00	2.13
Y1	0.47	0.56	0.43	0.49	N/A	N/A	N/A	N/A
Y2	0.59	0.67	0.50	0.57	0.49	0.59	1.01	0.89
M	0.63	0.79	0.51	0.63	0.53	0.65	0.96	0.87

^aY1 = yearling, Y2 = two-year old animal, and M = mature animal of five-years old or older. Female-N = non-reproductive female, Female-G = gestating female, and Female-L = lactating female, including calf.

Previous AUM equivalents for adult elk (sex not specified) include 0.4 (Murie 1951, Meresczak et al. 1981, Loomis et al. 1989, Wisdom 1992), 0.5 (Stoddart and Smith 1955, Skovlin et al. 1968, Lacey et al. 1993), 0.6 (Lacey et al. 1988), 0.65 (Vallentine 1990), and 0.75 (Telfer and Scotter 1975).

Our results demonstrate the effects that age, gender, physiological state, and forage quality can have on forage intake. By accounting for these variables and dietary overlap, our model permits more precise description of the study case. These results also point to the hazards of using single, general predictions of AUM consumed by elk, because such predictions cannot account for species differences in food habits and distribution across rangelands (Vavra 1992).

Animal Use and Ranch Resources

Numbers of elk utilizing the ranches were likely conservative (Table 3). With only one yearly flight to determine the population characteristics of a herd for the

entire year, we assumed no recruitment of bachelor bulls took place, and average recruitment through reproduction occurred.

Elk use and numbers varied across ranches. All ranches showed an influx of elk in late fall that continued to early spring (Table 4). In general, there was a decline in elk numbers during the summer as elk migrated to higher elevation habitats, typically on state and federal lands. The exception to this was Ranch 5, which provided calving grounds to 250 cow elk. Four of the 5 ranches supported both resident and migratory populations of elk.

Elk-use data presented in Table 4 represent our best estimates for the product of spatial and dietary overlap between elk and cattle by season and reflect differences due to forage species, elevation, slope, ruggedness, and distance from water (also see review by Fuller 1997). Late fall and winter showed the highest percentages of resource overlap of up to 90%, with the exception of Ranch 2. The manager of Ranch 2 felt there was only 20% overlap due to the fact that all hay

Table 3. Summary of elk herds on individual ranches.^a

Ranch	Age Class	Male	Female-N	Female-R
1	Y0	9	9	
	Y1	8	13	2
	Y2	2	7	6
	M	9	28	25
2	Y0	32	32	
	Y1	30	45	8
	Y2	5	25	22
	M	29	102	91
3	Y0	24	24	
	Y1	21	31	6
	Y2	7	18	15
	M	19	71	62
4	Y0	26	26	
	Y1	4	17	3
	Y2	3	9	9
	M	5	41	35
5	Y0	34	33	
	Y1	10	25	4
	Y2	4	14	12
	M	9	56	49

^aNumbers shown are estimated maximum populations.

Y0 = calves, Y1 = yearlings; Y2 = 2 year olds; M = 3+years

Female-N = non-reproductive female; Female-R = reproductive female.

Table 4. Summary of elk use on individual ranches.

Ranch	Period of Use	Number of Elk	Overlap ^a	AUM
1	Oct 1 -Nov 30	118	90	110
	Dec 1 - May 15	118	75	262
	May 16 - May 31	118	75	22
	June 1 - Oct 1	71	40	68
2	Oct 1 - Nov 30	199	90	186
	Dec 1 - Mar 31	347	20	156
	Apr 1 - May 30	421	40	182
	June 1 - Sept 9	331	50	328
	Sept 10 - 30	199	80	70
3	Oct 1 - Nov 30	290	90	271
	Dec 1 - Apr 15	298	85	673
	Apr 16 - Jun 20	249	40	111
	Jun 21 - Sept 9	199	50	169
	Sept 10 - 30	290	80	101
4	Oct 1 - Nov 30	178	90	157
	Dec 1 -Mar 31	178	90	333
	Apr 1 - Jun 20	49	40	27
	Jun 21 - Sept 9	100	50	83
	Sept 10 - 30	178	80	61
5	Oct 1 - Nov 30	194	90	173
	Dec 1 - Apr 15	114	85	245
	May 15 - Aug 15	250	40	168
	Sept 10 - 30	194	80	66

^aOverlap=dietary and spatial overlap between elk and cattle, %.

Table 5. Simulated ranch performance without elk removal.^a

Ranch	Herd Size	Cattle AUM	Elk w/o Overlap	Cattle used by Elk
		(\$/kg)	---	(AUM) ---
1	241	1,835	1.62	674
2	368	2,820	1.65	2,189
3	838	7,750	1.53	1,836
4	902	7,760	1.58	857
5	1,147	9,200	1.80	987

^aHerd Size = number of beef cows exposed per year, including replacements. Cattle AUM = AUM used by cattle; \$/kg = unit cost of beef production; Elk AUM w/o overlap = AUM used by elk without considering dietary and spatial overlap; Cattle AUM used by Elk = AUM that could be used by cattle if elk were not present.

Table 6. Simulated effects of elk herd reduction on beef enterprise performance.

Ranch	Percentage Reduction in Elk Numbers					SEM
	0	10	20	30	100	
	Cattle Herd Size = Cows Exposed/Year					
1	241 ^c	247 ^d	253 ^c	260 ^b	301 ^a	0.74
2	368 ^c	381 ^d	394 ^c	404 ^b	486 ^a	1.10
3	838 ^c	851 ^d	867 ^c	881 ^b	979 ^a	1.54
4	902 ^c	905 ^d	917 ^c	924 ^b	978 ^a	1.08
5	1,147 ^d	1,148 ^d	1,155 ^c	1,166 ^b	1,228 ^a	2.46
	Ranch Gross Margin, \$/year					
1	64,879 ^c	66,185 ^c	65,925 ^c	67,981 ^b	71,193 ^a	586
2	88,682 ^b	89,126 ^b	89,961 ^b	90,996 ^b	100,487 ^a	827
3	176,715 ^c	181,066 ^b	181,010 ^b	183,084 ^b	197,867 ^a	1,099
4	232,861 ^c	234,829 ^c	234,227 ^c	237,534 ^b	242,151 ^a	919
5	237,756 ^b	241,457 ^{ab}	243,019 ^a	243,536 ^a	243,705 ^a	1637

^{abcde}Means within rows with different superscripts differ (P < 0.05).

was stored in “elk-proof” sheds, and elk did not generally intermingle with cattle during winter feeding of hay. In general, summer months showed only a 40% overlap mostly due to changes in dietary preferences of elk from grasses to forbs (Murie 1951, Mackie 1970).

Table 5 summarizes ranch performance under actual management and elk numbers. Differences in production costs (\$/kg) were due to several factors. Reproductive rates were similar among ranches; however, calf mortality was high for Ranch 5, spreading production costs over less output. Due to snow cover, Ranches 1 and 2 fed hay for extended periods, increasing feed costs.

By accounting for less than complete dietary and spatial overlap (Table 4), AUM harvested by elk in competition with cattle were considerably less than might be predicted otherwise (Vavra et al. 1989, Kingery et al. 1996). This highlights the importance of dietary overlap in quantifying potential competition between livestock and wildlife.

Forage Resources Gained From Elk Removal

Differences among ranches in gross margin reflect differences in herd size as well as differences in unit costs of production (Table 6). Recovering all forage resources used by elk (i.e., 100% elk removal) increased cattle carrying capacity and gross margin for each ranch (P < 0.05); however, responses were unique for each ranch. The ratio of added AUM to added cows ranged from 7.7 to 9.4, indicating how ranches differed in their dependence on range resources. Because of their short grazing seasons, Ranches 1 and 2 added more cows per AUM than Ranch 3, which was able to graze for nearly two months longer. Ranches 4 and 5 were intermediate.

The value of added AUM (added gross margin divided by added AUM) also differed among ranches; however, standard errors were large. Because this statistic was deemed important to the interpretation of results, we repeated the simulations for the base scenario, and the scenario assuming total removal of elk. This time we replicated each scenario 200 times. Estimated values of an added AUM ranged from \$8.55 to \$14.51 (Table 7). Differences were related to, but not totally explained by differences in grazing season. Ranches that grazed longer and fed less hay were generally more efficient (i.e., lower production costs, \$/kg) and recovered more gross margin per added

Table 7. Simulated added AUM value after removal of all elk.

Ranch	Added AUM Value ^a
1	\$11.95
2	\$11.87
3	\$14.51
4	\$13.73
5	\$8.55

^aAdded AUM value = Added ranch gross margin divided by added AUM, based on 200 replicates.

AUM. The exception was Ranch 5, where unit cost of production was high primarily due to high calf mortality. In a survey conducted by Lacey et al. (1993) landowners in southwestern Montana reported average annual losses to big game of 511 AUM (214 due to elk) and 7.5 metric tons of hay, valued at \$6,066—i.e., \$11.87/AUM.

Block Management

Incentives for ranchers to participate in the Montana Block Management Program include hunter management, monetary compensation, and potentially some reduction in elk numbers. According to Montana Session Laws (1995) ranches participating in the Block Management Program are entitled to some benefits, including a monetary benefit of up to \$8,000, depending on the type of habitat provided for wildlife, species and number of wildlife present, and access provided to adjacent private and public lands. We simulated 10, 20, and 30% reductions in elk numbers to evaluate economic effects on each ranch.

Responses to reduction in elk numbers (Table 6) were essentially linear because we assumed no change in elk sex or age structure, only population size. However, slopes of the responses were not the same across ranches, which reflect differences among ranches in elk population structure, as well as differences in dietary overlap. Ranches 1, 2, 3, and 4 were able to increase cattle numbers ($P < 0.05$) by reducing elk by 10%, and all ranches experienced significant increases in cattle numbers when elk were reduced by 20%. Only Ranch 3 increased gross margin ($P < 0.05$) with a 10% reduction in elk numbers. Ranch 2 was unable to increase gross margin with even a 30% reduction in elk numbers.

These results suggest that elk herd reduction is likely to be of only minor benefit to ranches participating in Block Management. However, expenses associated with elk were less than \$8,000 on Ranches 1 and 5, suggesting these ranches could potentially recover all elk costs through participation in the Block Management Program, even without a reduction in elk numbers.

Outfitter Lease

Sixteen of the 100 mail surveys were returned. Five surveys were removed from the data because they were not completed properly. Follow-up phone calls made to a random half of non-respondents indicated that many of the outfitters felt unqualified to value a lease on private land because their business was limited to public land. Follow-up calls increased the number of useable surveys back to 16.

Based on their comments, outfitters gave conservative estimates for the value of a 1-year lease on the individual ranches for elk hunting (Table 8). Some respondents noted that leases would be worth more if deer hunting were included and if leases were of longer duration than just 1 year. All respondents agreed that it was very difficult to gauge an accurate price quote for a ranch without actually having been on the ranch during a hunting season to see the behavioral patterns and population characteristics of the elk herd. Also, aesthetics, reputation, and rapport between client and outfitter are difficult to measure yet can have a large influence on the price an outfitter is able to get for a hunt (Knight et al. 1995), which in turn influences the value of the lease.

Mean values assigned by the outfitters were all below the simulated costs of providing elk habitat on private land; yet there was a wide range of estimates for each lease. Each ranch was valued by at least one outfitter above elk costs. Though not accounted for in the simulations, Ranches 3, 4, and 5 did receive some annual income from elk hunting. For example, Ranch 3 leased hunting access for \$25,000/yr, which is less than the maximum value assigned by the outfitter surveys but more than our estimated expenses associated with elk.

Exchange of Forage Use

In theory, exchange of forage use with a state or federal resource management agency should fairly recover all expenses associated with elk, except possibly repair costs for fences and other improvements (note, that in Montana FWP provides some ranchers with panels to protect haystacks from wildlife). This assumes that added AUM allotted to ranches on

public land are equal to or greater than the AUM consumed by elk on private land. Table 5 shows our estimates of the number of AUM needed for an equitable exchange of use.

The fair market value of an AUM lease is the price a person would expect to pay if he/she leased land for the purpose of grazing cattle. Average rates for a “cow-calf pair” in Montana were \$13.90 and \$15.60, in 1996 and 2000, respectively (NASS 2001). Reported lease rates do not account for differences in cattle mature size; hence, they are not easily compared to AUM values reported here. On average, 30% of a private grazing lease represents landlord services such as fence maintenance, water access, etc. (Torell and Fowler 1992, LaFrance and Watts 1995), which were not varied in our simulations. Following such adjustment, average Montana lease rates would be \$9.73 and \$10.92 for 1996 and 2000, respectively. Our estimates of the value of an AUM recovered from elk use for the 5 ranches are above and below these values (Table 7). Interestingly, these results suggest that it may be more advantageous for some ranchers to accept fair market value of AUM eaten by elk rather than accept a direct exchange of forage use. On the other hand, ranches that show returns per AUM higher than lease values may be better off exchanging use with a public agency, if available.

The main focus of exchange of use in this study was on the monetary value of such an alternative management scheme. Where feasible, a coordinated exchange of use has other beneficial elements than just recouping costs associated with elk. As noted by Alt et al. (1992) and Frisina and Morin (1991), a cooperative grazing system actually increased available AUM by improving forage on the range. This had a secondary effect of keeping elk on wildlife management areas for a longer period of time before elk migrated to private ranges in search of food. Potential benefits of grazing on subsequent forage nutritional quality may be due to removal of old growth and delayed senescence, though studies have shown mixed results (Anderson and Scherzinger 1975, Severson and Urness 1994, Hobbs et al. 1996a, Wambolt et al. 1997). Increased

Table 8. Lease value of ranches for elk hunting based on outfitter survey.

Ranch	1	2	3	4	5
Mean	\$2,919	\$3,900	\$10,375	\$7,175	\$2,953
Maximum	\$6,700	\$15,000	\$30,000	\$17,700	\$7,500
Standard deviation	\$2,288	\$3,850	\$7,386	\$5,129	\$2,520

landowner tolerance of elk, while increasing cattle and elk numbers able to use the land (Frisina and Morin 1991) are other advantages to exchanging use of forage.

Discussion

Simulation is a tool to examine scenarios that are beyond the scope of experimentation. It is used to address questions that are too expensive or too time consuming to address with experimentation. Often these questions take the form of: "How would the system respond if _____?" The assumptions made and the boundaries of the models used define what inferences can be made from the studies. Our work represents an attempt to integrate a large amount of published research into a systems framework, and make a science-based application to a real-life issue; in this case estimating costs of providing wildlife habitat on private land, and evaluating methods to recoup these costs.

The accuracy of our predicted costs could be improved by more precise measures of elk population parameters, including diet composition. However, it should be noted that the type of data available to us in this study is the type of data available to resource managers, policy makers, and ranchers. Ranch managers know the number and classes of livestock. On the other hand, data on wild ungulates are "generally obtained from state wildlife agencies or collected in cooperation with such agencies" (Cooperrider and Bailey 1984). To account for imprecision in elk population parameters, using results presented in Tables 5 and 6 one could decrease or increase the number of elk to bracket a range of costs. Similar tactics could be employed if our methods were used to study different ranches.

Our model to predict forage harvest by elk has not been validated from energy metabolism studies with elk. We expect the precision of our estimates to be lower than expected from validated models of domestic animal metabolism; yet, better than simple predictions made from an "average elk," or using some average definition of animal unit equivalency. Importantly, our approach accounts for differences among elk populations in sex ratios and age distributions. Compared to domestic animals, there are few scientific studies of energy metabolism in elk. Clearly our ability to model digestion and metabolism of elk would be improved if more studies were completed with elk. Our approach was to use equations specific for elk when available. However, for

many equations we assumed that relationships for elk were similar to domestic cattle, scaling the equations for differences in mature size and output rates. Many aspects of energy metabolism are similar among ruminants of different species (e.g., sheep and cattle, ARC 1980). Several previous studies have applied relationships from cattle studies to wild ungulates (e.g., Moen 1973, 1978, 1983, Nelson and Legee 1982, Hudson and White 1985).

Our approach in this study was to allocate all forage to cattle and elk, defining the forage resource as the amount of forage that could be harvested without damaging the range resource. In other words, to manage a range resource responsibly, we assumed that forage harvest must be limited to a certain degree of use – the degree of use currently experienced by each ranch. Hence, under this assumption, forage consumed by elk (accounting for dietary overlap) reduced forage available to cattle. An increase in elk herd size would lead to a reduction in cattle herd size, and conversely an increase in cattle herd size would require a reduction in the number of elk. Hobbs et al. (1996a,1996b) showed that elk grazing led to decreased forage intake, and reduced weight gains for cattle. Some responses demonstrated threshold effects—i.e., if sufficient forage was available to cattle after elk grazing, then cattle showed little response to elk grazing. Our assumptions and the results of Hobbs et al. (1996a,1996b) are both consistent with accepted definitions of competition, i.e., for competition for forage to occur, both cattle and elk must be consuming the same forage species in the same area and the forage species must be in short supply (Vavra 1992).

Simulating ranches as if no elk existed was used as a tool to quantify the economic impact elk had on beef cattle enterprises. We emphasize, however, that it is seldom possible or legal to remove all elk from a ranch (Youmans 1992). In our experience, very few ranchers desire to remove all elk (or other wildlife) from their properties. Further, an increasing number of people outside of agriculture recognize the importance of livestock operations in providing/conserving wildlife habitat. Alternatives for managing elk, i.e., strategies to maintain herd sizes at reasonable levels and (or) recoup income lost or foregone by providing habitat, are vital to the sustainability of many ranches.

Implications

Our results show that providing elk habitat on private land does represent an

economic cost to ranches. Importantly, our results also suggest that Montana ranches represented by our sample can recover most if not all of these costs, and in some cases actually profit from elk by implementing various elk management strategies. Our study focused on expenses associated with forage use. Elk may also be responsible for damage to fences and other facilities. Lacey et al. (1993) reported that annual non-feed expenses associated with wildlife were \$401 per ranch.

Feed costs generally represent one of the largest expenses for beef cattle producers. Grazed forage is often a more economical feed source than harvested or purchased feed. Our results suggest that the more dependent ranches are on rangeland, and the more efficiently they produce beef (i.e., lower unit cost of production, \$/kg), the more these ranches have to lose from providing elk habitat. More efficient ranches stand to benefit most from exchange of use programs, while ranches that are less efficient should benefit most from direct compensation. The greatest benefits from the Montana Block Management program appear to come from improved hunter management and compensation for access and habitat rather than from reduction in elk numbers.

Our survey of outfitters suggests that leasing of hunting access may be a viable method to recoup costs for some ranches. Commercial recreation values associated with elk provide incentives for ranches to provide elk habitat (Anderson and Hill 1995). Multiple factors determine the market values of recreational leases. However, market incentives may not address needs associated with non-game species or opportunities for low income people (Burger and Teer 1981, Jordan and Workman 1989), nor longer term management objectives related to biodiversity (Freese and Trauger 2000, Gowdy 2000).

The ranches studied illustrate that solutions to wildlife-livestock issues are situation specific. A single, universal recommendation is not likely to be acceptable. We considered only 3 options for recovering costs associated with elk utilizing private ranges. Other options may play important roles in solutions to wildlife-livestock problems (e.g., conservation easements, different types of leases, owner-managed recreational enterprises, etc.) (Knight 1996a,1996b, 1996c). Wildlife-livestock interactions are complex and dynamic. Improved understanding of these systems and cooperative approaches are needed to identify sustainable and equitable solutions (Swensson and Knight 1998).

Appendix: Description of Elk Forage Consumption Model

The model is based on a 1-day time step. Metabolizable energy (ME) requirements for maintenance (MEM, Mcal) are predicted from current animal weight (WT) and adjusted for season to reflect energy expenditures for travel (Nelson and Legee 1982, Jiang and Hudson 1993).

$$MEM = \frac{BM(WT^{0.75})}{KM} \quad (1)$$

where, BM = 0.1002, 0.1094, 0.1138, 0.1072 in winter, spring, summer, and fall, respectively. Efficiency of ME use for maintenance (KM), is predicted as a function of diet energy density (ME/kg dry matter [MEDM]) following NRC (1984).

$$KM = \frac{1.37 MEDM - 1.38 MEDM^2 + 0.0105 MEDM^3 - 1.12}{MEDM} \quad (2)$$

Postweaning growth is simulated based on WT, asymptotic mature weight (AWT), and weight gain (WTG) following data presented by Murie (1951) and equations by Moen (1973) as:

$$WTG = B1(AWT - WT) \quad (3)$$

where B1 = 0.0030 for bulls and 0.0035 for cows, and AWT is assumed to be 350 and 260 kg for bulls and cows, respectively (Nelson and Legee 1982). Predictions of ME requirements for gain (MEG) are based on NRC (1984), and assume that the composition of gains for elk and cattle are similar at similar stages of maturity and similar relative rates of growth. For bulls,

$$MEG = \frac{0.0493WT^{0.75}(WTG^{1.097})ARATIO^{0.847}}{KG} \quad (4)$$

and for cows,

$$MEG = \frac{0.0686WT^{0.75}(WTG^{1.119})ARATIO^{0.869}}{KG} \quad (5)$$

where ARATIO is the ratio of mature weights for cattle and elk (e.g., 525/260 = 2.02 in this study). See below for derivation. Postweaning rates of growth for elk are expected to be slower and with lower percent fat than for domestic cattle fed concentrate diets. This prediction accounts for such differences. The efficiency of ME use for gain (KG) is computed based on NRC (1984) as:

$$KG = \frac{1.42 MEDM - 0.174 MEDM^2 + 0.0122 MEDM^3 - 1.62}{MEDM} \quad (6)$$

For pregnant females, ME requirements for gestation (MEU) is measured as uterine energy deposition (UTE) which has a 15% efficiency rate and is modeled after Ferrell et al. (1976). Gain in uterine development (UTEG) is computed by the equation:

$$UTEG = \frac{0.06973e^{DT(0.0323-0.0000275DT)}16.0}{40.0} - UTE \quad (7)$$

where, the ratio 16.0/40.0 accounts for difference in birth weight between elk and cattle, and UTE is the accumulated UTE on the day of gestation (DT). Then,

$$MEU = \frac{UTEG}{0.15} \quad (8)$$

For cows nursing a calf, it is necessary to calculate the fraction of the calf's requirements satisfied by milk, and the cow's added energy requirement to produce milk. First, we assume a 50:50 distribution of male and females calves. Second, we assume that the average nursing time is 120 days, and that calf growth is linear over this period for both sexes. During the nursing period calf ME requirements (CMEI) are:

$$CMEI = MEM + MEG \quad (9)$$

The fraction (FRACT) of MEI supplied by milk is assumed to decrease with calf age, and estimated as:

$$FRACT = 1.0 + \frac{16.0 + CWT}{WWT - 16.0} \quad (10)$$

where, CWT = current calf weight, and WWT = weaning weight (note that birth weight = 16 kg). Weaning weights are assumed to be 85.2 kg for bulls and 79.5 kg for cows (Nelson and Legee 1982). Then, CMEI supplied by forage is computed as:

$$CMEIF = CMEI(1.0 - FRACT) \quad (11)$$

The ME required by the cow to produce the milk consumed by the calf (MEL) is estimated as:

$$MEL = \frac{CMEI(FRACT)}{0.85KM} \quad (12)$$

where, 0.85 accounts for metabolizability of milk consumed by the calf (NRC 1989).

For all animals past weaning age, total ME consumed (MEI) is:

$$MEI = MEM + MEG + MEU + MEL \quad (13)$$

where MEG, MEU, or MEL could be zero, depending on animal age, sex, and physiological state. Metabolizable energy consumed was translated into animal unit months (AUM = 360 kg dry matter, SRM 1989) as:

$$AUM = \frac{MEI + CMEIF}{360(MEDM)} \quad (14)$$

The amount of forage consumed by elk that could have been consumed by cattle is then predicted as:

$$ADJAUM = AUM(OVERLAP) \quad (15)$$

where, OVERLAP is the product of spatial and dietary overlap expressed in decimal form.

For the purposes of this study we assumed that average birth and weaning dates for elk calves were June 1 and September 28, respectively (Skovlin 1982, Taber et al. 1982, Nelson and Legee 1982). To recognize that the number of elk using a ranch was not constant throughout the year, the model was constructed to simulate forage intake by elk during different periods of time specific for each ranch. For each period, inputs to the model included descriptions of the elk population, average forage quality during the period (i.e., MEDM), and OVERLAP.

Derivation of energy cost of gain for elk

From NRC (1984) the net energy of live weight gain for female cattle is:

$$NE_{GC} = 0.0686WTC^{0.75}(WTGC^{1.119}) \quad (16)$$

where, WTC = current live weight (kg) and WTGC = live weight gain (kg/d).

Dividing by WTGC, net energy per kg WTGC is:

$$NEKG_{GC} = 0.0686WTC^{0.75}(WTGC^{0.119}) \quad (17)$$

Our assumption is that the net energy for gain for elk is similar to that of cattle when gains and weights are at similar stages of maturity (i.e., fraction of mature size). Hence, if the current weight (WTE) and gain (WTGE) for elk are proportional to the ratio of mature weights for elk (AWTE) and cattle (AWTC), then:

$$WTE = WTC \left(\frac{AWTE}{AWTC} \right) \quad (18)$$

$$WTGE = WTGC \left(\frac{AWTE}{AWTC} \right) \quad (19)$$

Finally, solve for an adjustment factor (Z) that equalizes the net energy for gain for cattle and elk when gains are at similar fractions of mature weight.

$$0.0686WTC^{0.75}(WTGC^{0.119}) = 0.0686 \left(WTC \frac{AWTE}{AWTC} \right)^{0.75} \left(WTGC \frac{AWTE}{AWTC} \right)^{0.119} (Z) \quad (20)$$

$$Z = \left(\frac{AWTC}{AWTE} \right)^{0.869} \quad (21)$$

Note, that the coefficient $0.869 = 0.75 + 1.119 - 1.0$. Similarly, the coefficient for male elk is $0.847 = 0.75 + 1.097 - 1.0$.

Literature Cited

- Adams, A. W. 1982.** Migration, p. 301-321. *In*: J. W. Thomas and D. E. Toweill (eds.), *Elk of North America: ecology and management*. Stackpole Books, Harrisburg, Penn.
- Alt, K. L., M. R. Frisina, and F. J. King. 1992.** Coordinated management of elk and cattle, a perspective—Wall Creek Wildl. Manage. Area. *Rangelands* 14:12-15.
- Anderson, T. L. and P. J. Hill. 1995.** From a liability to an asset: developing markets for wildlife, p. xi-xv. *In*: T. L. Anderson and P. J. Hill (eds.), *Wildlife in the Marketplace*. Rowman and Littlefield Publishers, Inc., Lanham, Md.
- Anderson, E. W. and R. J. Scherzinger. 1975.** Improving quality of winter forage for elk by cattle grazing. *J. Range Manage.* 28:120-125.
- ARC. 1980.** The nutrient requirements of ruminant livestock. Commonwealth Agr. Bureaux, Farnham Royal, U.K.
- Arychuk, C. E. 2000.** Setting stocking rates for pastures. *The Tracker* 4:72-73.
- Begon, M., J. L. Harper, and C. R. Townsend. 1990.** *Ecology, individuals, populations and communities*. Blackwell Sci. Publ., Inc., Cambridge, Mass.
- Burger, G. V. and J. G. Teer. 1981.** Economic and socioeconomic issues influencing wildlife management on private land, p. 252-263. *In*: R. T. Dumke, G. V. Burger, and J. R. March (eds.), *Wildlife Management on Private Lands*. Wisconsin Wildl. Soc., Madison, Wis.
- Cooperrider, A. Y. and J. A. Bailey. 1984.** A simulation approach to forage allocation, p. 525-560. *In*: *Developing Strategies for Rangeland Management*. Westview Press, Boulder, Colo.
- Edge, W. D. and C. L. Marcum. 1990.** Elk and cattle on public lands: a new look at an old conflict. *West. Wildl.* 16(2):12-15.
- Ferrell, C. L., W. N. Garrett, N. Hinman. 1976.** Growth, development and composition of the udder and gravid uterus of beef heifers during pregnancy. *J. Anim. Sci.* 42:1477-1489.
- Freese, C. H. and D. L. Trauger. 2000.** Wildlife markets and biodiversity conservation in North America. *Wildl. Soc. Bull.* 28:42-51.
- Frisina, M. R. and G. Morin. 1991.** Grazing private and public land to improve Fleecer elk winter range. *Rangelands* 13:291-294.
- Fuller, W. L. 1997.** Elk management strategies for sustainable beef cattle enterprises. M. S. Thesis, Montana State Univ.-Bozeman, Bozeman, Mont.
- Gordon, F. A. 1968.** Range relationships of elk and cattle on elk winter range, Crow Creek, Montana. Master's Thesis, Montana State Univ., Bozeman, Mont.
- Gowdy, J. M. 2000.** Terms and concepts in ecological economics. *Wildl. Soc. Bull.* 28:26-33.
- Hart, R. H., K. W. Hepworth, M. A. Smith, and J. W. Waggoner, Jr. 1991.** Cattle grazing behavior on a foothill elk winter range in southeastern Wyoming. *J. Range Manage.* 44:262-266.
- Henderson, R. E. and A. O'Herren. 1992.** Winter ranges for elk and deer: victims of uncontrolled subdivisions? *Western Wildl.* 18(2):20-25.
- Hobbs, N. T., D. L. Baker, G. D. Bear, and D. C. Bowden. 1996a.** Ungulate grazing in sagebrush grassland: Mechanisms of resource competition. *Ecol. Appl.* 6:200-217.
- Hobbs, N. T., D. L. Baker, G. D. Bear, and D. C. Bowden. 1996b.** Ungulate grazing in sagebrush grassland: Effects of resource competition on secondary production. *Ecol. Appl.* 6:218-227.
- Holechek, J. L. 1980.** Concepts concerning forage allocation to livestock and big game. *Rangelands* 2:158-159.
- Hudson, R. J. and R. G. White. 1985.** Computer simulation of energy budgets. p. 261-290. *In*: R. J. Hudson and R. G. White (eds.), *Bioenergetics of wild herbivores*. CRC Press, Boca Raton, Fla.
- Jiang, Z. and R. J. Hudson. 1993.** Seasonal energy requirements of wapiti (*Cervus elaphus*) for maintenance and growth. *Can. J. Anim. Sci.* 74:97-102.
- Jordan, L. A. and J. P. Workman. 1989.** Economics and management of fee hunting for deer and elk in Utah. *Wildl. Soc. Bull.* 17:482-487.
- Kasworm, W. F., L. R. Irby, and H. B. Ihle Pac. 1984.** Diets on ungulates using winter ranges in northcentral Montana. *J. Range Manage.* 37:67-71.
- Kingery, J. L., J. C. Mosley, and K. C. Bordwell. 1996.** Dietary overlap among cattle and cervids in northern Idaho forests. *J. Range Manage.* 49:8-15.
- Knight, J. E. 1996a.** Minimizing controversy in wildlife and livestock grazing management. *Trans. 61st No. Amer. Wildl. and Natur. Resour. Conf.* 137-141.
- Knight, J. E. 1996b.** Noncontroversial techniques to manage rangeland resources, p. 107-111. *In*: *Sharing Common Ground on Western Rangelands*. U.S.D.A. For. Ser. Intermountain Research Section. Gen. Tech. Rep. INT-GTR-343.
- Knight, J. E. 1996c.** Conservation easements on Montana ranches. *MontGuide* 9618 AG.
- Knight, J. E., J. M. Fowler, and C. M. Morgan. 1995.** Expenses and income associated with fee hunting enterprises. *RITF Report No. 41*.
- Lacey, J. R., K. Jamtgaard, L. Riggle, and T. Hayes. 1993.** Impacts of big game on private land in south-western Montana: Landowner perceptions. *J. Range Manage.* 46:31-37.
- Lacey, J. R., S. B. Laursen, J. C. Gilchrist, R. M. Brownson, J. Anzick, and S. Doggett. 1988.** Economic and social implications of managing wildlife on private land in Montana. *Northwest Sci.* 62:1-9.
- LaFrance, J. T. and M. J. Watts. 1995.** Public grazing in the West and "Rangeland Reform '94". *Amer. J. Agr. Econ.* 77:447-461.
- Loomis, J., D. Donnelly, and C. Sorg-Swanson. 1989.** Comparing the economic value of forage on public lands for wildlife and livestock. *J. Range Manage.* 42:134-138.
- Mackie, J. R. 1970.** Range ecology and relations of mule deer, elk, and cattle in the Missouri River Breaks, Montana. *Wildl. Monogr.* 20.
- Mereszczak, I. M., W. C. Krueger, and M. Vavra. 1981.** Effects of range improvement on Roosevelt elk winter nutrition. *J. Range Manage.* 34:184-187.
- Moen, A. 1973.** *Wildlife ecology, an analytical approach*. W. H. Freeman, San Francisco, Calif.
- Moen, A. N. 1978.** Seasonal changes in heart rates, activity, metabolism, and forage intake of white-tailed deer. *J. Wildl. Manage.* 42:715-738.
- Moen, A. N., 1983.** *Agriculture and Wildlife Management*. CornerBrook Press, Lansing, N.Y.

- Montana Session Laws. 1995.** House Bill 195, p 2216-2225. *In: Laws and Resolutions of the State of Montana, Fifty-fourth Legislature.* Montana Legislative Services, Helena, Mont.
- Murie, O. J. 1951.** The Elk of North America. The Stackpole Company, Harrisburg, Penn.
- NASS. 2001.** Agricultural Prices (PAP-BB). National Agricultural Statistics Service, Agricultural Statistics Board, U.S. Department of Agriculture. <http://usda.mannlib.cornell.edu/> - accessed 4/27/01.
- Nelson, J. R. 1982.** Relationships of elk and other large herbivores, p 415-442. *In: J. W. Thomas and D. E. Toweill (eds.), Elk of North America: Ecology and Management.* Stackpole Books, Harrisburg, Penn.
- Nelson, J. R. and T. A. Leege. 1982.** Nutritional requirements and food habits, p 323-367. *In: J.W. Thomas and D.E. Toweill (eds.), Elk of North America: Ecology and Management.* Stackpole Books, Harrisburg, Penn.
- NRC. 1984.** Nutrient requirements of beef cattle (6th Ed.). National Academy Press, Washington, DC.
- NRC. 1989.** Nutrient requirements of dairy cattle (6th Ed.). National Academy Press, Washington, DC.
- Peek, J. M. 1982.** Elk, p 851-861. *In: Joseph A. Chapman and George A. Feldhamer (eds), Wild Mammals of North America, Biology, Management, and Economics.* John Hopkins University Press, Baltimore, Md.
- SAS. 1992.** SAS user's guide: statistics. SAS Inst., Inc., Cary, N.C.
- Severson, K. E. and P. J. Urness. 1994.** Livestock grazing: A tool to improve wildlife habitat p. 232-249. *In: M. Vavra, W. A. Laycock, and R. D. Pieper (eds.), Ecological Implications of Livestock Herbivory in the West.* Soc. for Range Manage., Denver, Colo.
- Sheehy, D. P. and M. Vavra. 1996.** Ungulate foraging areas on seasonal rangeland in northeastern Oregon. *J Range Manage.* 49:16-23.
- Skovlin, J. M. 1982.** Habitat requirements and evaluations, p 369-413. *In: J. W. Thomas and D. E. Toweill (eds.), Elk of North America: ecology and management.* Stackpole Books, Harrisburg, Penn.
- Skovlin, J. M., P. J. Edgerton, and R. W. Harris. 1968.** The influence of cattle management on deer and elk. *Trans. N. A. Wildl. Natur. Resour. Conf.* 33:169-178.
- Smith, D. R. 1961.** Competition between cattle and game on elk winter range. *Univ. of Wyoming Agr. Exp. Sta.*
- Society for Range Management. 1989.** A glossary of terms used in range management. Denver, Colo.
- Stevens, D. R. 1966.** Range relationships of elk and livestock, Crow Creek Drainage, Montana. *J. Wildl. Manage.* 30:349-363.
- Stoddart, L. A. and A. D. Smith. 1955.** Range management. McGraw-Hill, N.Y.
- Swenson, E. J. and J. E. Knight. 1998.** Identifying Montana hunter/rancher problems and solutions. *J. Range Manage.* 51:423-428.
- Swenson, E. J. and J. E. Knight. 2001.** Hunter management strategies used by Montana ranchers. *Wildl. Soc. Bull.* 29:306-310.
- Taber, R.D., K. Raedeke, and D. A. McCaughran. 1982.** Population Characteristics, p 279-298. *In: J. W. Thomas and D. E. Toweill (eds.), Elk of North America: ecology and management.* Stackpole Books, Harrisburg, Penn.
- Tefler, E. S. and G. W. Scotter. 1975.** Potential for game farming in boreal aspen forests of western Canada. *J. Range Manage.* 28:172-181.
- Tess, M. W. and B. W. Kolstad. 2000a.** Simulation of cow-calf production systems in a range environment. I. Model development. *J. Anim. Sci.* 78:1159-1169.
- Tess, M. W. and B. W. Kolstad. 2000b.** Simulation of cow-calf production systems in a range environment. II. Model evaluation. *J. Anim. Sci.* 78:1170-1179.
- Torell, L. A. and J. M. Fowler. 1992.** Grazing fees: how much is fair? *Agr. Exp. Sta. Rept.* 666. New Mexico State Univ., Las Cruces, N.M.
- Vallentine, J. F. 1990.** Grazing management. Academic Press, Inc., San Diego, Calif.
- Vavra, M. 1992.** Livestock and big game forage relationships. *Rangelands* 14:57-59.
- Vavra, M., M. McInnis, and D. Sheehy. 1989.** Implications of dietary overlap to management of free-ranging large herbivores. *Proc. West. Sect. ASAS.* 40:489-495.
- Wagner, F. H. 1969.** Ecosystem concepts in fish and game management. p. 259-307. *In: G. M. Van Dyne (Ed.), The ecosystem concept in natural resource management.* Academic Press, New York, N.Y.
- Wambolt, C. L., M. R. Frisina, K. S. Douglass, and H. W. Sherwood. 1997.** Grazing effects on nutritional quality of bluebunch wheatgrass for elk. *J. Range Manage.* 50:503-506.
- Wisdom, M. 1992.** The Starkey Project: new technologies chase old questions about deer and elk management. *Western Wildl.* 18:32-38.
- Witmer, G. W. and D. S. deCalesta. 1983.** Habitat use by female Roosevelt elk in the Oregon coast range. *J. Wildl. Manage.* 47:933-939.
- Yeo, J. J., J. M. Peek, W. T. Wittenger, and C. T. Kvale. 1993.** Influence of rest-rotation cattle grazing on mule deer and elk habitat use in east-central Idaho. *J. Range Manage.* 46:245-250.
- Youmans, H. B. 1992.** Editor: Elk Management Plan. Montana Dept. of Fish, Wildl., and Parks, Helena, Mont.

Evaluating the ecological relevance of habitat maps for wild herbivores

MARC E. STALMANS, ED T.F. WITKOWSKI, AND KEVIN BALKWILL

Authors are respectively Ecologist, Head of the Restoration and Conservation Biology Research Group and Curator of the C.E. Moss Herbarium, Department of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag 3, Wits 2050, Republic of South Africa. Present address of the first author is Mpumalanga Parks Board, PO Box 1990, 1200 Nelspruit, Republic of South Africa.

Abstract

Informed management of large herbivores depends largely on how well habitat availability and suitability are understood. The aims of the study were to quantify and map the distribution of sour and mixed grasslands in the 48,000 ha Songimvelo Game Reserve, Mpumalanga, South Africa. Mixed grassland retains its forage quality and hence its ability to sustain animal production for longer in the year than sour grassland. An unsupervised classification technique was applied to a LANDSAT 5 TM image acquired in 1993. The probability that each resulting cluster represented either sour or mixed grassland was calculated based on the proportional allocation of 428 sample plots. The 2 resulting probability maps were combined into a single image by selecting the class image that contained the maximum posterior probability and assigning that class to the output pixel. The accuracy of the vegetation map was assessed by ground-truthing with an independent set of 85 plots. This yielded a correct classification of 84.8% for the sour and 76.9% for the mixed plots. The mixed grasslands covered only 31.0% of the area but accounted for 66.1% of the game stocking. Water is widely distributed and is not a limiting factor to habitat selection. Based on a GIS analysis, the qualitative difference between mixed and sour grasslands overrides quantitative differences in forage availability, fire history and human disturbance in influencing herbivore distribution. The integration of field data and satellite imagery into a GIS system thus offers a powerful tool for the objective quantification and mapping of available habitat.

Key Words: wildlife, GIS, remote sensing, LANDSAT, ground-truthing

The informed management of large herbivores in conservation areas depends largely on how well habitat availability and suitability are understood. The Songimvelo Game Reserve (henceforth SGR) is spatially very diverse in terms of its average annual rainfall, underlying geological substrate, elevation, slope, and aspect (Barnes 1998). This results in a very diverse vegetation pattern with marked differences in habitat suitability for herbi-

Resumen

El manejo actualizado de los grandes herbívoros depende en gran parte de que tan bien son entendidos la disponibilidad y lo apropiado del hábitat. Los objetivos de este estudio fueron cuantificar y mapear la distribución de los pastizales mixtos y ásperos en las 48,000 ha de la reserva de fauna Songimvelo en Mpumalanga, South Africa. Los pastizales mixtos conservan su calidad, y de aquí su habilidad para mantener la producción animal durante un mayor periodo de tiempo durante el año que los pastizales ásperos. Una técnica de clasificación no supervisada se aplicó a una imagen LANDSAT 5 TM adquirida en 1993. La probabilidad de que cada conglomerado resultante represente el pastizal mixto o el áspero se calculó en base a la asignación proporcional de 428 parcelas de muestra. Los 2 mapas de probabilidades resultantes se combinaron en una sola imagen seleccionando la clase de imagen que contenía la probabilidad máxima posterior y asignando esa clase a la salida de pixel. La certeza del mapa de vegetación se evaluó mediante un reconocimiento terrestre con un juego independiente de 85 parcelas. Esto produjo una clasificación correcta en 84.4% de las parcelas de pastizal ásperos y en 76.9% de las parcelas de pastizal mixto. El pastizal mixto cubría solo el 31% del área, pero sostenía el 66.1% de la carga animal de fauna. El agua esta ampliamente distribuida y no es un factor limitante en la selección del hábitat. Basado en un análisis de Sistemas de Información geográfica (GIS) las diferencias cualitativas entre los pastizales mixtos y los ásperos anulan las diferencias cuantitativas en la disponibilidad de forraje, la historia de fuego y el disturbio humano en influenciar la distribución de los herbívoros. La integración de datos de campo e imagen de satélite en un sistema de GIS ofrece una herramienta poderosa para el objetivo de cuantificación y mapeo del hábitat disponible.

vores (Stalmans et al. 1999). This diverse vegetation can be generalised into 2 herbivore habitats, 'sourveld' and 'mixed veld' (Stalmans et al. 1999) based on forage quality characteristics.

Within the South African ecological context, 'sourveld' refers to range in which the forage plants become unacceptable and less nutritious to large herbivores on reaching maturity. Sourveld consequently is utilised only during spring and summer (Trollope et al. 1990). 'Sweetveld' in contrast retains its acceptability and nutritive value after maturity and is used throughout most of the year. In essence, herbivores feeding on sourveld lose body weight during the dry winter season due to a decline in forage quality below the level for efficient digestion, whereas in sweetveld, for-

Funding and logistical support were provided by the Mpumalanga Parks Board. Authors wish to acknowledge the support by Wilna Heymans who collected the independent data set used for the validation of the satellite map. Magda Rall, Annelize Steyn and other management staff assisted with the collection of vegetation, fire and game monitoring data. Dr Y. Bai and 2 anonymous reviewers provided useful comments and recommendations.

Manuscript accepted 12 Apr. 2001.

age quality never declines such that animals cannot maintain growth (Ellery et al. 1995). 'Mixed veld' is intermediate between sourveld and sweetveld. Prior to this study, little quantitative information existed on the spatial extent and distribution of sour and mixed range across the reserve. This quantification is necessary in order to determine appropriate stocking levels of game. The range of game species present, their numbers and their distribution determine the potential for tourism development which is required in the face of the great socio-economic needs experienced by rural communities bordering the SGR (Heinsohn et al. 1992).

Remote sensing is a useful tool for inventory and evaluation of wildlife habitat because of its multispectral and multi-temporal capabilities at different spatial scales (Quattrochi and Pelletier 1991). Processed remotely sensed data may be used as input to a Geographic Information System (GIS) and together with ancillary data be used for environmental modelling and analysis (Wilkinson 1996). Wildlife habitat maps derived from remote sensing need to be evaluated for accuracy and ecological relevancy before they are used for management purposes. Accuracy assessment relies on independent reference data, not used during the process of classification (Fairbanks and Thompson 1996).

The aim of the study was to evaluate the ecological relevance of habitat maps derived from multispectral remote sensing by first comparing the spatial distribution of the spectrally-derived habitats to the distribution obtained through field sampling and by secondly evaluating the actual herbivore distribution in relation to the spectrally-identified habitats.

Materials and Methods

Study Area

The Songimvelo Game Reserve (SGR) is located in the southeastern part of Mpumalanga on the South African-Swaziland border (25°45' to 26°06'S and 30°46' to 31°16'E) and is approximately 48,000 ha in extent (Fig. 1). The terrain is generally rugged with elevation ranging from 600 m above sea level along the Komati River in the south to over 1,900 m in the north and northeast. The geology is very diverse and ranges from alluvium and mafic and ultramafic lavas in the Komati Valley, to felsic lavas, conglomerates, shales, sandstones and quartzites at higher elevations.

Rainfall is concentrated between

Fig. 1. Locality map of the Songimvelo Game Reserve in southern Africa.

November and March, and varies from less than 800 mm per year in the south-west to over 1,400 mm in the north-east (Gamble 1988). Mean minimum monthly temperatures are 5.4°C and 8°C in July and mean maximum temperatures are 22°C and 34°C in January for the highland and lowland areas respectively (Stalmans et al. 1999). The generally acid and arenaceous geological substrates in the north-east, combined with a higher rainfall, result in leached acidic soils. In contrast, relatively nutrient-rich soils are found in the Komati Valley.

The SGR is characterised by a long and diverse history of small-scale cropping and livestock in the more fertile lowlands (Van der Merwe and Retief 1995). Since its inception in 1986, 20 species of large herbivores have been re-introduced within the 31,700 ha game-fenced portion of the reserve.

The vegetation of the higher-lying regions of the SGR belongs to the grassland biome. The lower-lying Komati Valley falls within the savanna biome (Rutherford and Westfall 1986). Three of Acocks (1975) vegetation types occur in the SGR. These are veld types 8 (North Eastern Mountain Sourveld) and 63 (Piet Retief Sourveld) which correspond to the North-eastern Mountain Grassland of the grassland biome as defined by Low and Rebelo (1996). Veld type 9 (Lowveld Sour Bushveld) corresponds to the Sour Lowveld Bushveld of the savanna biome. The forest biome is represented in the SGR by numerous isolated patches of for-

est, mostly at higher elevation and along drainage lines (Stalmans et al. 1999).

Conceptual approach

Three basic steps were followed. First, a classification into habitats was produced based on spectral differences in the vegetation. Field data were used to assign classification results into habitats with distinct differences in forage quality. Secondly, the accuracy of the resultant habitat map was assessed using a set of independent field data. Lastly, the ecological relevance of the map produced was evaluated using actual herbivore distribution patterns.

Vegetation field data

Reference data on the spatial spread of the sour and mixed range were collected for use in developing the wildlife habitat map from remote sensing imagery. A total of 428 sample plots of 30 X 30 m were subjectively located across the Songimvelo Game Reserve (SGR) during the period 1993–1995. Cover and height classes for individual woody and grass species within the 30 X 30 m plots were estimated using the semi-quantitative measures of the Braun-Blanquet approach (Mueller-Dombois and Ellenberg 1974) and structural measurements of Edwards (1983). Records of environmental data included elevation (by means of an altimeter (± 20 m) and the 1:50 000 topocadastral maps), geology (according to 1:250 000 geological survey maps (Geological Survey 1986) and locally at a finer scale through personal observations), landscape position (Land

Type Survey Staff 1989), aspect (whether predominantly N, E, S or W), slope steepness (class estimate), soil texture (using the sausage method (National Working Group for Vegetation Ecology 1986)) and rockiness (estimated as a percentage of the ground cover). The sampling adequately covered the different combinations of environmental factors (Stalmans et al. 1999), in particular elevation and geology which are known to be major determinants of plant community composition and distribution in this montane setting (Deall and Theron 1990). Grazing pressure within each plot was rated according to 3 broad subjective classes: none to light, medium, and heavy.

Ordination and classification of the data set resulted in the delimitation of 18 plant communities identifiable in the field (Stalmans et al. 1999). These 18 communities were combined into 3 main vegetation units: mixed communities, forest and thicket communities, and sour communities. Mixed and sour communities are distinguished using criteria developed by Ellery et al. (1995) regarding the proportion of 'sour' (unpalatable), 'sweet' (palatable) and 'mixed' species. Forest and thicket communities are dominated by woody species with a closed canopy cover.

Manipulation of satellite imagery

Landsat Thematic Mapper quarter scene WRS 168-3-078, acquired on 8 January 1993, was used. The image was radiometrically corrected. Geometric corrections were applied in both the along-scan and across-scan directions using ground control points. Pixel size is 30 X 30 m. Bands 3, 4, and 5 were selected. Bands 3 (red) and 4 (near infrared) have been shown to give a good measure of vegetation density, especially as it relates to leaf area, whereas band 5 (middle infrared) provides a good measure of canopy closure (Rey-Benayas and Pope 1995). This combination of bands has been used successfully in rangeland (Mackay and Zietsman 1996) and forest studies (Fuller et al. 1998).

A hybrid approach was adopted for the classification of the LANDSAT data. Unsupervised classification allocates each pixel to a certain class based on its spectral characteristics only. In contrast, supervised classification of the imagery requires pre-defined training sites to assign each pixel of the image to a certain class. The drawback to the supervised approach is that it is often difficult to locate and define homogenous training sites for all plant communities of interest. The considerable

pixel to pixel variation generally results in many pixels being misclassified (Tueller 1989). Unsupervised classification approaches have worked better in rangelands. The drawback of the unsupervised classification is that subjectivity in the interpretation of the resulting classes is unavoidable.

In this instance, no *a priori* assumptions were made regarding the information content of the LANDSAT image or of the classification clusters. Instead, the emphasis was on the interpretation of the classification results and the improvement of the classification by incorporating ancillary data (Hutchinson 1982, Medler and Yool 1997). An adequate spatial spread of the ground data was considered key to a successful interpretation of the different classification clusters, in particular where it is known that clusters could be the result of differential spectral response linked to slope and aspect characteristics (Quattrochi and Pelletier 1991). The available sample of 428 vegetation plots adequately covered the different elevation, aspect and geology combinations on the Songimvelo Game Reserve (SGR) (Stalmans et al. 1999) and thus enabled the combination of 2 or more different clusters (based on spectral characteristics) into a single vegetation unit (based on field data).

As a first step, the composite image of the 3 bands was subjected to an unsupervised classification using a histogram peak technique of cluster analysis in the IDRISI Geographical Information System (Eastman 1992). Based on its spectral characteristics, each pixel is assigned to a particular cluster or class. This resulted in 46 classes or clusters, each consisting of multiple individual polygons. Twenty-one clusters each covered less than 100 ha (or 0.2% of the SGR) scattered across the area. In view of the very small spatial extent of these scattered fragments, these 21 clusters were discarded and the original composite image was again classified with a maximum limit of 25 clusters to ensure that each remaining cluster covered at least 100 ha. In terms of managing the reserve, very small areas cannot realistically be managed differently than the surrounding matrix.

The available field data were used in an objective manner to determine the probability of the classification results representing certain communities. The 428 sample plots were each assigned to one of the 3 vegetation units, namely sour grasslands, mixed grasslands, or forests and thickets. Each point was buffered to cover a window of 3 rows X 3 columns of pixels from the LANDSAT image. This trans-

lates into a physical dimension of 90 X 90 m which takes into account inaccuracies inherent to the Global Positioning System (henceforth GPS) positioning (see Fuller et al. 1998 for a similar approach). Habitat type assignments for pixels in the cluster image were compared to that of the buffered sample points. A crosstabulation of the cluster image with the buffered image was made. The resulting matrix was used to assign probabilities for each cluster to represent respectively mixed or sour vegetation based on the percentage mixed and sour sample plots occurring in each cluster. These probabilities were used to produce 2 probability images; one for the mixed and one for the sour vegetation unit. These 2 probability images were combined into a single image by selecting the class image that contains the maximum posterior probability, and assigning that class to the output pixel.

Only 43 of the vegetation plots (10% of the total sample) represented forests and thickets. Their GPS position was likely to be less accurate because of the thick canopy cover, which when combined with the generally narrow linear distribution of these formations, renders the above approach less meaningful. An alternative approach was therefore followed. Six known and clearly identifiable forest patches were digitized from 1:10,000 scale orthophotos. The classification clusters corresponding best to these patches were identified. All other clusters with the same identity were consolidated across the whole image into a forest/thicket unit. The forest/thicket unit was superimposed on the mixed/sour habitat map.

The habitat map obtained was further refined by assigning any mixed vegetation pixels occurring above 1,300 m elevation to the sour range. Based on their composition, none of the 112 sample plots situated above 1,300 m elevation represented mixed vegetation. Secondly, a median 3 X 3 pixel filter was applied to remove random noise and unwanted speckle (Fuller et al. 1998). Lastly, the known extent of the non-native pine (*Pinus* spp.) plantations occurring within the boundaries of the SGR was superimposed on the map resulting in a final map with 4 habitat units.

Ground-truthing of the satellite-derived map

Three measurements of error were used to assess the accuracy of the habitat map derived from the satellite imagery. Errors of omission occur when the satellite map fails to recognise the actual habitat class of an independent sample plot. Errors of

commission result when the satellite map misclassifies the sampling plot from the independent data set. A Kappa Index of Agreement (KIA), both for all classes and on a per category basis, constitutes the third measure of error. The KIA ranges from 0.0 indicating no correlation to 1.0 indicating perfect correlation (Eastman 1992).

A data set collected during 1989 prior to, and independently from the present study was used to assess the accuracy of the habitat map. Grasslayer composition of 85 plots of 25 X 100 m, subjectively located across the Songimvelo Game Reserve (SGR), was assessed by means of 100 points per plot using the nearest-rooted plant criterion (Mentis 1984). These plots were assigned to the mixed and sour vegetation units based on species composition. A crosstabulation was performed between the assigned plots and the satellite-derived image. Habitat categories from the plots were compared with those of the satellite map. A tabulation was kept of the number of cells in each category combination. No tabulations were made for cells marked with a 0 on the ground-truth map. Omission, commission and KIA were calculated from the crosstabulation results.

Ecological significance of the satellite-derived map

Overall stocking densities for the Songimvelo Game Reserve (SGR) (1815 kg km⁻² during 1994 and 3288 kg km⁻² during 1999) fall well below the estimated grazing capacity for this part of the country (5,000 kg km⁻² or higher) (Barnes 1990). Given these overall low stocking densities on the reserve and large contiguous areas of different habitats being available to game, the spatial distribution of large herbivores should reflect the spatial distribution of mixed and sour grasslands. This would particularly apply during winter when forage resources are most limiting both in terms of quality and quantity (Voeten and Prins 1999).

Two helicopter game counts were conducted during the winter months of August 1994 and September 1999 respectively as herbivores were more easily visible due to the lower leaf cover (as the vast majority of savanna trees are deciduous). Counts were conducted by means of a Bell Jetranger helicopter seating a pilot, navigator and 2 observers in the back recording game within 300 m wide parallel strips. The helicopter was maintained at a constant height of 53 m above the ground. Airspeed was maintained at around 96 km hour⁻¹ (60 knots). Each count was conducted

within a period of 3 days. Extensive field experience from the pilot and observers indicates that no large-scale movement of game occurs within such a limited time period. Breaks during the counting were made along natural boundaries across which little or no short-term movement of game is expected. Double-counting of individual animals or herds is avoided by herding animals from the counting strip deeper into strips already counted. A GPS co-ordinate was recorded for each game sighting. Viljoen and Retief (1994) found the measured errors between actual and recorded localities using GPS technology for game counts to be well within the requirements for ecological work of this kind. Each GPS point was compared with the habitat map to establish whether the sighting fell within mixed or sour range. A value in kg km⁻² was calculated for each point based on the species and number of animals involved in each sighting.

The underlying assumption in distinguishing between mixed and sour habitats is that nutritional value represents the overriding factor determining herbivore distribution. Three other important factors however could influence herbivore distribution across the landscape. These are water availability, feed availability and fire history. Another complicating factor in the SGR is the presence of a number of human settlements within the game-fenced area. It is critical to ascertain that the assessment of the value of the mixed and sour habitats delimited on the satellite map is not biased through 1 of these factors.

Distance to the nearest watering point is known to be important in determining herbivore use intensity (Thrash et al. 1995). With the GIS a distance analysis was performed from all known perennial streams and rivers in order to establish whether any parts of the SGR might be unavailable to water-dependent species such as impala (*Aepyceros melampus* Lichtenstein) (Young 1970).

A crude index of grass quantity available in the sour and mixed habitats was calculated as follows during the survey of the 428 vegetation plots. The class value for the grass cover estimate (1 = sparse, 2 = open, or 3 = closed) (structural terminology and categories follow Edwards (1983)) in each sample plot was multiplied by the square root of the midpoint of the 3 following height classes (1 = < 0.5 m, 2 = 0.5 to 1.0 m, 3 = 1.0 to 2.0 m). Trollope and Potgieter (1986) used a similar approach to measuring standing phytomass.

Many African ungulates are attracted to recently burnt grassland (Wilsey 1996). The extent of areas burnt during the 12 months preceding the 1994 and 1999 winter helicopter counts was determined for the mixed and sour habitats. Fires have been mapped since 1987 in the Songimvelo Game Reserve (SGR) and the data have been consolidated in the GIS. A crosstabulation of burnt and unburnt areas was performed with the GPS positions of the game to assess relative and absolute stocking densities.

Illegal hunting and snaring are not considered to have a major effect around the settlements within the SGR. However, competition from livestock, habitat modification through cultivation and exclusion through protective fencing around croplands could negatively influence wild herbivores. A distance analysis was performed from the GPS positions of the settlements. An overlay of the buffered image was made with the habitat map. The resulting distance-habitat map was crosstabulated with the GPS positions of the game.

Throughout the assessment of the ecological significance of the satellite-derived map, a Chi-square goodness-of-fit analysis (Zar 1984) was used to evaluate differences between the observed crosstabulation results and the expected patterns of occurrence based on proportional habitat availability.

Results and Discussion

Habitat units

Twenty-five out of the 428 sample plots represented wetland and non-native communities dominated by planted pine or closed-canopy stands of self-seeded Black wattle (*Acacia mearnsii* De Wild.) and were not considered further. Of the remainder, 43 plots represented forests or thickets. No single plot was classified as sweet range requiring more than 30% of the total cover to consist of 'sweet' species and less than 20% cover by 'sour' species (Ellery et al. 1995). A total of 224 plots were classified as sour range with 'sour' species contributing more than 60% of the cover of the plot and 'sweet' species contributing less than 20% cover. The remaining 136 plots were by definition mixed range by not conforming to either the sweet or sour criteria. The grazing intensities recorded in the field indicate a dramatic and significant difference in usage of the mixed and sour vegetation units ($\chi^2 = 101.64$, $\chi^2_{0.05,1} = 3.481$, $P < 0.001$).

Fig. 2. Satellite-derived range map of the Songimvelo Game Reserve. Note mixed range in the south-western lower-lying Komati River valley and sour range in the north-eastern high mountains.

Whereas 57.3% of the mixed plots were assessed as being medium to heavily grazed, only 7.6% of the sour plots were similarly rated. This indicates that the split into sour and mixed range based on floristic composition criteria translates into an ecologically meaningful difference to herbivores.

Habitat map

Crosstabulation of the 25 classification clusters with the vegetation plots generally resulted in a high individual probability for each of the clusters to represent either sour or mixed range. More than half of the surface area of the Songimvelo Game Reserve (SGR) has a cluster probability above 80%. For 92.2% of the total area, the cluster probability is above 65%. Only 2 clusters have less than a 65% probability factor of representing only sour or only mixed vegetation. These 2 clusters only make up 7.8% of the total area. Their spatial distribution is of interest. The 2 clusters are spread in a horseshoe marking the transition from the low-lying Komati Valley to the higher mountains to the north and east (Fig. 2). The *Themeda triandra* Forssk. (Rooigras)–*Cymbopogon* spp. short Grassland community which is a transitional community intermediate between typical mixed woodland communities and sour grassland communities was identified for this zone (Stalmans et al. 1999). The low probability scores for these clusters probably reflect the heterogeneous and intermediate nature of the vegetation in this particular area.

The final habitat map clearly depicts the

mainly mixed vegetation in the low-lying Komati Valley and Msoi Valley (Fig. 2). The higher-lying mountains to the north and east are mainly covered by sour vegetation. The forest and thickets also occur mostly at higher elevation as small pockets and linear formations in drainage lines. Pine plantations are located in the north-east. The mixed vegetation is the smallest of the 3 main units covering 8,504 ha or 17.3% of the SGR, followed by the thickets and forests (10,119 ha or 20.6%). The sour habitat occupies 29,684 ha which represent 60.4% of the game reserve.

Ground-truthing of satellite-derived map

The habitat map conforms in broad terms to the understanding of the vegetation as obtained through ordination and classification of the 428 sample plots (Stalmans et al. 1999). Mixed communities occur mostly in the Komati Valley and sour communities at higher elevation.

The independent sample of 85 plots used for the validation consisted of 52 mixed and 33 sour plots. The unsupervised

procedure correctly classified 76.9% of the mixed and 84.8% of the sour sample plots. The Kappa coefficient (KIA) was 0.59. The overall percentage correct classification was 80% (obtained by dividing the sum of the diagonal entries in the error matrix by the total number of sample plots) (Table 1).

A good correspondence between the 6 digitized forest patches and the satellite-derived forest patches was obtained. The overall correct classification for the 6 patches was 78.4%. The KIA was 0.74. The satellite map overestimated the actual forest cover by 13.6%. The forest/thicket coverage was simply used to identify those parts of the SGR not dominated by grasslands which were the focus of the present study.

Classification accuracy reported by other researchers mapping landcover (Brondizio et al. 1996, Fuller et al. 1998, Hodgson et al. 1988, Lunetta and Balogh 1999), forest cover (Congalton et al. 1993) and grassland cover (Lauver and Whistler 1993) ranged from 69 to 94%. The accuracy figures of 78 to 80% achieved for the mixed/sour vegetation and forest patches on the SGR are thus considered to be satisfactory for an operational product of this kind.

Ecological significance of the habitat map

During 1994 a total of 22,800 ha was covered by the helicopter survey whereas during 1999 the whole game-fenced area of 31,700 ha was flown. A total of 705 GPS coordinates of wild herbivores were recorded for the 1994 count and 865 for the 1999 count. The associated animal biomass per GPS locality ranges from 10 kg (1 klipspringer (*Oreotragus oreotragus* Zimmermann)) to 16,560 kg (a herd of 36 eland (*Taurotragus oryx* Pallas)). Elephant (*Loxodonta africana* Blumenbach) constituted 11.4% of the total metabolic mass of wild herbivores present on the Songimvelo Game Reserve (SGR) in 1999. They generally move around in 1 or 2 herds and large daily movements across the land-

Table 1 Error matrix resulting from the crosstabulation of the 85 independent sample plots with the habitat map of the Songimvelo Game Reserve obtained through unsupervised classification of LANDSAT Thematic Mapper quarter scene WRS 168-3-078.

Independent data set	Satellite-derived habitat map			
	Mixed range	Sour range	Row total	Commission error (%)
Mixed range	40	12	52	23.1
Sour range	5	28	33	15.2
Column total	45	40	85	
Omission error (%)	11.1	30.0		

scape have been observed in the field. Elephant were not considered further for this study as a single GPS observation could dramatically bias the evaluation of habitat selection.

The results from the crosstabulation clearly indicate the proportionally greater selection of the mixed compared to the sour vegetation (Fig. 3). Although only representing 31.0% (range 26.4 to 35.7%) of the available habitat, the mixed vegetation holds 66.1% (range 60.4 to 71.9%) of the game. In contrast, 54% (range 50.4 to 57.7%) of the surveyed area consisted of sour vegetation that held only 26.5% (range 22.9 to 30.1%) of the game. This differential pattern in stocking rate according to range type remained similar for the 1994 and 1999 surveys. The forests and thickets represented 14.9% (range 13.9 to 15.8%) of the available habitat but contributed only 7.3% (range 5.2 to 9.5%) to the game stocking. The possibility exists that game numbers were undercounted for forests and thickets because of the difficulty of observing animals under the canopy. Field observations however suggest that few herbivores are found in this vegetation formation and particularly not in the dense and moist forests.

In terms of absolute values, the mixed portion of the landscape had an average stocking density 4 times higher than the sour portion (Table 2). This difference reflects the general stocking densities of 10^3 to 10^4 kg km⁻² for medium and high

Table 2 Stocking densities during winter in the different habitats of the Songimvelo Game Reserve.

Habitat	Stocking density		
	1994	1999	Weighted mean ¹
	----- (kg km ⁻²) -----		
Mixed	3415	2989	3198
Sour	771	684	717
Forest/thicket	629	784	724
Weighted mean ¹	1694	1309	1470

¹ weighted to take into account different extent of habitat and differences in area surveyed during 1994 and 1999 respectively.

soil nutrient status dystrophic savannas with a rainfall of approximately 1,000 mm as compared to only 10^2 to 10^3 kg km⁻² for low soil nutrient status savannas reported by East (1984). As mentioned in the description of the SGR, the lower-lying Komati Valley receives a much lower rainfall and is characterised by more fertile substrates compared to the higher-

Fig. 3. Mean relative habitat availability and stocking densities in the Songimvelo Game Reserve for the 1994 and 1999 game counts. Note the proportionally greater stocking of the mixed range.

lying north-easterly parts.

Differences in stocking rates between 1994 and 1999 cannot be directly compared. They are more a consequence of the differences in flight areas covered than a biologically significant change in animal numbers. The total recorded wild herbivore biomass, excluding elephant, was 391,367 kg in 1994 and 412,471 kg in 1999. The 1999 figure is 5.4% higher but is spread across an area 30% larger than 1994 resulting in an apparent drop of 23% in stocking rates (Table 2). During the intervening years, game numbers were controlled and a total of 272,478 kg was removed, mostly through live capture and relocation to other conservation areas. The higher total biomass figure recorded during 1999 therefore reflects the larger area surveyed and not an increase in wildlife numbers.

The overall stocking rate for the Songimvelo Game Reserve (SGR) is low compared to the agricultural guidelines for this part of the country (Barnes 1990). In view of the overall conservative stocking rates one can assume a fair degree of choice being available to the herbivores regarding area selection. The other factors that could influence herbivore distribution are the availability of water, availability of forage, fire history and human disturbance. No artificial waterpoints are provided in the SGR. The perennial Komati River bisects the game-fenced area.

Numerous other perennial rivers and streams occur. Fully 98.9% of the SGR is located within 2 km from perennial water. No part is situated further than 3 km from perennial water. The average radius of range utilisation around watering points in winter in the Kruger National Park has been documented as respectively 3.5 km for impala, 11.25 km for zebra (*Equus burchellii* Gray) and 11.5 km for blue wildebeest (*Connochaetus taurinus* Burchell) (Young 1970). Water is therefore not considered a major constraint to, or determinant of herbivore distribution in the SGR.

The crude index of grass quantity based on the 3 cover and 3 height classes has a possible range from 1 to 5.2. Based on the actual recorded values a mean of 2.9 (SD 1.02) was obtained for the mixed habitat (n = 136 sample plots) and 3.3 (SD 0.83) for the sour habitat (n = 224 plots). A larger quantity of grass is thus generally available in the sour habitat. This difference is however not significant ($\chi^2 = 0.03$, $\chi^2_{0.05,1} = 3.481$, $0.75 < P < 0.90$). The greater standard deviation for the mixed range reflects the figure of 57.3% of the plots assessed as being medium to heavily grazed, compared to only 7.6% of the sour plots being grazed. The mixed range consists of short-ly grazed areas as well as little grazed areas, whereas the sour range is generally uniformly non-utilised. In the field, the availability of grass, particularly in winter, is clearly more limited on the mixed areas.

Table 3. Stocking densities during winter in the different habitats of the Songimvelo Game Reserve in relation to fire history and distance from human settlements.

		Stocking density		
		1994	1999	Weighted mean
		----- (kg km ⁻²) -----		
Habitat and fire history				
Mixed				
	unburnt	3537	2858	3207
	burnt	49	3979	3100
Sour				
	unburnt	882	653	736
	burnt	366	886	624
Habitat and distance from settlements				
Mixed				
	< 4 km	1758	1073	1398
	> 4 km	3896	3571	3732
Sour				
	< 4 km	424	606	536
	> 4 km	1256	790	970

Taking into account the lower stocking densities on the sour habitat, herbivore distribution is clearly not primarily governed by the absolute quantitative availability of feed.

The difference in order of magnitude of stocking density was maintained for mixed and sour habitats regardless of burning history (Table 3). Overall, mixed range in the SGR is stocked at a rate 4 to 5 times higher than sour range whether burnt or unburnt. This difference is significant ($\chi^2 = 18120.6$, $\chi^2_{0.05,1} = 3.481$, $P < 0.001$). Differences were observed between individual years. The burnt areas were stocked at a lower density during 1994 within each habitat. The inverse pattern, with higher stocking densities on burnt areas, was observed during 1999. Objective evaluation of this pattern was complicated by the relatively small extent of the burnt areas. The burnt portion covered only 279 ha (3.4%) of the total mixed habitat surveyed in 1994 and only 970 ha (11.7%) of the mixed habitat in 1999. Burnt areas covered 2451 ha (21.6%) and 2407 ha (13.4%) of the sour habitat respectively in 1994 and 1999. Chance events and daily movements of herbivores could be an important factor in the evaluation of the relatively small burnt areas. Field observations (Unpublished data, M.E. Stalmans) certainly indicate a greater use of burnt areas at a smaller spatial scale and for a limited period of time. In summary, at a large spatial scale and a temporal scale of one year, the fundamental difference in the nature of the mixed and sour habitat overrides fire history.

Some 30 human settlements occur mostly in the southern and eastern boundary

areas of the game-fenced portion of the SGR. Each settlement is occupied by a single and sometimes extended family which practices subsistence agriculture and receives remittances from family members employed outside the Songimvelo Game Reserve (SGR). Mean herd size in 1992 was 27 head of cattle (range 0 to 126) (Heinsohn et al. 1992). Cultivation mainly consists of maize. Mean area of lands cultivated by a single family was 2.9 ha (range 0.4 to 9 ha). Trees and branches are cut down for building purposes and as firewood. The maximum distance in the SGR away from settlements is between 12 and 13 km. A cut-off value of 4 km was used for the habitat evaluation as 48.5% of the SGR is less than 4 km from a settlement leaving 51.5% of the area to be further than 4 km away.

The stocking density of wild ungulates on areas less than 4 km away from settlements was less than half that of areas further away for both mixed and sour habitat for both counts (Table 3). This apparent negative effect from human settlements on game stocking density tested significant ($\chi^2 = 1653.9$, $\chi^2_{0.05,1} = 3.481$, $P < 0.001$). Nevertheless, mixed areas close to settlements are still stocked at values two to three times higher than equivalent sour areas. Furthermore, the stocking density on mixed areas close to settlements still remains higher than the stocking density on sour areas further away from settlements.

Human settlements have been documented as having a negative impact on wild herbivore densities for a distance of at least 7 km in a forest environment (Eltringham 1990) and 10 km in arid envi-

ronments (Verlinden 1997). The definite negative impact within the 4 km cut-off selected for the SGR is therefore not unexpected but it does not override the fundamental difference in habitat quality between mixed and sour range.

At the landscape scale and at temporal scales of a year or more, the broad differences in habitat quality and its spatial distribution clearly outweigh the effects of any short-term, localised management action or human disturbance. Senft et al. (1987) hypothesised that in the absence of overriding constraints, foraging behaviour by large herbivores should produce a landscape stocking rate that is a linear function of landscape productivity. The mixed range, although limited in extent, is critical to wild herbivores in the SGR.

The habitat make-up of the SGR as derived from remote sensing and as confirmed by ground data, forms the base upon which further studies can be undertaken regarding individual herbivore species preference, performance and stocking.

Conclusions

The broad habitat map, which was derived from the satellite imagery, identified mixed and sour range units differing in terms of composition and palatability. Broad herbivore distribution patterns were well correlated with the spatial distribution of these habitat units derived from remote sensing. At the landscape scale, the habitat quality in terms of grass layer composition and palatability overrides its quantitative availability and its smaller-scale fire history. Because of its ubiquitous nature, water distribution is not a significant factor in the Songimvelo Game Reserve (SGR). Although stocking densities of wild ungulates are lower close to human settlements, the overall high ratio in stocking densities between mixed and sour habitat is maintained. These findings, applying to both the 1994 and 1999 game surveys, suggest the fundamental differences in forage quality between range types persist across seasons. Anecdotal field evidence from intervening years supports this assumption.

The integration of field data and satellite imagery into a GIS system for analysis offers a powerful tool for the objective quantification and mapping of the spatial distribution of available habitat. The resulting image is ecologically relevant and of practical value to the manager and ecologist dealing with this heterogeneous system. As such this approach could be

applied to other nature reserves and to the growing number of game farms in southern Africa and elsewhere.

Literature Cited

- Acocks, J.P.H. 1975.** Veld types of South Africa. Mem. Bot. Surv. So. Afr. 40:1–128.
- Barnes, D.L. 1990.** A survey of grazed and ungrazed grasslands in the south-eastern Transvaal highveld. 1. Palatability composition and grazing capacity. J. Grassl. Soc. So. Afr. 7:217–222.
- Barnes, K.N. (ed.). 1998.** The important bird areas of southern Africa. Avian Demography Unit, BirdLife South Africa, Johannesburg, So. Afr.
- Brondizio, E., E. Moran, P. Mausel, and Y. Wu. 1996.** Land cover in the Amazon estuary: Linking of the thematic mapper with botanical and historical data. Photogramm. Eng. Remote Sens. 62:921–929.
- Congalton, R.G., K. Green, and J. Tepley. 1993.** Mapping old growth forests on National Forests and Park Lands in the Pacific Northwest from remotely sensed data. Photogramm. Eng. Remote Sens. 59:529–535.
- Deall, G.B. and G.K. Theron. 1990.** Ordinations as a tool for substantiating and interpreting floristic classifications: A case study. Bothalia 20:223–227.
- East, R. 1984.** Rainfall, soil nutrient status and biomass of large African savanna mammals. Afr. J. Ecol. 22:245–270.
- Eastman, J.R. 1992.** IDRISI. Clark University Graduate School of Geography, Worcester, Mass.
- Edwards, D. 1983.** A broad-scale structural classification of vegetation for practical purposes. Bothalia 14: 705–712.
- Ellery, W.N., R.J. Scholes, and M.C. Scholes. 1995.** The distribution of sweetveld and sourveld in South Africa's grassland biome in relation to environmental factors. Afr. J. Range For. Sci. 12:38–45.
- Eltringham, S.K. 1990.** Wildlife carrying capacities in relation to human settlement. Koedoe 33:87–97.
- Fairbanks, D.H.K. and M.W. Thompson. 1996.** Assessing land-cover map accuracy for the South African Land-Cover database. So. Afr. J. Sci. 92:465–470.
- Fuller, R.M., G.B. Groom, S. Mugisha, P. Ipuet, D. Pomeroy, A. Katende, R. Bailey, and R. Ogutu-Ohwayo. 1998.** The integration of field survey and remote sensing for biodiversity assessment: a case study in the tropical forests and wetlands of Sango Bay, Uganda. Biol. Conserv. 86:379–391.
- Gamble, F. 1988.** Climate of the Transvaal Escarpment, p. 1–4. In: A.A. Ferrar, G. Isaacs and J.R. Stacey (eds.), Environmental conservation features of the Transvaal Escarpment. Occasional Rep. 31. CSIR, Pretoria.
- Geological Survey. 1986.** Geology map 1:250,000 geological series: 2430 Barberton. Government Printer, Pretoria.
- Heinsohn, R-D., S.J. Woodburne, and S.E. Alexander. 1992.** Demographic, socio-economic and attitudinal surveys of affected communities in and around Songimvelo Game Reserve. A.C.E.R. (Africa) Tech. Rep. to Dept. Development Aid, Pretoria.
- Hodgson, M.E., J.R. Jensen, H.E. Mackey, and M.C. Coulter. 1988.** Monitoring wood stork foraging habitat using remote sensing and geographic information systems. Photogramm. Eng. Remote Sens. 54:1601–1607.
- Hutchinson, C.F. 1982.** Techniques for combining Landsat and ancillary data for digital classification improvement. Photogramm. Eng. & Remote Sens. 48:123–130.
- Land Type Survey Staff. 1989.** Land types of the map 2530 Barberton. Memoirs of the Agric. Natur. Resources of So. Afr. 13, Pretoria.
- Lauver, C.L. and J.L. Whistler. 1993.** A hierarchical classification of Landsat TM imagery to identify natural grassland areas and rare species habitat. Photogramm. Eng. Remote Sens. 59:627–634.
- Low, A.B. and A.G. Rebelo. (eds.) 1996.** Vegetation of South Africa, Lesotho and Swaziland. Dept. Environ. Affairs and Tourism, Pretoria.
- Lunetta, R.S. and M.E. Balogh. 1999.** Application of multi-temporal Landsat 5 TM imagery for wetland identification. Photogramm. Eng. Remote Sens. 65:1303–1310.
- Mackay, C.H. and H.L. Zietsman. 1996.** Assessing and monitoring rangeland condition in extensive pastoral regions using satellite remote sensing and GIS techniques: An application to the Ceres Karoo region of South Africa. Afr. J. Range For. Sci. 13:100–112.
- Medler, M.J. and S.R. Yool. 1997.** Improving thematic mapper based classification of wildfire induced vegetation mortality. Geocarto Int. 12:49–58.
- Mentis, M.T. 1984.** Monitoring in South African grasslands. South African Nat. Sci. Programmes Rep. 91, CSIR, Pretoria.
- Mueller-Dombois, D. and H. Ellenberg. 1974.** Aims and methods of vegetation ecology. John Wiley & Sons, New York.
- National working group for vegetation ecology. 1986.** Soil classification according to the binomial classification system. Tech. Commun. 3, Pretoria.
- Quattrochi, D.A. and R.E. Pelletier. 1991.** Remote sensing for analysis of landscapes: An introduction. p. 52–76. In: M.G. Turner and R.H. Gardner (eds.), Quantitative methods in landscape ecology. Springer-Verlag, New York.
- Rey-Benayas, J.M. and K.O. Pope. 1995.** Landscape ecology and diversity patterns in the seasonal tropics from Landsat TM imagery. Ecol. Appl. 5: 386–394.
- Rutherford, M.C., and R.H. Westfall. 1986.** Biomes of southern Africa - An objective categorisation. Mem. Bot. Surv. So. Afr. 54:1–98.
- Senft, R.L., M.B. Coughenour, D.W. Bailey, L.R. Rittenhouse, O.E. Sala, and D.M. Swift. 1987.** Large herbivore foraging and ecological hierarchies. BioSci. 37:789–799.
- Stalmans, M., E.R. Robinson, and K. Balkwill. 1999.** Ordination and classification of vegetation of Songimvelo Game Reserve in the Barberton Mountainland, South Africa as a basis for the assessment of wildlife habitat distribution and quality. Bothalia 29:305–325.
- Thrash, I., G.K. Theron, and J. du P. Bothma. 1995.** Dry season herbivore densities around drinking troughs in the Kruger National Park. J. Arid Environ. 29:213–219.
- Trollope, W.S.W. and A.L.F. Potgieter. 1986.** Estimating grass fuel loads with a disc pasture meter in the Kruger National Park. J. Grassl. Soc. So. Afr. 3:148–152.
- Trollope, W.S.W., L.A. Trollope, and O.J.H. Bosch. 1990.** Veld and pasture management terminology in southern Africa. J. Grassl. Soc. So. Afr. 7:52–61.
- Tueller, P.T. 1989.** Remote sensing technology for rangeland management applications. J. Range Manage. 42:442–453.
- Van der Merwe, P.D.R. and E.F. Retief. 1995.** The Songimvelo Game Reserve inhabitants: individual data and background information. Tech. Rep. Dept. of Constitutional Development, Pretoria, So. Afr.
- Verlinden, A. 1997.** Human settlements and wildlife distribution in the southern Kalahari of Botswana. Biol. Conserv. 82:129–136.
- Viljoen, P.C. and P.F. Retief. 1994.** The use of the Global Positioning System for real-time data collecting during aerial surveys in the Kruger National Park. Koedoe 37:149–154.
- Voeten, M.M. and H.H.T. Prins. 1999.** Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania. Oecologia 120:287–294.
- Wilkinson, G.G. 1996.** A review of current issues in the integration of GIS and remote sensing. Int. J. Geographical Information Systems 10:85–101.
- Wilsey, B.J. 1996.** Variation in use of green flushes following burns among African ungulate species: the importance of body size. Afr. J. Ecol. 34:32–38.
- Young, E. 1970.** Water as faktor in die ekologie van wild in die Nasionale Krugerwildtuin. Ph.D. Thesis, Univ. Pretoria, So. Afr.
- Zar, J.H. 1984.** Biostatistical analysis. Prentice-Hall, N.J.

Intensive-early stocking for yearling cattle in the Northern Great Plains

E. E. GRINGS, R. K. HEITSCHMIDT, R. E. SHORT, AND M. R. HAFERKAMP

Authors are Research Animal Scientist, Supervisory Rangeland Scientist, Research Physiologist, and Rangeland Scientist, USDA-ARS, Fort Keogh Livestock and Range Research Laboratory, Miles City, Mont. 59301.

Abstract

A 3-year study was conducted to evaluate grazing strategies for production of growing cattle during summer on Northern Great Plains rangeland. Crossbred yearling steers (N = 123 per year, avg initial weight = 275 kg) were allotted to 1 of 2 treatments replicated in 3 pastures. Treatments were season-long grazing of pastures at recommended stocking rates assuming a 4-month grazing period or intensive-early grazing of pastures stocked at the same rate assuming only a 2-month grazing season. Precipitation in 1993 was 169% of normal resulting in greater forage quality than in other years and no differences were observed in weight gains between treatments during 1993. In 1994 and 1995, steers in the intensive-early stocked pastures gained less weight during the 2 months of grazing than did those in the season-long stocked pastures; however, gain per hectare was greater in the intensive-early stocked pastures. Intensive-early stocking with growing steers may be a viable means to overcome limited forage quality during late summer in the Northern Great Plains and to maximize forage utilization in years of abundant forage.

Key Words: grazing management, beef cattle, protein supplementation

Growing season precipitation in the Northern Great Plains occurs mainly during May and June. Drier, hotter conditions in late summer result in lowered forage quality and quantity with an associated decreased rate of gain of steers grazing these forages (Heitschmidt et al. 1993). By monitoring daily weight of grazing steers, Currie et al. (1989) found gains to decline in late July to early August, and some steers lost weight during late summer, indicating that keeping steers on rangeland after this time could be counterproductive.

Decreased gains during late summer may be avoided by removing steers from rangeland before the decrease in forage quality. Intensive-early stocking strategies that employ high stocking rates

Resumen

Se condujo un estudio de tres años para evaluar las estrategias de apacentamiento para la producción de ganado en crecimiento durante el verano, el estudio se realizó en el pastizal de las Grandes Planicies del Norte. Novillos un año de cruza de razas (N = 123 por año, peso inicial promedio = 275 kg) se asignaron a 1 de 2 tratamientos repetidos en tres potreros. Los tratamientos fueron: 1) apacentamiento del pastizal durante estaciones largas con la carga animal recomendada, asumiendo un periodo de apacentamiento de 4 meses y 2) apacentamiento intensivo temprano de los pastizales con la misma carga animal asumiendo un periodo de apacentamiento de solo 2 meses. La precipitación en 1993 fue 169% de la precipitación normal resultando una mayor calidad de forraje que en otros años, por lo que no se observaron diferencias en las ganancias de peso entre los tratamientos. En 1994 y 1995 los novillos en el tratamiento de apacentamiento intensivo y temprano ganaron menos peso durante los dos meses de apacentamiento que los novillos en el tratamiento de apacentamiento de estación larga, sin embargo, la ganancia por hectárea fue mayor en el tratamiento de apacentamiento intensivo y temprano. El apacentamiento intensivo con novillos en crecimiento puede ser un medio viable para sobreponer la calidad limitada del forraje a fines del verano en las Grandes Planicies del Norte y para maximizar la utilización del forraje en años en que este es abundante.

but remove cattle from range in mid-summer have been used in the central and southern Great Plains to effectively utilize early season forage for the production of growing cattle (McCollum et al. 1990, Olson et al. 1993, Smith and Owensby 1978). Economic analyses of intensive-early stocking strategies in Oklahoma (Bernardo and McCollum 1987) indicate that these systems require high rates of gain early in the growing season. Heitschmidt et al. (1993) found that gains over 1 kg/day can be expected for steers on Northern Great Plains rangelands in early summer, indicating good potential for intensive-early stocking strategies. The objective of this study was to evaluate intensive-early stocking compared with season-long stocking for the production of growing cattle grazing Northern Great Plains rangelands.

Methods

The study was conducted at the Fort Keogh Livestock and Range Research Laboratory near Miles City, Mont. (46°22'N 105°5'W). Climate is continental and semi-arid with vegetation

The authors express appreciation to Norm Bellows, Richard Bonine, JoAnne Gresens, Byron Hould, Caralea Leidholt, Susan Reil, and Brooke Shipp for assistance with this research.

This paper is a contribution from the U.S. Department of Agriculture, Agricultural Research Service and the Montana Agricultural Experiment Station, Miles City, Mont.

U.S. Department of Agriculture, Agricultural Research Service, Northern Plains Area, is an equal opportunity/affirmative action employer, and all agency services are available without discrimination.

Manuscript accepted 9 May 01.

dominated by western wheatgrass [*Pascopyrum smithii* (Rydb.) Love], threadleaf sedge [*Carex filifolia* Nutt.], needle and thread [*Stipa comata* Trin. and Rupr.], blue grama [*Bouteloua gracilis* (H.B.K.)], and downy [*Bromus tectorum* L.] and Japanese bromes [*B. japonicus* Thunb.]. Average annual rainfall in the area is 338 mm with 60% received during the 150-day, mid-April to mid-September growing season.

During each of 3 years, 123 crossbred yearling steers of British-type breeding (avg initial weight = 275 kg) were allotted to 1 of 2 treatments replicated in 3 pastures (6 pastures total) in a completely random design. Treatments were season-long stocking with pastures stocked at the recommended rate assuming a 4-month grazing period and intensive-early stocking with pastures stocked with about twice the number of steers for a shorter period of time. The timing of grazing varied among years due to forage conditions (Table 1). Pasture size varied from 36 to 90 hectares. Stocking rate was based on SCS (1983) guidelines for range sites in good condition. Hectares available per steer averaged 4.9 for season-long and 1.9 for intensive-early stocked pastures. Animal numbers per pasture were assigned based on range site composition, therefore, number of hectares per steer for the season-long-stocked treatment did not equal twice that of intensive-early stocked pastures. Pastures were assigned the same treatment each year, allowing evaluation of any short-term carryover effects of grazing management on pasture quality and animal performance.

Before the study, steers were implanted with a 200-day estradiol implant. Steers were weighed initially and then about every 14 days on a non-shrunk basis. Decisions concerning removal of cattle from intensive-early stocked pastures were based on biweekly weight changes and visual estimates of forage quality and utilization. Steers were removed from intensive-early stocked pastures when weight gains began to diverge from those of steers in season-long stocked pastures and when cool-season forages became dormant. During 1993, forage quality and quantity were visibly above average and cattle remained on intensive-early stocked pastures until 17 September.

Standing crop was estimated each year before grazing, after removal of intensive-early stocked steers and after remaining steers were removed from pastures. Two sites per pasture were chosen, representing an average of 48.5% of the pasture area

Table 1. Dates of the beginning and ending of the grazing periods for season-long (SS) and intensive-early stocked (IES) pastures.

Year	Start of grazing	IES cattle removed	SS cattle removed
1993	19 May	17 Sep.	4 Oct.
1994	17 May	15 Jul.	8 Sep.
1995	15 May	4 Aug.	26 Sep.

with a range from 26.2 to 73.1%. Three total range sites were sampled as not all pastures were comprised of the same range sites. Botanical composition of each site was visually estimated by the dry weight rank method (t'Mannetje and Haydock 1963) and is presented in Table 2. For standing crop, 4 non-random refer-

(Robertson and Van Soest 1977), and in vitro organic matter digestibility (IVOMD; Tilley and Terry 1963).

Analysis of variance of weight gain data was conducted with a model that included treatment, year, and pasture within treatment (SAS 1989). Treatment means were tested with the pasture within treatment

Table 2. Botanical composition of 3 range sites found within pastures used for intensive-early or season-long stocking of pastures.

Species group	Range site		
	Silty clay	Claypan	Silty-Shallow
	------(%)-----		
<i>Pascopyrum smithii</i>	35.9	63.0	18.3
<i>Stipa comata</i>	25.2	1.3	26.5
Other cool-season grasses	1.3	2.7	5.2
Warm-season grasses	12.7	17.0	18.3
Annual bromes	9.2	8.8	3.7
<i>Carex filifolia</i>	3.3	0.0	23.5
Forbs	12.4	7.2	4.5

ence plots (0.25 m²) per range site were chosen based on a range of biomass densities from least to most abundant. Additionally, 10 random plots per site per pasture were estimated. The 4 reference plots and every fifth random plot were clipped for calibration of the estimates. Herbage was clipped to the ground, sorted by grass and forbs, dried at 55°C for 48 hours, and weighed. The non-random reference plots were not included in standing crop estimates for the pasture. Samples were composited by site within grazing treatment and saved for chemical analysis. Chemical analyses on herbage included dry matter, ash (AOAC 1990), crude protein (Hach 1987), neutral detergent fiber

mean square as the error term. Year effects were tested with the residual error term. Standing crop was evaluated with a model including year, treatment, and the interaction which were tested with pasture within treatment as the error term. The model also included sampling time, year x sampling time, treatment x sampling time, and year x treatment x sampling time which were tested using the residual mean square as the error term. The model for forage quality included year and time of sampling (pre-grazing, mid-grazing, and end of grazing). Due to compositing of samples for chemical analysis, the residual error was used to test effects on chemical analysis of forage.

Table 3. Forage standing crop for 2 range sites within pastures used for intensive-early stocking (IES) and season-long stocking (SS), SEM = 32.6.

Item	Treatment		Year		
	IES	SS	1993	1994	1995
	------(kg/ha)-----				
Initial pre-grazing ¹	1,406	1,576			
Pre-grazing	1,425	1,803	1,491	1,807	1,544
Mid-grazing	1,483	1,814	1,804	1,711	1,431
Post-grazing	1,418	1,904	1,636	1,722	1,625
Average	1,442	1,840	1,644 ^{a2}	1,747 ^a	1,533 ^b

¹May 1993.

²Means by year with differing superscripts differ, P < 0.05.

Fig. 1. Temperature and precipitation throughout 1993 to 1995 compared to a 115 year average.

Results and Discussion

Environmental Conditions

Precipitation during May through August 1993 was about 169% of normal, with rain falling throughout the grazing period (Fig. 1). July 1993 precipitation was 400% above normal. Precipitation in 1994 was 44% of normal, with all months being below normal. Precipitation in 1995 was close (104%) to the average for the area, with a fairly typical monthly pattern.

Seasonal Changes in Herbage Quantity and Herbage

At the initial pre-grazing sample in 1993, available forage did not differ between treatments (Table 3). The increase in forage availability between 1993 and 1994 may be related to carry-over of biomass from 1993 into 1994. Quantity of forage was less in 1995 than it had been the previous 2 years. No interactions ($P > 0.10$) of grazing treatment with year or sampling time on forage availability were observed.

As forage quantity did not differ between treatments at any time, we hypothesize that pastures could have been stocked at a heavier rate with little detriment to cattle performance. However, care should be taken to not overstock pastures with an intensive-early stocking system. Olson et al. (1993) compared season-long

to intensive-early stocking in the Central Great Plains at either 2- or 3-times the number of animals in the intensive-early stocked pastures for 9-years and found vegetation shifted to more warm-season grasses with the heavier intensive-early stocking. Willms and Jefferson (1993) also suggested shifts to warm-season grasses will occur with heavy early grazing in the Northern Great Plains.

Forage quality declined throughout the summer as evidenced by a consistent decline in crude protein between pre-graz-

ing samples and those collected later in the season (Table 4). Crude protein did not differ between mid- and post-grazing samples. Greater forage crude protein was observed in 1993 than in other years and is related to the greater amounts of precipitation and cooler temperatures observed in 1993. Forage IVOMD did not differ among years for the pre-grazing sample, but was greater for mid- and post-grazing samples in 1993 than in other years. Mid- and post-grazing IVOMD were lowest in 1995.

The only forage quality measure to be affected by grazing treatment was neutral detergent fiber. These values were higher ($P < 0.05$) for samples collected from intensive-early stocked (81.1%) than season-long (79.2%) treatments. This could be the result of increased grazing intensity in the intensive-early stocked pastures.

Grazing Management

At the end of the early grazing period, cattle grazing intensive-early stocked pastures weighed about 10 kg less than the cattle grazing season-long stocked pastures (Table 5). In 1993, steers were lighter at the beginning of grazing than in other years, but were heavier by the end of both grazing periods. This was related primarily to the increased length of grazing in 1993.

There was a year x treatment interaction ($P < 0.05$) for average daily gain during the early grazing period as no differences were observed in gains between the treatments during 1993 (Table 6). This occurred even though the intensive-early stocked pastures were grazed for 4 months rather than the proposed 2 months (Table 1). The increased length of grazing greatly

Table 4. Forage quality of pastures used during the summer with intensive-early stocking (IES) or season-long stocking (SS) and sampled before grazing, at the time steers were removed from IES pastures, and at the end of SS grazing.

Item	Time of sampling			SEM
	Before grazing ¹	IES steers removed	Post-SS grazing	
Crude protein ¹	-----(% OM)-----			
1993 ^{A2}	9.7	7.8	7.3	0.19
1994 ^B	8.1	5.4	4.9	0.17
1995 ^B	7.8	5.2	5.2	0.17
Neutral detergent fiber				
1993	77.0 ^{aA}	81.6 ^{bA}	82.1 ^{bA}	0.79
1994	78.6 ^{aA}	82.9 ^{bA}	82.4 ^{bA}	0.72
1995	73.7 ^{aB}	78.9 ^{bB}	84.5 ^{cB}	0.73
IVOMD				
1993	61.4 ^a	58.9 ^{bA}	54.8 ^{cA}	0.67
1994	60.4 ^a	51.7 ^{bB}	50.6 ^{bB}	0.61
1995	59.6 ^a	48.2 ^{bC}	45.9 ^{cC}	0.62

¹There was a main effect of sampling time with pre-grazing differing from mid- and post-grazing samples, $P < 0.05$.

²Means within year with differing lowercase superscripts differ by sampling time. Means within sampling time with differing uppercase superscripts differ by year, $P < 0.05$.

Table 5. Weight changes of yearling steers grazing Northern Great Plains rangeland in summer and intensive-early-stocked (IES), season-long stocked (SS).

	Treatment		Year			SEM
	IES	SS	1993	1994	1995	
	------(kg)-----					
Initial weight	276	275	268 ^{A1}	278 ^B	280 ^B	0.87
Weight, after IES	391	401	432 ^A	370 ^B	386 ^C	1.16
Weight, at end of SS grazing	-	429	451 ^A	408 ^B	426 ^C	2.11

¹Year means with differing superscripts differ, $P < 0.01$.

increased the gain per hectare (Table 6) for this treatment in 1993 (treatment x year interaction) and indicates a potential advantage to the intensive-early stocking system. It was possible to take advantage of a season of high forage production for additional weight gains in steers. In 1994 and 1995, steers in the intensive-early stocked pastures gained less weight per day during the 2 months of grazing than did those grazing season-long; however, gain per hectare was greater in the intensive-early stocked pastures. The decreased gain per steer but increased gain per hectare is typical of intensive-early stocked grazing systems (Smith and Owensby 1978, McCollum et al. 1990). Olson et al. (1993) did not observe this response on shortgrass range in Kansas and suggested that this may be related to a slower decline in forage quality on those ranges. In the current study, forage quality had substantially declined in 1994 and 1995 by the time intensive-early stocking cattle were removed from pastures and associated gains of season-long stocking steers were reduced in the second half of the grazing season.

High rates of gain early in the grazing

season (1.3 kg/day) are reflective of the high forage quality available at this time of the year. Average daily gain over the entire grazing season for the season-long stocked steers was 1.19, 1.07, and 1.11 kg/day in 1993, 1994, and 1995, respectively. Average daily gain throughout the season-long grazing period was greater ($P < 0.05$) for 1993 (1.2 kg/day) than for 1994 and 1995 (1.1 kg/day). This was related to the increased available forage crude protein and IVOMD observed in 1993 compared with other years.

Implications

Gain per hectare was improved with the use of intensive-early stocking for yearling steers; therefore, the use of this strategy for growing cattle may be a viable means to overcome limited forage quality during late summer in the Northern Great Plains and to maximize utilization of the rangeland resource in years of abundant forage. Additional long-term research is required to define optimal stocking rates for this environment.

Table 6. Average daily gain and gain per hectare for steers grazing intensive-early stocked (IES) or season-long stocked (SS) pastures.

	Treatment		SEM
	IES	SS	
ADG, during IES period	------(kg/day)-----		0.01
1993	1.22 ^{A1}	1.24 ^A	
1994	1.29 ^{aB}	1.48 ^{bB}	
1995	1.25 ^{aA}	1.38 ^{bC}	
ADG after IES period			0.02
1993	-	1.11 ^A	
1994	-	0.59 ^B	
1995	-	0.66 ^B	
Gain per hectare	------(kg gain/ha)-----		0.69
1993	82.8 ^{aA}	39.8 ^{bA}	
1994	43.2 ^{aB}	26.8 ^{bB}	
1995	52.8 ^{aC}	30.0 ^{bB}	

¹Means with differing lowercase superscripts differ by treatment within year, $P < 0.05$. Means with differing uppercase superscripts differ by year within treatment, $P < 0.05$.

Literature Cited

- AOAC. 1990. Official methods of analysis. 16th ed. Assoc. Official Anal. Chem., Washington, D.C.
- Bernardo, D.J. and F.T. McCollum. 1987. An economic analysis of intensive-early stocking, season-long stocking and prescribed burning programs for stocker cattle operations in central Oklahoma. Okla. Agric. Exp. Sta. Anim. Sci. Res. Rep. MP-119 238-242.
- Currie, P.O., J.D. Volesky, D.C. Adams, and B.W. Knapp. 1989. Growth patterns of yearling steers determined from daily live weights. J. Range Manage. 42:393-396.
- Hach. 1987. Feed analysis manual. Hach Co., Ames, Iowa.
- Heitschmidt, R.K., J.D. Volesky, M.R. Haferkamp, and P.O. Currie. 1993. Steer performance on native and modified Northern Great Plains rangeland. J. Range Manage. 46:529-533.
- McCollum, F.T., R.L. Gillen, D.M. Engle, and G.W. Horn. 1990. Stocker cattle performance and vegetation response to intensive-early stocking of Cross Timbers rangeland. J. Range Manage. 43:99-103.
- Olson, K.C., J.R. Brethour, and J.L. Launchbaugh. 1993. Shortgrass range vegetation and steer growth response to intensive-early stocking. J. Range Manage. 46:127-132.
- Robertson, J.B. and P.J. Van Soest. 1977. Dietary fiber estimation in concentrate feed-stuffs. J. Anim. Sci. 45 (Suppl. 1):254 (Abstr.).
- SAS. 1989. SAS users guide: Basics. SAS Institute, Cary, N.C.
- SCS. 1983. Technical guide, Section II-E-8. 10-14" Precipitation zone. Eastern Sedimentary Plains. Mont.
- Smith, E.F. and C.E. Owensby. 1978. Intensive-early stocking and season-long stocking of Kansas Flint Hills range. J. Range Manage. 31:14-17.
- Tilley, J.M.A. and R.A. Terry. 1963. A two-stage technique for the in vitro digestion of forage crops. J. Brit. Grassl. Soc. 18:104-111.
- t'Mannetje, L. and K.P. Haydock. 1963. The dry-weight-rank method for the botanical analysis of pasture. J. Br. Grassl. Soc. 18:268-275.
- Willms, W.D. and P.G. Jefferson. 1993. Production characteristics of the mixed prairie: constraints and potential. Can. J. Anim. Sci. 73:765-778.

Nutritional value and intake of prickly pear by goats

ZENO McMILLAN, CODY B. SCOTT, CHARLES A. TAYLOR, JR., AND J. ED HUSTON

Authors are former Graduate Assistant, Associate Professor, Department of Agriculture, Angelo State University, San Angelo, Tex.; Supervisor, Texas Agricultural Experiment Station, Sonora, Tex; and Professor, Texas Agricultural Experiment Station, San Angelo, Tex.

Abstract

Prickly pear (*Opuntia* sp.) is both a benefit and hindrance to the livestock industry in the southwestern U.S. It competes with herbaceous forage but is sometimes used as emergency feed during drought. Spineless prickly pear (*O. ficus-indica* Engelm. and *O. rufida* Engelm.) has been planted in some regions of the southwest but little is known about its nutritional value. Our objectives were to determine: (1) the nutritional value of both spined (*O. macrorhiza* Engelm.) and spineless prickly pear (*O. rufida* Engelm.); (2) if goats can be conditioned to eat prickly pear after prescribed burning; and, (3) if goats would consume prickly pear when alternative forage was available. In Experiment 1, 8 goats were placed in metabolism stalls and fed either spineless or spined prickly pear with singed spines in both summer and winter. Intake, digestibility, and nitrogen balance were measured. In Experiment 2, 18 goats were placed in individual pens, and 9 were fed spineless prickly pear to determine if this increased acceptance of spined prickly pear with singed spines. In the third experiment, we varied the amount of alfalfa pellets fed to goats (below, near, and above maintenance) to determine if level of alfalfa intake affected prickly pear intake. Spineless prickly pear was higher ($P < 0.05$) in digestibility and crude protein than singed prickly pear, but nitrogen balance was similar for goats consuming the 2 species. Goats ate more spineless prickly pear on an as fed basis, but on a dry basis, intake was similar. Familiarity with spineless prickly pear increased ($P < 0.05$) subsequent intake of singed prickly pear. Level of alfalfa intake did not affect prickly pear intake. We concluded that both species are moderately nutritious, spineless prickly pear is more digestible than spined prickly pear, and once a preference for prickly pear has developed, goats may continue to eat prickly pear even though other forage is available.

Key Words: *Opuntia*, food novelty, learning, diet preference, browsing, protein, nitrogen balance, forage digestibility

The perceived value of prickly pear (*Opuntia* sp.) varies depending on geographic location and species. Most livestock producers in the southwestern United States attempt to control prickly pear because of its competitive nature with herbaceous forages (Mayeux and Johnson 1989, Ueckert et al. 1988). Most species of prickly pear also contain spines that cause injury to

Resumen

El "Prickly pear" (*Opuntia* sp.) es benéfico pero a la vez también es un estorbo para la ganadería del sudeste de los Estados Unidos. El compite con la vegetación forrajera herbácea, pero en ocasiones es utilizado como forraje de emergencia durante la sequía. En algunas regiones del sudeste se ha plantado una especie de "Prickly pear" sin espinas (*O. ficus-indica* Engelm. and *O. rufida* Engelm.), pero poco se sabe acerca de su valor nutricional. Nuestros objetivos fueron determinar (1) el valor nutricional del "Prickly pear" con espinas (*O. macrorhiza* Engelm.) y sin espinas (*O. rufida* Engelm.); (2) si las cabras pueden ser acondicionadas para comer "Prickly pear" después de un fuego prescrito y (3) si las cabras consumirían "Prickly pear" cuando otro forraje alternativo esta disponible. En el experimento 1, 8 cabras se colocaron en jaulas metabólicas individuales y durante el invierno y verano fueron alimentadas con "Prickly pear" sin espinas o con espinas marcadas y se midió el consumo, la digestibilidad y el balance de nitrógeno. En el experimento 2, 18 cabras fueron colocadas en corrales individuales y 9 se alimentaron con "Prickly pear" sin espinas para determinar si esto incrementa la aceptación sobre el "Prickly pear" con espinas marcadas. En el tercer experimento variamos la cantidad de pellets de alfalfa con la que se alimento a las cabras (abajo, cerca y arriba del nivel de mantenimiento) para determinar si el nivel de consumo de alfalfa afectó el consumo de "Prickly pear". La especie de "Prickly pear" sin espinas fue mayor en digestibilidad y proteína cruda ($P < 0.05$) que la especie con espinas marcadas, pero el balance de nitrógeno fue similar en cabras consumiendo las 2 especies. En base al alimento, las cabras consumieron mas "Prickly pear" sin espinas, pero en base de materia seca el consumo fue similar. La familiaridad del "Prickly pear" sin espinas incremento ($P < 0.05$) el consumo subsecuente de "Prickly pear" con espinas marcadas. El nivel de consumo de alfalfa no afecto el consumo de "Prickly pear". Concluimos que ambas especies son moderadamente nutritivas, que el "Prickly pear" sin espinas es mas digestible que la especie con espinas y que una vez que la preferencia por "Prickly pear" ha sido desarrollada las cabras pueden continuar comiendo "Prickly pear" aunque otro forraje este disponible.

livestock after ingestion (Ueckert et al. 1990). In other areas, spineless prickly pear (*Opuntia ficus-indica* Engelm. and *O. ficus-indica* (L.) Miller) has been introduced as an alternative feed (Brutsch and Zimmerman 1993). Spined prickly pear is used as forage for livestock, especially during droughts (Griffiths 1905, Bement 1969, Lehman 1969, Hanselka and Paschal 1991). Before feeding or grazing prickly pear, the pads are generally singed with a propane burner to remove the spines thereby improving acceptance and reducing the health hazards (i.e., phys-

Funding was provided by the Management, Instruction, and Research Center, Angelo State University, San Angelo, Tex.; Texas Agricultural Experiment Station, Sonora, Tex. The authors would like to acknowledge B.S. Engdahl for her assistance with laboratory analysis.

Manuscript accepted 8 Jul. 01.

ical damage to the lips, mouth, and upper gastrointestinal tract) (Ueckert et al. 1990, Hanselka et al. 1993).

Throughout most of western and central Texas, prescribed burning is used to reduce prickly pear abundance, but mortality rates are low unless winter burning is followed with herbicide application (Ueckert 1997, Ueckert et al. 1988). The high cost of herbicides limits the economic feasibility of controlling prickly pear. Given that livestock will consume prickly pear after the spines have been removed, prescribed burning could be followed by livestock grazing. Grazing after burning may also reduce prickly pear density because the plant does not tolerate heavy defoliation (Maltsberger 1989).

Prickly pear species are common throughout the southwestern U.S. and many produce substantial phytomass that can serve as emergency forage (Garcia de Cortazar and Nobel 1992). Prickly pear is moderately high in sugars, starch, ether extract, crude protein, amino acids, and fiber (Teles et al. 1984, Retamal et al. 1987). However, the availability of nutrients for ruminant animals has not been assessed. To assess the potential value of singing prickly pear as an emergency forage resource, it is important to know its forage value. Thus, the first objective of this study was to quantify *in vivo* digestibility of prickly pear and nitrogen balance of goats consuming prickly pear.

Our second objective was to determine if we could improve acceptance of prickly pear as a forage. Recent studies on livestock training have suggested that previous experiences with certain foods increases intake, and preferences may develop and persist (Provenza 1994). Thus, it may be possible to train livestock to consume more prickly pear, thereby increasing the effectiveness of livestock herbivory after prescribed burning as a biological control. We hypothesized that feeding spineless prickly pear immediately after weaning would improve acceptance of singed (spined) prickly pear.

Given the presence of spines, livestock generally avoid eating prickly pear when other forage is available. However, livestock have been observed to eat prickly pear throughout the year even though they develop health problems and alternative forage is available (Hanselka et al. 1993). Our third objective was to determine how dietary feed level affected intake of prickly pear by goats. We hypothesized that goats meeting or exceeding maintenance requirements would avoid eating prickly pear while goats unable to meet maintenance

requirements because of limited feed intake would consume prickly pear.

Methods

All experiments were conducted at the Texas Agricultural Experiment Station, Sonora, Tex. (30° N, 100° W) beginning in June 1999. Spined (*O. macrohiza* Engelm.) and spineless (*O. rufida* Engelm.) prickly pear were fed to goats in 3 studies. The spineless prickly pear was grown on site under ambient conditions, and the spined prickly pear was harvested from a natural stand nearby. The spined prickly pear was singed with a propane burner in the field each day immediately before harvesting to remove all spines. Both types of prickly pear were cut into 5 cm wide strips, and fed fresh to individual goats in each of the 3 experiments.

Metabolism Study

Eight female Boer-Spanish cross goats (11 months-old and weighing about 45 kg) were randomly allocated to 1 of 2 treatments in a Latin square design. Goats were housed in an open-air building in individual 2.4 x 1.1 x 1.7 m metabolism stalls with expanded steel floors to allow feces and urine separation and collection. Goats were given *ad libitum* access to either spined prickly pear with singed spines or spineless prickly pear daily. Intake, fecal output and urine output were recorded daily. All goats used in this study were accustomed to the stalls from a previous experiment.

Treatments consisted of feeding either singed or spineless prickly pear to individual goats (8 goats/treatment). Two periods were conducted with treatments reversed (i.e., 4 goats fed spineless prickly pear in Period 1 were fed singed prickly pear in Period 2). Period 2 was initiated 10 days after the completion of Period 1. Goats were maintained on alfalfa pellets (15 g kg⁻¹) between periods. Goats were fed the appropriate prickly pear during a 3-day adjustment period followed by a 5-day collection period. Relatively short adjustment and collections periods were used because of the short retention time of goats (Huston et al. 1986). A 2 x 2 Latin square design was used for Experiment 1 because of a limited number of metabolism stalls.

Feces and urine were collected daily during each 5-day collection period for each trial. Ten ml of 25% H₂SO₄ was added to 1-gallon plastic collection containers to prevent volatilization of ammo-

nia from urine (A.O.A.C. 1984). Urine and feces were frozen at -26°C until analysis. Composite diet and fecal samples were dried at 60°C for 48 hours, ground to pass through a 1 mm screen, dried at 105°C, and ashed at 600°C to determine percent dry matter and organic matter, respectively. Nitrogen contents of prickly pear, feces, and urine were analyzed using standard micro-Kjeldahl procedures (Holechek et al. 1982). The fecal and urinary nitrogen content was subtracted from the nitrogen intake from the prickly pear to estimate nitrogen balance (Boutouba et al. 1990). Dry matter and organic matter digestibility of prickly pear were estimated using *in vivo* techniques and compared between prickly pear species (Holechek et al. 1982, Nunez-Hernandez et al. 1992).

Preliminary evidence suggested that nutrient content of prickly pear varied among seasons (Huston et al. 1981, Retamal et al. 1987). The metabolism trial was repeated in winter (December) to estimate differences in prickly pear quality between summer and winter. The same goats and protocol used in the summer trial were used in the winter trial.

Previous Dietary Experiences

In Experiment 2, 9 intact male and 9 female Boer-Spanish cross goats, 4-5 months of age, and weighing 20 kg, were used to determine how experience with spineless prickly pear at weaning affected intake of singed prickly pear. Goats were placed in individual pens and allocated randomly to 1 of 2 treatments (9 goats/treatment). Four males were assigned to Treatment 1 with 5 females, and 5 males and 4 females were assigned to the other Treatment 2.

Treatments consisted of goats either naive or familiar with spineless prickly pear. All goats were raised in pens to control exposure to prickly pear before the test period, and all goats were naive to prickly pear before initiation of the study. The naive goats received only alfalfa pellets (15 g kg⁻¹ BW) to meet maintenance requirements (NRC 1981). In addition to feeding alfalfa pellets at maintenance levels, experienced goats were also fed spineless prickly pear in excess for 1 hour daily until consumption leveled off (8 days). After the initial 8 days, all naive and experienced goats were fed singed prickly pear for 1 hour daily over 4 days, and intake was recorded daily. Prickly pear was harvested fresh daily, spines were singed, and pads were chopped into 5 cm wide strips to facilitate feeding. All goats continued to receive fresh water and 15 g kg⁻¹ BW of alfalfa daily throughout the study.

Feed and Prickly Pear Intake

Experiment 3 began 14 days after the completion of Experiment 2. Goats from Experiment 2 were re-randomized to 1 of 3 treatments and placed in individual pens. An equal number of goats from Treatments 1 and 2 used in Experiment 2 were assigned to treatments for Experiment 3 to minimize the effect of previous experience with prickly pear. Goats were fed a maintenance diet of alfalfa pellets (15 g kg⁻¹ BW) until the experiment began (14 days).

For this experiment, goats were allocated to 1 of 3 treatment groups. Treatment 1 was fed 10 g kg⁻¹ BW of alfalfa pellets daily to represent a diet below maintenance, Treatment 2 was fed 20 g kg⁻¹ BW of alfalfa pellets daily to represent a near maintenance diet, while Treatment 3 was fed 30 g kg⁻¹ BW of alfalfa pellets daily to exceed maintenance requirements. Freshly chopped singed prickly pear was fed to all 3 groups for 2 hours each morning before they were fed their pre-assigned alfalfa diet. Singed prickly pear intake was recorded daily over 5 days. The effects of basal diet feeding level on prickly pear consumption were compared among the 3 treatments.

Statistical Analysis

For each experiment, data were analyzed using analysis of variance (Hicks 1993). A 2 x 2 Latin square design (2 treatments and 2 periods) was used in Experiment 1. A nested design was used in all experiments with goats nested within treatments as replicates. Treatment (naive vs. familiar) served as the primary effect and sex as the secondary effect in Experiment 2. For Experiment 3, level of alfalfa intake was the primary effect and familiarity with prickly pear (from Exp. 2) was the secondary effect. Intake data for all 3 experiments were converted to g kg⁻¹ body weight (BW) on a dry matter basis to eliminate the effects of moisture content

and body size on intake data. Data from Experiments 2 and 3 were analyzed using repeated measures analysis of variance because intake was measured for individual goats daily. Means were separated using least significant difference (LSD) when $P < 0.05$ (Gomez and Gomez 1984). Data were analyzed using the statistical computer package JMP (SAS 1994).

Results

Metabolism Trial

Goats readily consumed both prickly pear species. Goats consumed more ($P < 0.05$) spineless prickly pear on an as fed basis (g kg⁻¹ BW), whereas dry matter intake was similar for both species of prickly pear (Table 1). Moisture content of prickly pear was high for both species and for both seasons (summer 95% and 90%; winter 90% and 75% for spineless and spined prickly pear, respectively).

Digestibility varied between prickly pear species, but was similar between seasons. Digestibility of spineless prickly pear was greater than singed prickly pear for both dry matter ($P < 0.05$) and organic matter ($P < 0.07$) when data were combined across seasons (Table 1). Percent crude protein was also greater ($P < 0.05$) for spineless prickly pear.

Nitrogen balance of goats did not differ when fed spined or spineless prickly pear (Table 1). Values were negative for both species in the summer (-0.21 g vs -0.42 g for spined and spineless, respectively). During the winter, nitrogen balance for goats consuming spined prickly pear were 0.36 g while goats consuming spineless prickly had a positive nitrogen balance of 4.0 g.

Previous Dietary Experiences

During the 8-day familiarization period, goats ate on average 1.3 g kg⁻¹ BW DM of

spineless prickly pear. Following initial exposure to spineless prickly pear, goats familiar with spineless prickly pear ate more ($P < 0.05$) singed prickly pear than naive goats (3.1 vs. 1.0 g kg⁻¹ BW for goats familiar vs. naive to prickly pear). Intake of prickly pear differed ($P < 0.05$) among days over the 4-days of feeding (Fig. 1). Nevertheless, familiar goats consistently ate more singed prickly pear than naive goats. Intake of prickly pear was similar ($P > 0.05$) between males and females.

Feed and Prickly Pear Intake

Varying intake of alfalfa did not affect intake of singed prickly pear ($P > 0.05$, 3.2 ± 0.6 , 3.3 ± 0.6 , 3.5 ± 1.3 , g kg⁻¹ BW for below, near, and above maintenance, respectively). Goats familiar with spineless prickly pear in the previous experiment continued to eat more ($P < 0.08$) singed prickly pear than naive goats (4.2 vs. 2.5 g kg⁻¹ BW, for familiar vs. naive goats, respectively), regardless of the amount of alfalfa fed.

Discussion

Nutritive Value of Prickly Pear

Both species were moderately digestible (58–85% DMD) and met nitrogen requirements for goats during the winter (Exp. 1). Goats readily consumed both species of prickly pear and consumed some prickly pear when another forage was fed to meet or exceed nutrient requirements (Exp. 3). We contend that prickly pear can be a viable alternative forage, especially when used as an emergency feed. Producers typically rely on prickly pear when other forage sources are depleted or dormant. Under these circumstances and given the negative nitrogen balance values during the summer trial (Exp. 1), protein supplementation may be required in addition to feeding prickly pear.

The prickly pear used in this study was only collected from 1 site and may vary nutritionally in other areas. Future studies should identify variations in nutritional value of prickly pear growing on different soil types and in different locations.

Consumption of spined prickly pear after singeing the spines suggests strongly that goats will consume prickly pear after prescribed burning. Prescribed burning or singeing spines with a propane torch would be required to reduce health hazards (Ueckert et al. 1990). In addition, livestock herbivory after burning should reduce prickly pear cover and density

Table 1. Mean nutritional parameters of spine (singed) and spineless prickly pear fed to goats for Experiment 1. Crude protein values were measured using the 2 outermost prickly pear cladodes.

Parameter	Singed	SEM	Spineless	SEM
Dry matter (%)	11.5		23.7	
Organic Matter (%)	74.0		71.0	
Intake, as fed basis (g kg ⁻¹ BW)	91.0 ^b	4.1	154.0 ^a	3.9
Dry matter intake (g kg ⁻¹ BW)	14.0	1.3	12.0	1.3
Fecal Output (g day ⁻¹)	462.5 ^a	20.3	304.8 ^b	19.5
Dry matter digestibility (%)	58.0 ^b	0.1	79.0 ^a	0.1
Organic matter digestibility (%)	70.0 ^b	1.0	83.0 ^a	1.0
Crude protein (%)	4.8 ^b	0.9	8.1 ^a	0.5
Nitrogen balance (g/d)	0.4	0.2	1.8	0.2

^{a,b}Means within rows with different superscripts differ (Intake $P < 0.05$; DMD, $P < 0.05$; OMD, $P < 0.07$; CP, $P < 0.05$).

Fig. 1. Intake ($\text{g kg}^{-1} \text{ BW}$) of singed prickly pear by goats familiar or naïve with spineless prickly pear over a 4 days (days 9 through 12) in Experiment 2. The first 8 days involved the familiarization period when experienced goats were fed spineless prickly pear. Average consumption of spineless prickly pear for the familiarization period was $1.3 \text{ g kg}^{-1} \text{ BW}$ on dry basis.

given that this plant has a low tolerance to herbivory (Griffiths 1905). However, goat herbivory may need to occur quickly after burning before pads begin to spoil from heat damage (Ueckert pers. comm.).

Spineless prickly pear was more digestible and had a higher crude protein content than spined prickly pear. Thus, spineless prickly pear could serve as a palatable and nutritious alternative feed source for livestock and wildlife. Establishing spineless prickly pear can be highly successful, but requires at least 4 years to accumulate sufficient biomass (Turpin and Gil, 1928). Palatability of spineless prickly pear will necessitate fencing to reduce herbivory until establishment. Providing spineless prickly pear as a forage may be more cost effective than burning spined prickly pear when forage is limited because of the high cost of labor and propane fuel for burning.

Spineless prickly pear also could be established in food plots to serve as emergency forage for wildlife. Most forages grown on food plots for deer in central and western Texas were developed in areas that receive higher and more consistent precipitation, and most are not adapted to xeric climates. Because spineless prickly pear evolved in dry conditions, it should remain productive even during drought.

Previous Dietary Experiences

Previous foraging experiences improve acceptance, foraging skills, and may result in physiological adaptations to metabolize some toxins (Distel and Provenza 1991, Provenza 1994, Bisson et al. 2001). Foraging experiences are particularly

important in the formation of dietary preferences when forages are nutritious and nonaversive (Villalba and Provenza 1997a, 1997b, 1997c, 1999). Prickly pear is moderately nutritious (Exp. 1) and lacks mechanical defenses after singeing. Feeding of spineless prickly pear increased consumption of singed prickly pear (Exp. 2), and this acceptance persisted (Exp. 3).

Weaning may be an important time for molding diet selection because of limited maternal influences on dietary habits (Hinch et al. 1987, Howery et al. 1998). Conditioning the acceptance of prickly pear could be accomplished during weaning when replacement animals are separated from their dams and housed in separate facilities. Once goat kids acquire a preference for spineless prickly pear, the acceptance of singed prickly pear is easily attainable as observed in Experiment 2. As an alternative to growing and hand-feeding spineless prickly pear, producers could wean goat kids in a pasture after singeing prickly pear spines.

Prickly Pear Intake

Level of alfalfa intake did not affect intake of prickly pear in this study. Goats consumed prickly pear at a constant rate regardless of the level of intake of the basal diet. Goats may have consumed prickly pear because of an innate desire to consume a variety of foods. In another study, when lambs were offered 3 rations varying in nutrient quality (high, medium, and low), they consistently ate all 3 even though the high quality ration met all of their dietary requirements (Provenza et al.

1996). Food preferences change within meals often to less nutritious foods (Newman et al. 1994, Early and Provenza 1998) and ruminants prefer alternatives to forages they have consumed for several days (Newman et al. 1992, 1994, Ramos and Tennesen 1993) or even several hours (Parsons et al. 1994).

Prickly pear also may provide other essential nutrients that may be limited. Other studies have reported that livestock and wildlife often consume prickly pear even when forage quantity is not limited (Taylor et al. 1980, Fontenot et al. 1991). Phosphorous often is limited on central and western Texas rangelands. Ruminants occasionally consume atypical dietary items to rectify deficiencies (Provenza 1994).

Implications

Most southwestern livestock producers consider spined prickly a hindrance to forage production; spined prickly pear has increased in cover in the last 100 years because of overgrazing and the lack of fire. Controlling spined prickly pear in the southwestern U.S. is often not practical because of economic restraints, its use as emergency feed during droughts, and its importance for wildlife habitat.

Spineless prickly pear has the potential as an alternative forage for goats or other domestic livestock or deer. Nutritionally, it yields enough protein to meet protein requirements of goats under some levels or stages of production. In addition, for most current management systems, spined prickly pear is an unused forage source. However, combining prescribed burning with goat herbivory would allow prickly pear to be used as a forage resource without jeopardizing the animal health and reduce prickly pear cover and density.

Literature Cited

- A.O.A.C. 1984. Official Methods of Analysis (14th Ed.). Association of Official Analytical Chemists, Washington D.C.
- Bement, R.E. 1969. Plains pricklypear: relation to grazing intensity and blue grama yield on central Great Plains. *J. Range Manage.* 21:83–86.
- Bisson, M.G., C.B. Scott, C.A. Taylor, Jr., and R.A. Moen. 2001. Activated charcoal and experience affect intake of juniper by goats. *J. Range Manage.* 54:274–278.
- Boutouba, A., J.L. Holecchek, M.L. Galyean, G. Nunez-Hernandez, J.D. Wallace, and M. Cardenas. 1990. Influence of two native shrubs on goat nitrogen status. *J. Range Manage.* 43:530–534.

- Brutsch, M.O. and H.G. Zimmerman. 1993.** The prickly pear (*Opuntia ficus-indica* [Cactaceae]) in South Africa: utilization of the naturalized weed and of cultivated plants. *Econ. Bot.* 47:154-162.
- Distel, R.A. and F.D. Provenza. 1991.** Experience early in life affects voluntary intake of blackbrush by goats. *J. Chem. Ecol.* 17:431-450.
- Early, D.M. and F.D. Provenza. 1998.** Food flavor and nutritional characteristics alter dynamics of food preference in lambs. *J. Anim. Sci.* 76:728-734.
- Fontenot, N.J., G.R. Engdahl, G.L. Holland, and W.H. Schacht. 1991.** Seasonal diet selection of white-tailed deer (*Odocoileus virginianus*) in relation to forage availability in west central Texas. *MIR Prog. Rep.* No. R-5:8-9.
- Garcia de Cortazar, V. and P.S. Nobel. 1992.** Biomass and fruit production for the prickly pear cactus, *Opuntia ficus-indica*. *J. Amer. Soc. Hort. Sci.* 117:558-562.
- Gomez, K.A. and A.A. Gomez. 1984.** Statistical Procedures for Agricultural Research. pp. 187-207. John Wiley and Sons, New York.
- Griffiths, D. 1905.** The prickly pear and other cacti as food for stock. USDA Bureau of Plant Industries Bull. 74:46.
- Hanselka, C.W. and J.C. Paschal. 1991.** Prickly pear cactus: an important rangeland resource. In: Progress Report, pp. 141-143. Texas Agr. Exp. Sta., U.S.A.
- Hanselka, C.W., R.Q. Landers, and J.C. Paschal. 1993.** Prickly pear: friend or foe. Texas Agri. Ext. Ser. at Corpus Christi. Technical Rept. B-5046.
- Hicks, C.R. 1993.** Fundamental Concepts in the Design of Experiments. p. 201. Saunders College Publishing, New York.
- Hinch, G.N., E. Lecrivain, J.J. Lynch, and R.L. Elwin. 1987.** Changes in maternal-young associations with increasing age of lambs. *Appl. Anim. Behav. Sci.* 17:305-318.
- Howery, L.D., F.D. Provenza, R.E. Banner, and C.B. Scott. 1998.** Social and environmental factors influence cattle distribution on rangeland. *Appl. Anim. Behav. Sci.* 55:231-244.
- Holecchek, J.L., M. Vavra, and R.D. Pieper. 1982.** Methods of determining the nutritive quality of range ruminant diets: a review. *J. Anim. Sci.* 53:291-302.
- Huston, J.E., B.S. Rector, W.C. Ellis, M.L. Allen. 1986.** Dynamics of digestion in cattle, sheep, goats and deer. *J. Anim. Sci.* 62:208-215.
- Huston, J.E., B.S. Rector, L.B. Merrill, and B.S. Engdahl. 1981.** Nutritional Value of Range Plants in the Edwards Plateau Region of Texas. Texas Agr. Exp. Sta. Bull. B-1357.
- Lehman, V.W. 1969.** Forgotten legions, sheep in the Rio Grande Plains of Texas. Texas Western Press. U.S.A.: Univ. of Texas at El Paso. 226 pp.
- Maltsberger, W.A. 1989.** Prickly pear cactus - an unsung blessing of the Rio Grande Plains. pp. 19-30. In: C.W. Hanselka and J.C. Paschal (eds.) Developing Prickly Pear as a Forage, Fruit, and Vegetable Resource. Proc. of Conference July 14, 1989. Kingsville, Tex. Tex. Agr. Ext. Serv. College Station.
- Mayeux, H.S., Jr. and H. B. Johnson. 1989.** Absorption and translocation of picloram by Lindheimer pricklypear (*Opuntia lindheimeri*). *Weed Sci.* 37:161-166.
- Newman, J.A., A.J. Parsons, and A. Harvey. 1992.** Not all sheep prefer clover: diet selection revisited. *J. Agr. Sci. Cambridge.* 119:275-283.
- Newman, J.A., P.D. Penning, A.J. Parsons, A. Harvey, and R.J. Orr. 1994.** Fasting affects intake behaviour and diet preference of grazing sheep. *Anim. Behav.* 47:185-193.
- NRC. 1981.** Nutrient Requirements of Goats: Angora, Dairy, and Meat Goats in Temperate and Tropical Countries. National Academy Press, Wash. D.C.
- Nunez-Hernandez, G., J.L. Holecchek, D. Arthun, A. Tembo, J.D. Wallace, M.L. Galyean, M. Cardenas, R. Valdez. 1992.** Evaluation of fecal indicators for assessing energy and nitrogen status of cattle and goats. *J. Range Manage.* 45:143-147.
- Parsons, A.J., J.A. Newman, P.D. Penning, A. Harvey, and R.J. Orr. 1994.** Diet preference of sheep: effect of recent diet, physiological state and species abundance. *J. Anim. Ecol.* 63:465-478.
- Provenza, F.D. 1994.** Ontogeny and social transmission of food selection in domesticated ruminants. In press In: P. Valsecchi and B.G. Galef (eds.) Ontogeny and social transmission of food preferences in mammals: Basic and Applied Research. Harwood Acad. Press, London.
- Provenza, F.D. 1995.** Postingestive feedback as an elementary determinant of food preferences and intake in ruminants. *J. Range Manage.* 48:2-17.
- Provenza, F.D., C.B. Scott, T.S. Phy, and J.J. Lynch. 1996.** Preference of sheep for foods varying in flavors and nutrients. *J. Anim. Sci.* 74:2355-2361.
- Ramos, A. and T. Tennesen. 1993.** A note on the effect of dietary variety on food intake of cattle. *Anim. Prod.* 57:323-325.
- Retamal, N., J.M. Duran, and J. Fernandez. 1987.** Seasonal variations of chemical composition of prickly pear (*Opuntia ficus-indica* (L.) Miller). *J. Sci. Food Agr.* 38:303-311.
- SAS. 1994.** JMP User's Guide, Version 3.1. SAS Institute Inc., N.C.
- Taylor, C.A., M.M. Kothmann, L.B. Merrill, and D. Elledge. 1980.** Diet selection by cattle under high-intensity low-frequency, short duration, and Merrill grazing systems. *J. Range Manage.* 6:428-434.
- Teles, F.F.F., J.W. Stull, W.H. Brown, and F.M. Whitney. 1984.** Amino and organic acids of the prickly pear cactus (*Opuntia ficus-indica* L.). *J. Sci. Food Agr.* 35:421-425.
- Turpin, H.W., and G.A. Gill. 1928.** Insurance against drought. So. Africa Dept. Agr. Bull. 36:32.
- Ueckert, D.N. 1997.** Pricklypear ecology. Proc. of Brush Sculptors Symposium. pp. 35-38. Tex Agri. Exp. Sta. and Tex Agr. Ext. Ser. San Angelo.
- Ueckert, D.N., J.L. Petersen, R.L. Potter, J.D. Whipple and M.W. Wagner. 1988.** Managing pricklypear with herbicides and fire. Texas Agr. Exp. Sta. Prog. Rep. Pr-4570.
- Ueckert, D.N., C.W. Livingston, Jr., J.E. Huston, C.S. Menzies, R.K. Dusek, J.L. Petersen, and B.K. Lawrence. 1990.** Range and sheep management for reducing pear-mouth and other pricklypear-related health problems in sheep flocks. Sheep and Goat, Wool and Mohair, Res. Report. Tex Agr. Exp. Sta., San Angelo, Tex.
- Villalba, J.J. and F.D. Provenza. 1997a.** Preference for wheat straw by lambs conditioned with intraruminal infusions of starch. *Br. J. Nutr.* 77:287-297.
- Villalba, J.J. and F.D. Provenza. 1997b.** Preference for flavoured wheat straw by lambs conditioned with intraruminal infusions of acetate and propionate. *J. Anim. Sci.* 75:2905-2914.
- Villalba, J.J. and F.D. Provenza. 1997c.** Preference for flavoured foods by lambs conditioned with intraruminal administration of nitrogen. *Br. J. Nutr.* 78:545-561.
- Villalba, J.J. and F.D. Provenza. 1999.** Effects of food structure and nutritional quality and animal nutritional state on intake behaviour and food preferences of sheep. *Appl. Anim. Behav. Sci.* 63:145-163.

Day and night grazing by cattle in the Sahel

AUGUSTINE. A. AYANTUNDE, SALVADOR FERNÁNDEZ-RIVERA, PIERRE. H. HIERNAUX, HERMAN VAN KEULEN, AND HENK M. J. UDO

Authors are former graduate Fellow, Animal Scientist and Range Ecologist, International Livestock Research Institute, ILRI/ICRISAT, B.P. 12404, Niamey, Niger, professor and Associate Professor, Animal Production Systems Group, Wageningen Agricultural University, P.O. Box 338, 6700 AH Wageningen, The Netherlands. The correspondence author is Henk Udo.

Abstract

The influence of night grazing on feeding behavior, nutrition and performance of cattle was studied. Twenty-four steers weighing 367 kg (SD = 76) grazed either from 0900 to 1900 (day grazers), 2100 to 0700 (night grazers) or 0900 to 1900 and 2400 to 0400 (day-and-night grazers) during 13 weeks. Four esophageally fistulated steers were used in a cross-over design to sample the diet selected during the day and at night. No differences ($P > 0.05$) were observed in the diet selected in the day or at night. As the season progressed the fiber components of the diet increased ($P < 0.01$) significantly while nitrogen and in sacco dry matter disappearance declined ($P < 0.01$). Actual grazing time (min day⁻¹, SE = 16) were 352, 376, and 476 for day, night, and day-and-night grazers, respectively. Day-and-night grazers had a higher intake of organic matter than either day or night grazers. Night grazers had the lowest forage intake and also the slowest rate of consumption. Steers that grazed in the night had the lowest water intake: 22.7 liter day⁻¹ (SE = 1.5) in week 4; 19.9 liter day⁻¹ (SE = 1.1) in week 8. Average weight changes (g day⁻¹, SE = 62) were -435, -548 and -239 for day, night, and day-and-night grazers, respectively. These results show that during the dry season, grazing exclusively in the night cannot substitute for day time grazing, but that it is rather complementary to the latter. Timing (day or night) of grazing did not affect diet selection but nocturnal grazing decreased the need for water.

Key Words: cattle, forage intake, night grazing, Sahel

Night grazing is a common herd management practice in the West African Sahel, especially at the end of the dry season (Dicko-Touré 1980, Powell et al. 1996). This practice has also been reported for herded animals in the sub-humid zone of West Africa (Bayer 1986), East Africa (Wigg and Owen 1973, Nicholson 1987) and for free ranging sheep and cattle in the USA and Australia (Vallentine 1990). In addition to the advantage of increased grazing time, King (1983) reported that night grazing helps to reduce heat stress on the animals and may increase forage intake. It has the benefit of manure deposition on rangelands rather than in the enclosed sites (Wigg and Owen 1973). However, this is in conflict with the practice of corralling the animals on cropland for depositing manure (Powell et al. 1996). Previous research (Fernández-Rivera et al. 1996) on night grazing

Resumen

El objetivo del presente trabajo fue estudiar la influencia del pastoreo nocturno sobre el comportamiento alimenticio, el consumo de forraje, la excreción fecal y los cambios de peso en bovinos. Veinticuatro novillos con un peso inicial de 367 kg (desviación estándar = 76) pastorearon de 0900 a 1900 (pastoreo diurno), 2100 a 0700 (pastoreo nocturno) o de 0900 a 1900 y de 2100 a 0700 (pastoreo día y noche) durante 13 semanas. Cuatro novillos con fístula esofágica fueron utilizados en un diseño reversible para muestrear la dieta seleccionada durante el día y en la noche. No se observaron diferencias ($P > 0.05$) en la dieta seleccionada en el día o en la noche. A medida que la estación seca avanzó los componentes de fibra de la dieta aumentaron ($P < 0.01$), mientras que el contenido de nitrógeno y la desaparición *in sacco* de la materia seca disminuyeron ($P < 0.01$). El tiempo de pastoreo propiamente dicho (i.e. tiempo de consumo) fue 352, 376 y 476 min día⁻¹ (SE = 16) para novillos con pastoreo nocturno, pastoreo diurno o con pastoreo el día y la noche, respectivamente. Los novillos con pastoreo el día y la noche tuvieron un mayor consumo de materia orgánica que aquellos que pastorearon el día o la noche. Los novillos con pastoreo nocturno tuvieron los niveles y tasas de consumo de forraje más bajos. El consumo de agua fue también más bajo en los novillos que pastorearon durante la noche 22.7 liter día⁻¹ (SE = 1.5) en la semana 4 y 19.9 liter día⁻¹ (SE = 1.1) en la semana 8. El cambio promedio de peso fue -435, -548 y -239 g día⁻¹ (SE = 62) para los novillos con pastoreo nocturno, pastoreo diurno o con pastoreo el día y la noche, respectivamente. Estos resultados indican que durante la estación seca el pastoreo exclusivamente durante la noche no puede ser sustituto, sino más bien complemento del pastoreo durante el día. El momento (día o noche) de pastoreo no afectó la selección de la dieta, pero el pastoreo nocturno disminuyó el requerimiento de agua.

by cattle showed that diet selection during the day and at night were not different. However, the steers that grazed during the day consumed more forage and water than those that grazed in the night. Further studies on the influence of night grazing on feeding behavior, nutrition and performance of cattle are needed to improve understanding of the nutrition of grazing cattle and cattle's role in nutrient transfer processes in the landscape.

The objective of this study was to determine the effects of night grazing on diet selection, forage and water intake, fecal excretion, feeding behavior and performance of cattle.

Material and Methods

Study site

The experiment was conducted over 13 weeks at the end of the dry season (February to May) of 1995 at International Crop Research Institute for the Semi-Arid Tropics (ICRISAT-SC) in Sadorè (13° 14' N 2° 16' E), Niger.

Treatments, pasture and animals

Twenty-four intact steers with a body weight (W) of 367 (SD = 76) kg were randomly allotted to 3 treatments: grazing either from 0900 to 1900 (day grazing), 2100 to 0700 (night grazing) or 0900 to 1900 and 2400 to 0400 (day-and-night grazing). After return from the pasture, the steers were kept in individual pens in a barn located 150 m from the paddock. The animals grazed the same pasture in the day and at night, i.e. a fallow of 5.5 ha, dominated by annual grasses mainly *Ctenium elegans* Kunth, *Diheteropogon hagerupii* Hitchc., *Pennisetum pedicellatum* Trin. and forbs mainly *Borreria stachydea* (DC.) Hutch. & Dalz. and *Hibiscus sabdarifa* Linn. At the beginning of the trial, the standing herbage and litter mass of the pasture were estimated at 828 and 1,070 kg DM ha⁻¹, respectively (Table 1). The herbage mass consisted of standing hay composed of 59% grasses and 41% forbs.

The study included 2 periods of collection of feces and extrusa which started in weeks 4 and 8 of the experiment. Each period included 9 days of fecal collection. The animals were accustomed to carrying fecal collection bags during the last week before the collection started. In each collection period, fecal bags were emptied and the feces weighed, before and after grazing. Ten percent of the fecal excretion was sampled and frozen for subsequent analysis. Water intake was also measured in weeks 4 and 8 of the trial. All the animals were watered in the morning (0800) before grazing started. Water intake was measured daily during the collection periods, for which all animals had access to

water for 30 min. In week 8 of the experiment the grazing activities of all steers were observed. Observation was made every 5 min (24 hour/day) for 3 consecutive days by 6 observers. The observation was instantaneous and the recording included one of the following activities: searching for food, prehending, masticating, ruminating, walking, drinking, sleeping, and idling. Grazing time was defined as the time spent prehending, masticating and searching for food. Idling included time spent neither for grazing, ruminating, sleeping, walking, nor drinking. Activities such as drinking, fighting, and socializing were referred to as 'other'.

In the 2 collection periods, four esophageally fistulated steers were randomly grouped into 2 pairs and were used in a cross-over design for sampling the diet selected during the day and at night. The 2 pairs either grazed in the day (0900 to 1900) or at night (2100 to 0700). During the data collection period in weeks 4 and 8, samples of the diet selected by the fistulated steers (extrusa) were collected in the morning (1000) and afternoon (1500) for the day grazing pair, and at night (2200) and at dawn (0300) for the night grazing pair, for 3 consecutive days. At the end of the 3 days collection period, the 2 groups were switched. After switching the grazing schedule, the animals were allowed 3 days for adaptation after which extrusa samples were collected for another 3 days following the same collection schedule. The extrusa samples were frozen immediately after collection.

Sample processing and laboratory analyses

The daily fecal sub-samples were bulked by time of collection (before or after grazing) and analyzed for dry (DM) and organic matter (OM). The extrusa samples were dried at 55° C for 48 hours and were ground to pass a 1-mm screen. They were analyzed for DM, OM, nitrogen (N), ashless neutral detergent fiber (NDF), ashless acid detergent fiber (ADF)

and ashless lignin (Van Soest et al. 1991). Hemicellulose and cellulose were calculated as the differences NDF-ADF and ADF-lignin, respectively. Samples ground to pass a 2-mm screen were incubated in duplicate for 48 hours in 3 ruminally fistulated steers to determine in sacco DM (DMD) and OM (OMD) disappearance, treating the residues from the nylon bags in a HCl-pepsin solution for 24 hours. Samples collected from vegetation mass measurement, representing the available feed, were subdivided by functional group (grasses or forbs) and dominant species within a group for standing herbage and litter separately. These were analyzed for DM, OM, N, phosphorus (P), DMD, and OMD.

Animal measurements

Animals were weighed every two weeks for 3 consecutive days. Average daily gain (ADG) was estimated by regression of individual body weight (W) data over time. Individual animal feed intake was determined from individual data on fecal output and group (day or night schedule) means of OMD.

Statistical analysis

Data analysis were performed with SAS (Statistical Analysis System Institute 1987) using the General Linear Model (GLM) procedure for the variance and regression analyses. An analysis of variance model including treatments as fixed effects, was used to analyze data on fecal output, forage and water intake, and animal behavior (time spent grazing, ruminating, idling, walking, sleeping, and drinking). The model for analysis of water intake included live weight and dry matter intake in addition to the treatments studied. Multiple comparisons of treatment means (Day vs Night grazing and Day vs Day-and-night grazing) within and between the collection periods (weeks 4 and 8) were performed by contrasts. Extrusa components of diet selected in the day and at night were analyzed using the Cochran procedure for the t-test. Unless it is specified differently, the level of significance was declared at P < 0.05.

Results

There were no differences in the quality of diet (extrusa) selected (Table 2) in the day or at night for both collection periods (weeks 4 and 8), the only exception was observed in week 4 when the NDF (SE =

Table 1. Nutritional quality of standing herbage and litter mass at the beginning of the experiment (March 1995).

Component	Standing herbage	Litter	SE
	----- g kg ⁻¹ DM -----		
Organic matter	949	938	6
Nitrogen	3.5	3.4	0.5
Phosphorus	1.2	1.1	0.2
Dry matter digestibility	426	412	18
Organic matter digestibility	400	391	19
Digestible organic matter	380	367	13

Table 2. Chemical composition of forage selected (extrusa) by esophageally fistulated steers grazing in the day or at night.

Component	Week 4		Week 8		SE
	Day	Night	Day	Night	
	g kg ⁻¹ DM				
Organic matter	894	883	881	889	4
Nitrogen	9.0 ^a	8.1 ^a	7.5 ^b	7.1 ^b	0.4
NDF	649 ^a	675 ^a	817 ^b	821 ^b	6
ADF	507 ^a	521 ^a	635 ^b	637 ^b	6
Lignin	134 ^a	129 ^a	178 ^b	187 ^b	5
Cellulose	373 ^a	393 ^a	460 ^b	450 ^b	6
Hemicellulose	143 ^a	154 ^a	182 ^b	184 ^b	5
DMD ²	533 ^a	524 ^a	486 ^b	478 ^b	8
OMD ²	469	455	459	444	8
DOM ²	419	402	404	395	6

¹Values with different superscripts denote significant difference ($P < 0.05$) between means within rows.

²DMD=Dry matter digestibility; OMD = Organic matter digestibility; and DOM = Digestible organic matter (i.e. OMD x OM).

6) of the diet selected by night grazers (675 g kg⁻¹ DM) was significantly higher than that of the day grazers (649 g kg⁻¹ DM). As the dry season progressed (week 4 vs week 8, Table 2) diet's NDF, ADF, cellulose, hemicellulose and lignin increased significantly ($P < 0.01$) while nitrogen concentration (SE = 0.4) declined from 8.5 in week 4 to 7.3 g kg⁻¹ DM in week 8 and DMD (g kg⁻¹ DM, SE = 8) also declined significantly (week 4 = 529; week 8 = 482).

Steers grazing in the day, night, and day-and-night spent 352, 376, and 476 min day⁻¹ respectively for grazing (Table 3). Night grazers spent less time ruminating and walking than day grazers. Day-and-night grazers spent 124 minutes grazing more than day-grazers. The hourly distribution of time expenditure (Fig. 1.) for different activities showed that day grazers had 2 distinct grazing periods with the first in the morning till mid-day and the second before the sunset. The second grazing period accounted for over 60% of total time spent grazing. Day-and-night grazers also had 2 grazing periods in the day similar to day grazers with one additional period in the night of about 2 hours. Night grazers had 2 grazing periods with the initial period accounting for about 75% of the total grazing time. Steers that grazed in the day-and-night had lower time for resting (time spent sleeping + idling) than steers that grazed in the day (421 vs 560, SE = 25, $P < 0.05$) but there was no difference in resting time by day grazers compared to night grazers (560 vs 614, SE = 25).

Day, and day-and-night grazing steers consistently consumed more forage (g DM kg^{-0.75} W) than steers that grazed at night (Table 4). In weeks 4 and 8, day-and-night grazers consumed daily 93.2 and 67.1 g DM kg^{-0.75} W respectively whereas night

grazers consumed 62.5 g DM kg^{-0.75} W in week 4 and 53.6 g DM kg^{-0.75} W in week 8. Day grazers consumed significantly more digestible organic matter (g DOM kg^{-0.75} W) than night grazers (Week 4: 30.2 vs 20.4, SE = 1.6; week 8: 22.7 vs 18.3, SE = 1.4), but the differences between day grazers and day-and-night grazers were not statistically significant. Forage intake declined significantly from week 4 to week 8 for day grazers, and day-and-night grazers. Intake rate (mg OM kg^{-0.75} W min⁻¹) in week 8 (SE = 7) were 142 for day grazers, 110 for night grazers and 113 for day-and-night grazers.

There was a significant difference in water intake between steers that grazed in

Fig. 1. Hourly distribution of time expenditure for different activities by (a) day, (b) night, and (c) day-and-night grazing steers in the dry season in the Sahel.

Table 3. Time expenditure on different activities in Week 8 (May 1995) of the experiment by day, night, and day-and-night grazing steers.

Activity	Day	Night	Day-and-night	SE
	----- (min day ⁻¹) -----			
Grazing ²	352 ^a	376 ^a	476 ^b	16
Ruminating	463 ^a	389 ^b	447 ^a	21
Sleeping	88 ^a	99 ^a	50 ^b	12
Walking	37 ^a	28 ^a	55 ^b	3
Idling ²	472 ^a	519 ^a	371 ^b	27
Other	30	29	43	10

¹Values with different superscripts denote significant difference ($P < 0.05$) between means within rows.

²Grazing includes prehension, mastication and search for food; Idling includes time spent neither for grazing, ruminating, sleeping, walking nor drinking; and Other includes activities such as drinking, fighting and socializing.

the night and those that grazed either in the day or in the day-and-night in both periods of measurement (Table 4). As the season progressed water intake of day grazers (week 4 = 35.5, week 8 = 27.6 liter day⁻¹) and day-and-night grazers (week 4 = 35.5, week 8 = 27.6 liter day⁻¹) declined significantly but that of night grazers (week 4 = 22.7, week 8 = 19.9 liter day⁻¹) remained fairly constant. Relative to forage intake water consumption (liter kg⁻¹ forage DM) was constant for all treatments regardless of the period of measurement. Regression analyses of water intake on metabolic weight ($W^{0.75}$) and dry matter intake (DMI, kg DM day⁻¹) showed that water intake (ml day⁻¹) was correlated with metabolic weight in all treatments and with DMI for day grazers (equation 1), and day-and-night grazers (equation 3) but not for night grazers (equation 2). The following regression equations were estimat-

ed from the pooled data of weeks 4 and 8:

$$\text{water intake} = 148 (\text{SE} = 26) W^{0.75} + 3243 (\text{SE} = 343) \text{ DMI} (r^2 = 0.99, P < 0.01) \quad (1)$$

$$\text{water intake} = 263 (\text{SE} = 6) W^{0.75} (r^2 = 0.99, P < 0.01) \quad (2)$$

$$\text{water intake} = 126 (\text{SE} = 34) W^{0.75} + 3412 (\text{SE} = 429) \text{ DMI} (r^2 = 0.99, P < 0.01) \quad (3)$$

In week 4, fecal excretion by day grazers, night grazers, and day-and-night grazers were 9.3, 6.9, and 10.3 g DM kg⁻¹ W day⁻¹ (SE = 0.7), respectively. In week 8 (SE = 0.6), day grazers excreted 7.6 g DM kg⁻¹ W day⁻¹, the fecal output by night grazers was 6.9 g DM kg⁻¹ W day⁻¹ and day-and-night grazers voided 8.3 g DM kg⁻¹ W day⁻¹. A significant decrease in fecal excretion was observed in day grazers, and day-and-night grazers as the season progressed, whereas that of night graz-

ers remained essentially the same.

Average weight changes (g day⁻¹, SE = 62) was -435 for day grazers, -548 for night grazers and -239 for day-and-night grazers. There was no significant difference in weight changes between day grazers and night grazers.

Discussion

The results on diet (extrusa) quality show that the time (day or night) of grazing had no significant influence on dietary selection, which supports the findings by Arnold (1966) that sight does not play a major role in the selection of plant parts by grazing animals. Similar results were observed by Fernández-Rivera et al. (1996). However, there may be differences between the quality of diet selected during the day and at night if the grazing sites and species composition are different, which is often the case when the animals are herded during night grazing. The declining quality of the diet selected as the season progressed, as observed in this study, has also been reported by Schlecht (1995) for steers and by Becker et al. (1996) for zebu cows grazing natural pastures in the region. Nitrogen concentration (7.1–9.0 g kg⁻¹ DM) in the diet selected was similar to values reported in the dry season by Schlecht (1995) in Mali (53–82 g CP kg⁻¹ OM) and Becker et al. (1996) in Niger (64–75 g CP kg⁻¹ OM) for extrusa samples taken in the same season. The digestibility of OM (444–469 g kg⁻¹ DM) was similar to that observed by the latter authors and by Fernández-Rivera et al. (1996) in the region.

Regardless of the time of grazing, the steers spent about 60% of the time allowed for grazing (i.e. prehension, mastication, and searching for food). The actual grazing times of 5.9, 6.3, and 7.9 hours for day, night, and day-and-night grazing, respectively, compare well with reported values in the dry season of 6.3 hours for a day grazing herd in Kenya by Coppock et al. (1988); 7 to 8 hours for day-and-night grazers in Uganda by Harker et al. (1954) and 7.4 to 10.4 hours reported by Dicko-Touré (1980) for day-and-night grazers in Mali. The ruminating time (6.5 to 7.7 hours) also agrees with those reported by Dicko-Touré (1980) and Harker et al. (1954). Night grazers spent less time ruminating than either day grazers or day-and-night grazers, because they had a lower forage intake. This might also be associated with the natural inclination to ruminate in the night. The lower walking time for

Table 4. Daily intake of dry matter (DM), digestible organic matter (DOM) and intake rate, and water intake by day, night, and day-and-night grazing steers in the dry season in the Sahel.

Variable	Day	Night	Day-and-night	SE
Week 4				
Forage intake				
g DM kg ^{-0.75} W	86.3 ^{a†}	62.5 ^b	93.2 ^{a†}	4.8
g DOM kg ^{-0.75} W	30.2 ^{a†}	20.4 ^b	31.9 ^{a†}	1.6
Water intake				
liter animal ⁻¹ day ⁻¹	36.0 ^{a†}	22.7 ^b	35.5 ^{a†}	1.5
liter kg ⁻¹ forage DM	5.1 ^a	4.4 ^b	4.9 ^a	0.2
ml kg ⁻¹ W day ⁻¹	100 ^{a†}	62 ^b	105 ^{a†}	5
Week 8				
Forage intake				
g DM kg ^{-0.75} W	62.9 ^a	53.6 ^b	67.1 ^a	4
g DOM kg ^{-0.75} W	22.7 ^a	18.3 ^b	24.3 ^a	1.4
Intake rate				
g DM min ⁻¹	14.4 ^a	11.2 ^b	11.0 ^b	0.7
mg OM kg ^{-0.75} W min ⁻¹	142 ^a	110 ^b	113 ^b	7
Water intake				
liter animal ⁻¹ day ⁻¹	27.1 ^a	19.9 ^b	27.6 ^a	1.1
liter kg ⁻¹ forage DM	5.5 ^a	4.8 ^b	5.3 ^a	0.3
ml kg ⁻¹ W day ⁻¹	80 ^a	59 ^b	82 ^a	3

¹Values with different superscripts denote significant difference ($P < 0.05$) between means within rows.

²Different symbols (†) following the same variable in Weeks 4 and 8 within a treatment group (column) denote significant difference ($P < 0.05$) between values in the 2 periods.

steers that grazed in the night compared to the other groups, even though they grazed in the same pasture, supports the findings of Arnold (1966) that sight impairment (poor visibility) causes orientation problems, which limits the area for selective grazing by the animals. The cost of grazing in the night in addition to day grazing is a reduction in resting time as observed for day-and-night grazers. The general pattern of 2 grazing periods during the day, separated by a mid-day rest observed in day grazers, and day-and-night grazers has also been reported by Coppock et al. (1988) for Turkana cattle in Kenya. Night grazers had a longer initial grazing period (4.5 vs 2.7 hours) than day grazers, probably because they were not constrained by heat and high radiation. Resting between the grazing periods by night grazers may likely be induced by rumen fill or fatigue. Similar findings were reported by Fernández-Rivera et al. (1996) in a preliminary study on nocturnal grazing by cattle in the region.

Forage intake, in both weeks 4 and 8, was lower for night grazers than day grazers, which supports previous findings by Fernández-Rivera et al. (1996). This was due to a slow intake rate. Forage intake by day grazers ($64.6 \text{ g OM kg}^{-0.75} \text{ W}$), and day-and-night grazers (69.0 g) in week 4 falls within the range of $63\text{--}83 \text{ g}$ reported by Schlecht (1995) for unsupplemented steers in Mali and the values reported by Becker et al. (1996) for unsupplemented cows in Niger. The intake values in week 8, however, are lower than those reported by these authors. Day-and-night grazers spent longer time grazing than day grazers but intake was not significantly different. This means that in the day-and-night grazing group, intake (and intake rate) during the day decreased due to night grazing. The fecal excretion values found in this study ($6.3\text{--}11.0 \text{ g DM kg}^{-1} \text{ W day}^{-1}$) is similar to those reported by Schlecht (1995). Collectable manure, i.e. the amount of feces excreted while not in the pastures (manure excreted while in the corralling site), was higher than the feces deposited in the rangelands by day grazers (week 4: $1,786$ vs $1,521$, week 8: $1,322$ vs $1,236 \text{ g DM animal}^{-1} \text{ day}^{-1}$). The reverse was the case for the animals that grazed in the night, i.e. night grazers (week 4: $1,058$ vs $1,385$, week 8: 953 vs $1,304 \text{ g DM animal}^{-1} \text{ day}^{-1}$) and day-and-night grazers (week 4: $1,126$ vs $2,326$, week 8: 932 vs $1,836 \text{ g DM animal}^{-1} \text{ day}^{-1}$). This shows that more manure could be collected from animals that did not graze in the night compared to those that did. The amounts

of collectable manure estimated in this study fall within the range of 600 to $1,500 \text{ g DM TLU}^{-1}$ (TLU is Tropical Livestock Unit, animal of 250 kg body weight) reported by Khombe et al. (1992) and Fernández-Rivera et al. (1995).

Consumption of water relative to forage intake ($\text{liter kg}^{-1} \text{ forage DM}$) found in this study agrees with the value of $4.5 \text{ liter kg}^{-1} \text{ forage DM}$ reported by King (1983). The day, and day-and- night grazers, that consumed more forage drank more water than the night grazers. High water consumption by the former could also be associated with high temperatures during the day, as reported by Nicholson (1987) and King (1983), the latter suggesting an extra water cost of $0.35 \text{ liter km}^{-1}$ for walking in high solar heat. The range in water consumption ($56\text{--}110 \text{ ml kg}^{-1} \text{ W day}^{-1}$) observed in this study is below the theoretical maximum ($160 \text{ ml kg}^{-1} \text{ BW day}^{-1}$) suggested by King (1983) for cattle grazing tropical pastures. The lower water intake observed in the second period of measurement (week 8) could be attributed to an unexpected rainfall during the period and the concomitant fall in daily temperature for some days and the low ingestion of forage. Low water consumption by the night grazers observed in this study and the previous one (Fernández-Rivera et al. 1996) suggests that during a period of water scarcity, the water needs of grazing cattle could be reduced if nocturnal grazing is practiced without day grazing and the animals are restricted and protected from sunlight during the day.

Steers that grazed in the day-and-night had lower weight loss (239 g day^{-1}) than either day grazers (435 g day^{-1}) or night grazers (548 g day^{-1}). Similar results were reported by Wigg and Owen (1973) and Khombe et al. (1992) for steers that grazed day and night. These findings and that of the present study show that grazing exclusively in the night cannot substitute for day grazing. It rather complements day grazing and leads to better animal performance especially in the dry season. From the data on weight change and intake, day-and-night grazers lost significantly less weight than day grazers but had the same diet quality and intake, whereas day grazers had higher intake than night grazers but had the same weight loss. This discrepancy could be due to differential gut fill which might have influenced live weight measurement (t' Mannetje et al. 1976). The differential gut fill could be associated with the time of the day (0730 to 0800) at which all the animals were weighed. This implies that the night grazers were

weighed almost immediately after grazing, about 4 hours after night grazing for day-and-night grazers and 12 hours after grazing for day grazers. Perhaps, the weight loss for night grazers and day-and-night grazers could have been higher than the reported values if they had been weighed at the same time difference after grazing as the day grazers. However, this is not feasible due to the experimental design.

The results also show that the traditional practice of night corralling (i.e. no night grazing) of cattle in West African Sahel put a nutritional stress on the animals (by decreasing forage intake), thereby increasing weight losses especially in the dry season. It also increases the needs for supplementation. To resolve the conflict between night grazing and night corralling, it is necessary to determine the optimum use of the animal's time for grazing and manuring. Therefore, further research on combinations of timing (day and/or night) and duration of grazing is needed to identify practical and feasible recommendations on how to resolve the conflict.

Literature Cited

- Arnold, G.W. 1966. The special senses in grazing animals. I. Sight and dietary habits in sheep. *Aust. J. Agr. Res.* 17:521–529.
- Bayer, W. 1986. Agropastoral herding practices and grazing behaviour of cattle in the subhumid zone of Nigeria. *ILCA Bull.* 24:8–13.
- Becker, K., C. Gall, A. Susenbeth, and T. Rath. 1996. Nutrition and productivity of milking cattle on a semi-arid rangeland in West Africa, p. 153–184. *In: Adapted farming in West Africa. Rep. on results, Interim Rep. 1994 - 1996; Special programme 308, Univ. Hohenheim, Hohenheim, Germany.*
- Coppock, D.L., J.E. Ellis, and D.M. Swift. 1988. Seasonal patterns of activity, travel and water intake for livestock in south Turkana, Kenya. *J. Arid Environ.* 14:319–331.
- Dicko-Touré, M.S. 1980. The contribution of browse to cattle fodder in the sedentary system of the Office du Niger, p. 313–319. *In: H. N. Le HouËrou (ed.), Browse in Africa: the current state of knowledge. International Livestock Center for Africa, Addis Ababa, Ethiopia.*
- Fernández-Rivera, S., A. Ayantunde, P.H.Y. Hiernaux, and M. Turner. 1996. Nocturnal grazing effects on the nutrition of cattle. *J. Anim. Sci.* 74 (Suppl. 1) 200 (abstr.).
- Fernández-Rivera, S., T. O. Williams, P. Hiernaux, and J. M. Powell. 1995. Fecal excretion by ruminants and manure availability for crop production in semi-arid West Africa, p. 149–169. *In: J. M. Powell, S. Fernández-Rivera, T. O. Williams, and C. Renard (eds.), Livestock and sustainable nutrient cycling in mixed farming systems of*

- sub-saharan Africa. Volume II: Technical papers. International Livestock Center for Africa, Addis Ababa, Ethiopia.
- Harker, K.W., J.I. Taylor, and D.H.L. Rollinson. 1954.** Studies on habits of zebu cattle. I. Preliminary observations on grazing habits. *J. Agr. Sci. (Camb.)*. 44:193–198.
- Khombe, C.T., I.A. Dube, and P. Nyathi. 1992.** The effects of kraaling and stover supplementation during the dry season on body weight and manure production of Mashona steers in Zimbabwe. *African Livestock Res.* 1:18–23.
- King, J.M. 1983.** Livestock water needs in pastoral Africa in relation to climate and forage. ILCA (International Livestock Center for Africa) Res. Rep. 7, Addis Ababa, Ethiopia.
- t'Mannetje, L., R.J. Jones, and T.H. Stobbs. 1976.** Pasture evaluation by grazing experiments, p. 194–234. *In*: Shaw N.H and W.W. Bryan (eds.), *Tropical pasture research: principles and methods*. Commonwealth bureau of pastures and field crops, Hurley, Berkshire.
- Nicholson, M.J. 1987.** Effects of night enclosure and extensive walking on the productivity of zebu cattle. *J. Agr. Sci. (Camb.)*. 109:445–452.
- Powell, J. M., S. Fernández-Rivera, P. Hiernaux, and M.D. Turner. 1996.** Nutrient cycling in integrated rangeland/cropland systems of the Sahel. *Agr. Sys.* 52:143–170.
- Schlecht, E. 1995.** The influence of different levels of supplementation on feed intake and nutrient retention of grazing zebu cattle in Sahelian agro-pastoral systems. Ph.D Thesis, Univ. Hohenheim, Hohenheim, Germany.
- Statistical Analysis System Institute. 1987.** SAS/STAT guide for personal computers. SAS Institute Inc., Cary, N.C.
- Vallentine, J.F. 1990.** Grazing management. Academic Press, San Diego, Calif.
- Van Soest, P.J., J.B. Robertson, and B.A. Lewis. 1991.** Methods for dietary fiber, and nonstarch polysaccharides in relation to animal nutrition. *J. Dairy Sci.* 74:3583–3597.
- Wigg, P.M. and M.A. Owen. 1973.** Studies on water consumption, night grazing and growth of Boran and crossbreed steers at Kongwa, Tanzania. *East African Agr. and Fores. J.* 38:361–366.

Bud viability in perennial grasses: Water stress and defoliation effects

ANDREA C. FLEMMER, CARLOS A. BUSO,* AND OSVALDO A. FERNÁNDEZ

Authors are postdoctoral fellow of the Consejo Nacional de Investigaciones Científicas y Técnicas de la República Argentina (CONICET), CERZOS, Altos del Palihue, 8000 Bahía Blanca, Argentina; Full Professor, Departamento de Agronomía-CERZOS, Universidad Nacional del Sur (UNSur) and research scientist CONICET, Altos del Palihue, Bahía Blanca, and Consulting Professor, Departamento de Agronomía-CERZOS, UNSur and research scientist CONICET, Altos del Palihue, Bahía Blanca. Corresponding author: Departamento de Agronomía UNSur, Altos del Palihue, 8000-Bahía Blanca, Argentina; email=cebus-so@criba.edu.ar; fax 54-291-4595127; Phone 54-0291-4595102.

Abstract

Effects of the timing and frequency of defoliation under different levels of soil water availability were evaluated on bud metabolic activity and subsequent outgrowth in the desirable (i.e., palatable) *Stipa clarazii* Ball. and *S. tenuis* Phil. in competition with the undesirable (i.e., unpalatable) *S. gynerioides* Phil. Field studies on these native, perennial tussock grasses were conducted from 1995 to 1997 in temperate, semiarid Argentina. Our working hypotheses were 1) axillary bud activation and subsequent tillering are lower under water stress than under higher soil moisture conditions in *S. clarazii*, *S. tenuis*, and *S. gynerioides*, 2) when compared to undefoliated controls, activation, and subsequent outgrowth of axillary buds reach similar or greater values in *S. clarazii* and *S. tenuis* after early (vegetative stage of development), but not late (during internode elongation) defoliations or increased defoliation frequency (vegetative+ during internode elongation) during each growing cycle. Additionally, it was expected that the greatest reduction of axillary bud metabolic activity and outgrowth would occur on plants defoliated twice, and 3) axillary bud activation and succeeding tillering are greater in the undefoliated *S. gynerioides* when the desirable species are defoliated than when they remain undefoliated. With a few exceptions, our results led us to reject all 3 hypotheses. Responses of axillary buds were in general specific to the species and treatments, to sampling time, and to the cumulative effects of previous treatments. This makes predictions of plant responses of these species under natural field conditions difficult, where they are often defoliated under water stress.

Key Words: *Stipa clarazii*, *Stipa tenuis*, *Stipa gynerioides*, bud metabolic activity, bud outgrowth, water stress, defoliation, perennial grasses, semiarid Argentina

Successive tiller production by the development of axillary buds compensates for annual tiller mortality, allowing persistence of perennial grasses (Jewis 1972). Production of new tillers, and of leaf blades, stems, and sheaths from remaining apical and intercalary meristems after defoliation contributes to reestablishment of removed plant tissues (Briske 1991). However, regrowth will depend upon activation and subsequent outgrowth of axillary buds when most, if not all, apical and intercalary meristems are

Resumen

Se evaluó el efecto de la época y la frecuencia de defoliación bajo distintos contenidos hídricos del suelo sobre la actividad metabólica de las yemas axilares y rebrote subsiguiente en las especies desables (palatables) *S. clarazii* Ball. y *S. tenuis* Phil. en competencia con la especie indeseable (no palatable) *S. gynerioides* Phil. Los estudios se efectuaron en el campo en estas especies de gramíneas perennes nativas desde 1995 a 1997 en los pastizales templados, semiáridos de Argentina. Nuestras hipótesis de trabajo fueron 1) la activación y rebrote subsiguiente de las yemas axilares son menores bajo condiciones de estrés hídrico que bajo mayores contenidos hídricos del suelo en *S. clarazii*, *S. tenuis* y *S. gynerioides*, 2) en comparación a los controles no defoliados, la activación y rebrote subsiguiente de las yemas axilares alcanzan valores similares o mayores en *S. clarazii* y *S. tenuis* después de defoliaciones tempranas (estadio fenológico vegetativo) pero no luego de defoliaciones tardías (durante la elongación de los entrenudos) o ante una mayor frecuencia de defoliación (vegetativo+elongación de entrenudos) en cada ciclo de crecimiento. Además, se esperó que la mayor reducción en la actividad metabólica de las yemas axilares y rebrote subsiguiente se produjera en las plantas defoliadas con mayor frecuencia, y 3) la activación y subsiguiente rebrote de las yemas axilares son mayores en las plantas no defoliadas de *S. gynerioides* cuando las especies deseables son defoliadas que cuando permanecen sin defoliar. Con unas pocas excepciones, las 3 hipótesis fueron rechazadas con los resultados obtenidos. Las respuestas de las yemas axilares fueron en general específicas a las especies y tratamientos, a la época de muestreo, y a los efectos acumulativos de tratamientos previos. Esto enfatiza la dificultad de predecir la respuesta de estas especies bajo condiciones naturales, en las que normalmente son defoliadas bajo condiciones de estrés hídrico.

removed by defoliation (Busso et al. 1989). Any factor, such as water stress, which decreases availability, metabolic activity or capacity to grow out of axillary buds would limit reestablishment of photosynthetic canopy of grazed perennial grasses, compromising their persistence in the plant community (Briske and Richards 1995).

Tiller production can be lower on defoliated than on undefoliated plants in perennial grasses exposed to water stress, rainfed or irrigated conditions (Busso et al. 1989, Deregibus and Trlica 1990, Bullock et al. 1994, Hendrickson and Briske 1997). Water stress can also reduce tiller production in defoliated and undefoliated plants; this response has been observed under natural droughts (Bullock et al.

1994, Briske and Hendrickson 1998) or controlled environmental conditions (Busso et al. 1989). Mueller and Richards (1986) and Busso et al. (1989) suggested that the degree of bud metabolic activity would be comparatively more important than bud number or viability in explaining reduced tiller production after defoliation with or without water stress.

Timing of defoliation can also influence tiller production. For example, tiller production was stimulated by defoliation during internode elongation, but not during earlier growth stages in *Agropyron desertorum* (Fisch. ex Link) Schult. (Olson and Richards 1988). This response is partially due to apical meristem removal which stimulates axillary bud activation after eliminating the inhibition source (Murphy and Briske 1992). However, lack of apical meristem removal has also stimulated tiller production on defoliated plants (Deregibus and Trlica 1990). In addition to direct inhibitory effects of the apical meristem on bud outgrowth, both physiological mechanisms and their interaction with environmental variables and resource availability should be considered when studying factors involved in regulating tillering in perennial grasses (Murphy and Briske 1992). For example, bud activation and subsequent outgrowth can be stimulated or suppressed by modifying light quality and quantity at the plant stem bases (Casal et al. 1986, Deregibus and Trlica 1990, Devkota et al. 1997, Gautier et al. 1999).

Knowledge of axillary bud dynamics is essential when considering production and persistence of perennial grasses in the plant community. A few studies have evaluated the effects of various biotic and abiotic factors on this important component of plant growth and development. For example, they include evaluation of defoliation at different phenological stages (*Stipa tenuis* Phil. and *Piptochaetium napostaense* (Speg.) Hack: Becker et al. 1997), water stress with or without defoliation (*Agropyron* species: Busso et al. 1989), and fire (*S. tenuis*: Busso et al. 1993; *S. tenuis*, *S. gynerioides* Phil. and *P. napostaense*: Peláez et al. 1997). The objective of this study was to evaluate the effects of defoliation at different phenological stages and under different levels of soil water availability on the degree of bud metabolic activity and bud outgrowth in 3 perennial grasses: *Stipa clarazii* Ball., *S. tenuis* and *S. gynerioides*. *Stipa clarazii* and *S. tenuis* are 2 desirable, palatable species which compete with the undesirable, unpalatable *S. gynerioides* in the semiarid, temperate rangelands of Central Argentina. We hypothesized that activation of axillary buds and succeeding tiller-

ing 1) would be lower under water stress than under more favorable soil moisture conditions in *S. clarazii*, *S. tenuis*, and *S. gynerioides*, 2) when compared with undefoliated controls, would reach similar or greater values in *S. clarazii* and *S. tenuis* after early (vegetative stage of development), but not late (during internode elongation) defoliations or increased defoliation frequency (vegetative+ during internode elongation) during each growing cycle. Additionally, we expected that the greatest reduction of the studied plant variables would occur on plants defoliated twice, and 3) would be greater in the undefoliated *S. gynerioides* when the desirable species are defoliated than when they are not. However, values for these parameters in *S. gynerioides* will be greater after late or more frequent than early defoliations of *Stipa clarazii* and *S. tenuis*. Results of this study are important to gain understanding of the

responses of these species to the most common disturbances at the study region: grazing under water stress conditions.

Materials and Methods

Study Site

This study was conducted at the research field site of the Agronomy Department-CERZOS in Bahía Blanca (38° 48'S, 62° 13'W) during 1995, 1996, and early 1997. Soil is a typical Haplustol (Luis Sánchez, Dpto. Agronomía UNSur, pers. comm.) with a petrocalcic horizon at 1.8 m depth. A meteorological station at the experimental site measured rainfall, air temperature, relative humidity, wind speed, solar radiation, and potential evapotranspiration (Fig. 1).

Fig. 1. A) Monthly rainfall (mm) and number of rainy days, B) Absolute minimum and maximum and mean monthly air temperatures (°C) to 0.25 m above the soil surface, C) Mean monthly wind speed (km hour⁻¹) to 2 m above the soil surface and mean monthly relative humidity (%), and D) Mean monthly solar radiation (cal cm⁻² day⁻¹) and potential evapotranspiration (mm, Thornthwaite) during 1995, 1996 and early 1997. Measurements were taken using a meteorological station located 100 m away from the experimental plots.

Plant material

Studies were conducted on *Stipa clarazii* Ball., *S. tenuis* Phil. and *S. gynerioides* Phil., all C₃ perennial grasses native to the South of the Calden Phytogeographical District, a region of about 4 million hectares in Central Argentina. The first 2 species have a high forage value whereas the latter is an undesirable, unpreferred tussock grass (Cano 1988). Tillering starts with fall rains in all 3 species, although it extends into winter, spring, and even summer if rainfalls are abundant (Giorgetti et al. 2000). Recent studies have shown that *S. clarazii* has a greater competitive ability and tolerance to defoliation than *S. tenuis* (Saint Pierre et al. 2000a, 2000b) and the undesirable species *Stipa trichotoma* Nees, *S. gynerioides*, and *Stipa ambigua* Speg. (Moretto and Distel 1997, Saint Pierre et al. 2000a, 2000b).

Experimental design

During December 1993–April 1994, 28 experimental plots (1.8 x 1.8 m) were established at the field site from transplants on unplowed, weeded soil. Distance among plots was 4 m. Plants were obtained from a 20 year-exclosure to domestic animals located southeast of La Pampa Province (38° 45'S, 63° 45'W) at the South of the Calden Phytogeographical Region. Plants of the 3 species were placed 30 cm from one another in intersecting rows forming a matrix where each plant of *S. clarazii* and *S. tenuis* was surrounded by 4 plants of *S. gynerioides*. Desirable species plants were always present at each plot vertex. This matrix contributed to uniform competitive effects among plants. Plant responses within a plant community are better explained by using plants growing with nearby, competitive neighbors than by utilizing plants growing in isolation (Mueggler 1972, McNaughton 1992). There were 49 plants on each plot (12 of *S. clarazii*, 12 of *S. tenuis* and 25 of *S. gynerioides*) making a total of 1372 transplants for the whole study. At the time of transplanting, plant diameters at crown level were 13.47 ± 0.56 cm ($\bar{X} \pm 1$ SE, $n = 56$) for *S. clarazii*, 10.02 ± 0.51 cm for *S. tenuis*, and 12.27 ± 0.61 cm for *S. gynerioides*. In January 1995, during the plant quiescent period, all tussocks of *S. clarazii* and *S. tenuis* were manually clipped leaving 5 cm stubble height. In this manner, only current year growth was included in subsequent harvests to determine biomass. Two experimental plots (replicates) were randomly assigned to each water level x defoliation

Fig. 2. Periods of imposition of the different water levels and timing of defoliation (indicated as vertical solid bars) at the vegetative (V), internode elongation (E) or both (VE) phenological stages in 1995 and 1996.

treatment combination, giving a total of 14 treatments (see Water levels and Defoliation treatment headings in Fig. 2).

Measurements during the 3 growing seasons were repeated measures on the same groups of plants. Thus, we report on the cumulative effects of several water and defoliation treatments. Since we worked with an enormous unit of work, labor, and budget constraints made replication of our study in space and time impossible. Despite the fact that we place emphasis on statistical differences, caution is called for extrapolating our results. These should be better viewed under the specific conditions they were obtained. However, our study provided a unique opportunity for a simultaneous comparison of plant responses to various water levels, and to the timing and frequency of defoliation on species having differences in competitive ability.

Treatments

Soil water levels

Timing of application of water level and defoliation treatments during each year is shown in Fig. 2. A set of plots received rainfall all year round (rainfed plots). Irrigated plots received rainfall plus additional water with a drip irrigation system. In the irrigated treatment, plots were watered whenever soil moisture content dropped below 60% of field capacity as determined with soil tensiometers. The amount of water added to these plots was

calculated using software (Smith 1992, 1993) which accounted for soil and climate characteristics at the study site, and plant characteristics of species similar to those investigated. Water-stressed plots were covered with transparent plastic sheets (0.2 mm thick) whenever rain fell during the vegetative (V) or early internode elongation (E) or VE phenological stage of development (Fig. 2). Plants are often exposed to water stress conditions during any of these periods in their natural environment (Busso 1997, Fernández and Busso 1999). Plastic sheets were mounted on a specially designed wooden structure that provided an open-sided rain shelter. Lateral movement of water into the water-stressed plots was prevented by surrounding these plots with plastic sheets (0.2 mm thick) up to 1.8 m depth. Plants were exposed to water stress before, during and until 3 weeks after application of the defoliation treatments.

Except for plots exposed to water stress in the VE stage, the amount of water received when the different water levels were imposed (mid-April to mid-October in 1995 and late-April to late-October in 1996) was 373.2 mm in 1995 and 305.4 mm in 1996 in the irrigated plots, 87.2 mm in 1995 and 252.4 mm in 1996 in the rainfed plots, 76.4 mm in 1995 and 172.6 mm in 1996 after alleviation of water stress in the V stage, and 22.0 mm in 1995 and 133.2 mm in 1996 before imposition

Table 1. Midday leaf water potential (MPa) on plants of *S. clarazii*, *S. gynerioides* and *S. tenuis* during 1995. *Stipa clarazii* and *S. tenuis* were either defoliated or remained undefoliated (Controls: C) at the vegetative (V), internode elongation (E) or both phenological stages (VE) under rainfed, irrigated or water stress conditions. Plants of *S. gynerioides* grew in competition with the other 2 species but remained undefoliated. Each value is the mean (+/-SE) of n=2. Values without SE come from n=1.

Treatments			1995					
Water levels	Defoliation		1 Apr	17 May	31 Aug	26 Sep	24 Oct	29 Nov
(MPa)								
<i>S. clarazii</i>	Irrigation	C	-1.00 -	-2.10 (0.20)	-3.33 (0.28)	-3.33 (0.08)	-3.60 (0.40)	-1.98 (0.78)
		V	-0.88 (0.23)	-2.30 (0.00)	-2.75 (0.25)	-3.05 (0.55)	-3.28 (0.13)	-1.83 (0.83)
		E	-1.30 (0.40)	-2.65 -	-2.78 (0.28)	-3.28 (0.73)	-2.78 (0.38)	-2.00 (0.65)
		VE	-0.85 (0.55)	-2.33 (0.38)	-2.55 (0.10)	-2.95 (0.15)	-2.80 (0.30)	-2.03 (0.88)
	Rainfed	C	-1.75 (0.05)	-2.83 (0.38)	-2.33 (0.18)	-1.40 (0.10)	-1.43 (0.13)	-2.50 (0.55)
		V	-1.58 (0.43)	- -	-1.35 (0.15)	-1.28 (0.58)	-0.65 (0.15)	-1.30 (0.10)
		E	-1.43 (0.38)	-2.60 -	-2.03 (0.03)	-0.85 (0.35)	-1.18 (0.53)	-1.75 (0.15)
		VE	-1.68 (0.03)	-1.30 -	-1.63 (0.28)	-1.38 (0.58)	-1.10 (0.00)	-1.90 (0.10)
	Water stress V	C	-0.65 -	-2.80 (0.10)	-3.13 (0.03)	-3.25 (0.30)	-4.15 (0.80)	-2.28 (0.08)
		V	-1.65 (0.25)	-2.63 (0.43)	-2.93 (0.13)	-3.83 (0.38)	-3.78 (0.13)	-1.85 (0.15)
	Water stress E	C	-0.80 -	-2.60 (0.20)	-2.08 (0.08)	-3.33 (0.08)	-2.35 (0.15)	-2.50 (0.05)
		E	-1.10 (0.10)	-3.00 -	-3.80 (1.60)	-3.35 (1.00)	-2.03 (0.23)	-2.23 (0.23)
	Water stress VE	C	-0.80 -	-2.08 (0.98)	-2.85 (0.05)	-3.85 (0.55)	-1.83 (0.83)	-2.75 (0.25)
		VE	-1.25 (0.55)	-2.35 (0.45)	-2.45 (0.05)	-2.83 (0.18)	-2.13 (0.18)	-3.10 (0.45)
<i>S. gynerioides</i>	Irrigation	C	-0.50 -	-1.95 (0.85)	-3.28 (0.18)	-2.88 (0.18)	-3.60 (0.60)	-1.65 (0.35)
		V	-1.55 (0.75)	-1.70 (0.60)	-3.00 (0.05)	-3.05 (0.25)	-2.95 (0.15)	-2.40 (0.25)
		E	-0.70 (0.10)	-2.60 -	-2.50 (0.00)	-2.38 (0.68)	-3.25 (0.05)	-1.93 (0.23)
		VE	-0.35 (0.15)	-1.50 (0.60)	-2.50 (1.20)	-3.70 (0.70)	-3.15 (0.25)	-1.88 (0.63)
	Rainfed	C	-1.75 (0.75)	-2.88 (0.23)	-2.75 (0.45)	-1.83 (0.58)	-1.58 (0.28)	-1.63 (0.28)
		V	-1.80 (0.80)	- -	-2.10 (0.40)	-1.23 (0.28)	-1.25 (0.05)	-1.55 (0.85)
		E	-1.85 (0.95)	-2.30 -	-2.10 (0.60)	-1.08 (0.63)	-1.35 (0.15)	-1.73 (0.48)
		VE	-1.20 (0.70)	-2.80 -	-1.90 (0.70)	-1.05 (0.20)	-1.50 (0.10)	-1.28 (0.08)
	Water stress V	C	-1.80 -	-1.75 (0.55)	-2.90 (0.50)	-4.53 (0.73)	-2.88 (0.23)	-2.75 (0.25)
		V	-2.60 (0.70)	-2.58 (0.23)	-3.08 (0.63)	-3.45 (0.20)	-3.53 (0.08)	-2.33 (0.03)
	Water stress E	C	-0.30 -	-1.45 (0.95)	-2.10 (1.00)	-2.33 (0.88)	-2.05 (0.30)	-2.13 (0.28)
		E	-1.65 (0.85)	-2.90 -	-2.38 (0.73)	-2.60 (0.60)	-2.08 (0.18)	-2.25 (0.35)
	Water stress VE	C	-2.70 -	-2.08 (1.08)	-4.13 (0.23)	-3.60 (0.10)	-2.90 (0.90)	-1.80 (0.20)
		VE	-1.30 (1.10)	-1.45 (0.95)	-2.08 (0.63)	-2.35 (0.40)	-2.28 (0.03)	-2.38 (0.33)
<i>S. tenuis</i>	Irrigation	C	-1.20 -	-2.60 (0.60)	-2.75 (0.50)	-2.93 (0.18)	-2.90 (0.40)	-1.53 (0.48)
		V	-2.00 (0.30)	-2.35 (0.25)	-2.80 (0.35)	-2.63 (1.03)	-2.53 (0.43)	-2.10 (0.45)
		E	-1.70 (0.10)	-2.40 -	-2.28 (0.28)	-2.65 (0.10)	-2.75 (0.05)	-2.50 (0.15)
		VE	-1.95 (0.05)	-1.78 (0.28)	-3.15 (0.10)	-2.95 (0.45)	-3.00 (0.10)	-2.68 (0.13)
	Rainfed	C	-2.05 (0.05)	-2.45 (0.95)	-1.45 (0.35)	-1.20 (0.25)	-1.15 (0.05)	-1.18 (0.13)
		V	-1.78 (0.68)	- -	-2.68 (0.13)	-1.73 (0.78)	-1.48 (0.38)	-1.65 (0.00)
		E	-1.45 (0.25)	-2.10 -	-2.43 (0.23)	-1.73 (0.38)	-1.60 (0.50)	-1.20 (0.10)
		VE	-1.75 (0.15)	-1.10 -	-1.45 (0.10)	-1.88 (0.38)	-1.70 (0.50)	-1.23 (0.28)
	Water stress V	C	-1.90 -	-2.88 (0.53)	-4.00 (0.80)	-3.65 (0.15)	-3.03 (0.78)	-2.33 (0.48)
		V	-1.65 (0.75)	-2.05 (0.05)	-2.80 (0.30)	-3.05 (0.40)	-2.88 (0.58)	-1.78 (0.93)
	Water stress E	C	-1.60 -	-2.25 (0.15)	-3.13 (0.48)	-3.43 (0.23)	-2.78 (0.93)	-1.65 (0.55)
		E	-1.85 (0.05)	-2.40 -	-2.10 (0.60)	-2.78 (0.23)	-2.20 (0.40)	-1.75 (0.35)
	Water stress VE	C	-1.30 -	-1.65 (0.55)	-4.15 (0.75)	-2.80 (0.10)	-2.30 (0.20)	-2.10 (0.85)
		VE	-1.70 (0.10)	-1.95 (0.85)	-3.58 (0.53)	-3.43 (0.03)	-2.53 (1.53)	-2.23 (0.13)

of water stress at the E stage. Thereafter, all 28 experimental plots received 313.7 mm from mid-October 1995 to late-April 1996, and 487.8 mm from late-October 1996 to March 1997.

Defoliation treatments

Within each water level, plants of *S. clarazii* and *S. tenuis* remained undefoliated (Controls: C) or were defoliated at either V or E or VE stage of development during 1995 and 1996. Clipping left 5–7

cm stubble height on 23 May (V) or 27 September (E) in 1995, and 12 June (V) or 20 September (E) in 1996 (Fig. 2). *Stipa gynerioides* was not defoliated in 1995 and 1996 since it is not consumed by cattle (Cano 1988, Moretto and Distel 1997). However, all plants of this species were clipped to 5–7 cm stubble height at the end of the study (12 March 1997) to determine biomass production in the different treatments.

Leaf water potential

Determinations of leaf water potential provided a measure of plant water stress. Mid-day leaf water potential was periodically measured in all species using a pressure chamber during 1995, 1996, and early 1997 (Waring and Cleary 1967). Youngest, fully expanded leaves were taken for these measurements; one tiller was used per species and replicate on each sampling date. Leaves were kept in a plastic bag from excision to end of each determination to reduce water loss (Turner 1987).

Table 2. Midday leaf water potential (MPa) on plants of *S. clarazii*, *S. gynerioides* and *S. tenuis* during 1996 and early 1997. *Stipa clarazii* and *S. tenuis* were either defoliated or remained undefoliated (Controls: C) at the vegetative (V), internode elongation (E) or both phenological stages (VE) under rainfed, irrigated or water stress conditions during 1996. These plants had been defoliated under these water levels during 1995. Plants of *S. gynerioides* grew in competition with the other 2 species but remained undefoliated. Plants of all 3 species received natural rainfall during early 1997. Each value is the mean (+/-SE) of n=2.

Treatments			1996						1997
Water levels	Defoliation		19 Apr	11 Jun	15 Aug	22 Sep	14 Nov	21 Dec	22 Feb
-(MPa)									
<i>S. clarazii</i>	Irrigation	C	-1.88 (0.08)	-0.85 (0.45)	-1.80 (0.45)	-2.03 (0.13)	--	-2.38 (0.18)	-2.55 (0.25)
		V	-1.40 (0.10)	-1.13 (0.13)	-1.15 (0.15)	-2.13 (0.38)	--	-2.45 (0.10)	-2.40 (0.30)
		E	-1.68 (0.08)	-1.43 (0.73)	-1.68 (0.23)	-2.25 (0.35)	--	-2.48 (0.38)	-2.45 (0.05)
		VE	-1.30 (0.20)	-1.43 (0.53)	-1.98 (0.28)	-1.95 (0.55)	--	-2.10 (0.70)	-2.35 (0.05)
	Rainfed	C	-1.53 (0.28)	-0.98 (0.28)	-1.65 (0.65)	-1.70 (0.10)	-3.10 (0.40)	-1.95 (0.45)	-2.95 (0.45)
		V	-1.73 (0.28)	-1.68 (0.43)	-1.85 (0.15)	-1.90 (0.00)	-3.63 (1.03)	-2.65 (0.55)	-2.40 (0.40)
		E	-2.05 (0.25)	-1.25 (0.45)	-0.95 (0.25)	-2.35 (0.05)	-3.10 (0.20)	-2.55 (0.55)	-2.75 (0.75)
		VE	-1.93 (0.23)	-0.88 (0.28)	-1.30 (0.70)	-2.10 (0.10)	-2.40 (0.25)	-2.10 (0.20)	-2.25 (0.05)
	Water stress V	C	-2.38 (0.18)	-3.95 (0.35)	-2.38 (0.28)	-2.60 (0.30)	--	-2.83 (0.43)	-3.05 (0.25)
		V	-2.15 (0.35)	-4.68 (0.48)	-2.18 (0.33)	-2.40 (0.20)	--	-2.75 (0.20)	-3.15 (0.45)
	Water stress E	C	-2.00 (0.00)	-1.45 (0.20)	-2.30 (0.10)	-3.65 (0.05)	-6.15 (0.35)	-2.30 (0.30)	-2.90 (0.10)
		E	-1.85 (0.50)	-1.65 (0.15)	-1.73 (0.18)	-4.05 (1.65)	-3.60 (0.80)	-2.15 (0.35)	-2.75 (0.25)
	Water stress VE	C	-2.48 (0.33)	-3.28 (0.03)	-3.50 (0.10)	-3.35 (0.05)	-5.20 (0.50)	-2.88 (0.28)	-2.65 (0.15)
		VE	-1.68 (0.44)	-3.63 (0.38)	-2.73 (0.03)	-2.53 (0.18)	-4.38 (0.23)	-2.75 (0.30)	-2.50 (0.20)
<i>S. gynerioides</i>	Irrigation	C	-1.38 (0.13)	-1.58 (1.18)	-2.80 (0.60)	-2.63 (0.03)	--	-2.85 (0.15)	-2.60 (0.30)
		V	-1.70 (0.10)	-1.55 (0.05)	-1.65 (0.85)	-2.40 (0.20)	--	-2.50 (0.05)	-2.15 (0.05)
		E	-1.95 (0.80)	-2.25 (0.55)	-1.43 (0.60)	-2.48 (0.18)	--	-3.00 (0.15)	-1.85 (0.45)
		VE	-1.25 (0.15)	-2.05 (0.65)	-2.83 (0.68)	-2.33 (0.03)	--	-2.83 (0.38)	-2.40 (0.40)
	Rainfed	C	-1.48 (0.23)	-3.10 (0.00)	-1.85 (0.45)	-2.00 (0.30)	-3.03 (0.08)	-2.45 (0.45)	-2.90 (0.30)
		V	-1.78 (0.38)	-1.00 (0.10)	-1.00 (0.00)	-2.50 (0.20)	-2.85 (0.65)	-3.10 (0.00)	-2.40 (0.30)
		E	-2.33 (0.13)	-1.08 (0.38)	-1.93 (0.08)	-2.25 (0.15)	-2.55 (0.35)	-2.45 (0.55)	-2.20 (0.80)
		VE	-1.43 (0.43)	-1.08 (0.38)	-2.43 (0.23)	-1.65 (0.05)	-2.15 (0.45)	-2.63 (0.03)	-1.70 (0.20)
	Water stress V	C	-2.25 (0.15)	-4.25 (0.75)	-2.73 (0.23)	-2.83 (0.08)	--	-2.63 (0.03)	-2.45 (0.65)
		V	-1.43 (0.18)	-4.10 (0.60)	-1.70 (0.50)	-2.93 (0.03)	--	-2.70 (0.20)	-3.10 (0.40)
	Water stress E	C	-1.45 (0.35)	-1.18 (0.08)	-2.40 (0.30)	-3.70 (0.10)	-4.08 (0.28)	-2.88 (0.13)	-2.75 (0.35)
		E	-1.85 (0.05)	-1.28 (0.13)	-2.60 (0.50)	-4.95 (2.45)	-3.50 (0.60)	-2.73 (0.43)	-2.88 (0.28)
	Water stress VE	C	-1.80 (0.60)	-3.75 (0.15)	-4.05 (0.15)	-3.85 (0.75)	-6.08 (1.33)	-2.38 (0.13)	-2.60 (0.30)
		VE	-2.15 (0.55)	-2.15 (0.85)	-4.65 (0.15)	-4.20 (1.00)	-4.35 (0.35)	-2.65 (0.15)	-1.35 (0.75)
<i>S. tenuis</i>	Irrigation	C	-1.95 (0.05)	-1.30 (0.45)	-2.48 (0.03)	-2.40 (0.10)	--	-1.88 (0.18)	-2.33 (0.13)
		V	-2.10 (0.05)	-1.80 (0.70)	-2.20 (0.10)	-2.30 (0.30)	--	-1.85 (0.05)	-1.90 (0.70)
		E	-2.08 (0.18)	-1.63 (0.33)	-1.55 (0.45)	-2.15 (0.05)	--	-2.38 (0.13)	-1.85 (0.35)
		VE	-1.85 (0.45)	-1.63 (0.78)	-1.75 (0.60)	-1.80 (0.00)	--	-1.55 (0.30)	-2.10 (0.00)
	Rainfed	C	-2.10 (0.30)	-1.78 (0.83)	-1.35 (0.35)	-1.55 (0.25)	-2.80 (1.20)	-2.00 (0.25)	-2.45 (0.35)
		V	-1.63 (0.28)	-1.43 (0.38)	-1.10 (0.00)	-1.80 (0.00)	-2.50 (0.70)	-1.66 (0.28)	-2.25 (0.15)
		E	-2.00 (0.20)	-2.25 (0.05)	-1.40 (0.45)	-1.90 (0.20)	-2.60 (0.20)	-2.13 (0.13)	-2.40 (0.00)
		VE	-2.40 (0.50)	-1.20 (0.05)	-1.85 (0.35)	-1.90 (0.20)	-1.80 (0.50)	-2.03 (0.33)	-1.98 (0.28)
	Water stress V	C	-2.13 (0.13)	-3.35 (0.10)	-1.38 (0.13)	-1.80 (0.10)	--	-1.70 (0.30)	-2.48 (0.68)
		V	-1.60 (0.20)	-4.75 (0.45)	-1.93 (0.28)	-1.98 (0.28)	--	-2.05 (0.20)	-3.35 (1.05)
	Water stress E	C	-2.30 (0.20)	-1.33 (0.03)	-2.28 (0.13)	-4.35 (0.05)	-5.65 (0.65)	-2.10 (0.25)	-3.00 (0.50)
		E	-2.10 (0.35)	-1.73 (0.03)	-1.98 (0.03)	-3.35 (1.25)	-3.93 (0.73)	-1.70 (0.10)	-2.82 (0.29)
	Water stress VE	C	-1.90 (0.10)	-2.70 (0.50)	-2.75 (0.35)	-2.45 (0.15)	-3.75 (1.75)	-2.15 (1.15)	-2.10 (0.00)
		VE	-2.05 (0.55)	-2.40 (0.60)	-3.13 (0.38)	-2.63 (0.63)	-4.38 (0.13)	-2.20 (0.10)	-1.60 (0.30)

Bud metabolic activity and axillary bud outgrowth

These variables were evaluated on parent tillers produced during each growing season. At each observation date, 2 to 4 tillers were harvested per plant of *S. clarazii*, *S. tenuis*, or *S. gynerioides*; one plant was used per replicate in all treatments. Crown samples were maintained at 4°C until dissection. Number, metabolic activity, and outgrowth of axillary buds were determined on each tiller under a

binocular microscope. Three bud categories were considered: metabolically active (MAB), dormant or dead (DDB), and buds which grew out originating daughter tillers (DT). Total bud number (TBN) was calculated as MAB+DDB+DT. The potential maximum number of buds per stem base (total node number = TN) was calculated as MAB+DDB+DT+number of foliar scars. Font Quer (1982) reported that this number is equivalent to the number of produced leaves. Foliar

scars indicate presence of leaves which do not have buds or daughter tillers in their axilla (Hendrickson and Briske 1997).

Metabolic activity of axillary buds was determined using Triphenyl Tetrazolium Chloride (TTC) following Busso et al. (1989). Each stem base was longitudinally cut leaving entire buds at both sides of the cutting. Both halves were maintained in a solution of 0.6% (weight/volume) TTC-0.05 M Phosphate buffer (pH = 7.38) during 15 hours in darkness at 30°C.

Metabolically active buds were those whose apex stained pink or red indicating enzymatic reduction of colourless tetrazolium salt to red, insoluble formazan. Buds not-stained with TTC were considered dormant or dead.

Statistical analysis

Leaf water potentials were analyzed separately for each date using ANOVA. A split plot design was used with treatments (14 combinations of water x defoliation levels) as main factors and species as secondary factors. One-way ANOVA was used to analyze the bud metabolic activity data; analysis was performed separately for each date and species using a completely randomized design with 14 treatments. Whenever F tests were significant at $p < 0.05$, means were separated using Fisher LSD or Tukey-Kramer test for balanced or unbalanced data, respectively. Values for MAB and DDB were transformed to $\sqrt{x+1}$ to improve normality assumptions (Steel and Torrie 1985). Non-transformed values are presented in Figures.

Results and Discussion

Leaf water potentials

During 1995, 1996, and early 1997, leaf water potentials were similar ($p > 0.25$) among defoliation treatments within each water level in all 3 species (Tables 1 and 2). These results are similar to those of Becker et al. (1997) and Busso and Richards (1993) in these and other perennial grasses. Other studies, however, have reported higher leaf water potentials on defoliated than on undefoliated perennial tussock grasses (Briske and Anderson 1990, Brown 1995, Williams et al. 1998). This positive response to herbivory has been attributed to a reduced transpiratory leaf surface area after defoliation which would conserve soil water (Anderson and Briske 1995, Brown 1995).

At the beginning and end of each growing cycle, leaf water potential was similar ($p > 0.25$) among water levels in *S. clarazii*, *S. tenuis* and *S. gynerioides*. In August, September, and October 1995, however, these species had lower ($p < 0.05$) leaf water potentials under water stress than under irrigated conditions. Similar results were obtained in 1996 during this period, except on plants of the desirable species by the end of September ($p > 0.15$). Leaf water potentials were more variable on plants of the 3 species in the rainfed plots. Under these conditions, leaf

Table 3. Number of total nodes (TN), buds which originated daughter tillers (DT), and metabolically active (MAB) and dead and dormant (DDB) buds on parent tillers of *S. gynerioides* at the different treatments in 1995, 1996 and early 1997. C: Undefoliated controls, and defoliation at the vegetative (V), internode elongation (E) or both phenological stages (VE). Each value is the mean (+/-SE) of n=2.

Dates	Treatments		TN	DT	MAB	DDB
	Water levels	Defoliation				
23/5/95	Irrigation	C	6.25 (0.75)	3.00 (0.00)	1.25 (0.25)	0.25 (0.25)
		V	5.75 (0.75)	2.00 (0.50)	0.50 (0.00)	1.00 (1.00)
		VE	8.00 (0.00)	5.00 (0.00)	1.00 (0.00)	0.00 (0.00)
	Rainfed	C	7.00 (0.00)	3.50 (0.00)	0.50 (0.00)	0.00 (0.00)
		V	7.75 (1.25)	3.00 (1.00)	0.75 (0.25)	0.50 (0.00)
		VE	7.25 (1.25)	2.25 (0.25)	0.75 (0.25)	1.75 (0.75)
	Water stress V	C	6.75 (0.75)	3.75 (1.25)	0.75 (0.75)	0.75 (0.75)
		V	7.75 (0.25)	3.75 (0.25)	1.00 (0.00)	0.25 (0.25)
	Water stress VE	C	8.25 (0.75)	4.00 (1.00)	0.50 (0.00)	1.00 (1.00)
		VE	6.25 (0.75)	3.25 (0.75)	1.00 (0.00)	0.00 (0.00)
	7/9/95	C	7.13 (0.13)	2.63 (0.13)	0.88 (0.13)	2.00 (0.00)
		V	7.25 (2.00)	2.88 (1.13)	0.88 (0.38)	1.00 (0.75)
		VE	6.25 (0.50)	3.13 (0.13)	0.88 (0.38)	0.25 (0.00)
27/9/95	Rainfed	C	7.25 (0.75)	3.00 (0.25)	0.50 (0.25)	1.75 (1.50)
		V	5.88 (0.63)	2.25 (0.50)	0.75 (0.00)	1.63 (0.38)
		VE	7.13 (1.13)	2.83 (1.17)	0.71 (0.04)	1.25 (0.25)
	Water stress V	C	6.50 (0.00)	2.50 (0.00)	1.50 (0.50)	0.75 (0.50)
		V	8.08 (0.58)	3.38 (0.63)	0.79 (0.46)	1.38 (0.38)
	Water stress VE	C	6.42 (0.08)	2.71 (0.04)	1.09 (0.42)	0.88 (0.13)
		VE	7.75 (0.00)	3.13 (0.13)	0.88 (0.38)	1.00 (0.75)
	Irrigation	C	7.38 (0.38)	3.38 (0.38)	0.38 (0.13)	2.00 (0.50)
		E	7.88 (0.13)	3.13 (0.63)	0.88 (0.38)	1.25 (0.00)
		VE	8.88 (0.13)	3.75 (0.50)	1.00 (0.00)	1.50 (0.50)
	Rainfed	C	8.00 (0.75)	2.88 (0.38)	0.50 (0.50)	2.38 (0.63)
		E	9.13 (0.38)	4.00 (0.25)	0.88 (0.13)	2.00 (0.00)
		VE	8.50 (1.00)	3.38 (0.13)	1.25 (0.25)	2.00 (1.00)
	Water stress E	C	7.75 (0.50)	2.88 (0.13)	0.25 (0.00)	1.88 (0.63)
		E	7.88 (0.38)	3.00 (0.75)	0.63 (0.13)	1.00 (0.00)
	Water stress VE	C	7.50 (0.50)	2.75 (0.25)	1.38 (0.13)	1.38 (0.63)
		VE	9.63 (0.13)	4.00 (0.25)	0.63 (0.38)	1.50 (0.25)
	14/12/95	C	6.88 (0.13)	2.75 (1.25)	0.00 (0.00)	2.13 (0.63)
		E	7.75 (0.75)	2.38 (0.38)	0.00 (0.00)	3.00 (0.00)
		VE	7.13 (0.38)	2.63 (0.63)	0.00 (0.00)	2.13 (0.38)
	Rainfed	C	7.63 (0.63)	3.00 (0.50)	0.13 (0.13)	2.25 (0.25)
		E	8.63 (1.38)	3.50 (0.25)	0.25 (0.25)	2.63 (1.63)
	Water stress E	C	7.88 (0.63)	3.88 (1.13)	0.00 (0.00)	2.50 (0.50)
		E	7.88 (0.63)	2.88 (0.63)	0.00 (0.00)	2.50 (0.25)
	Water stress VE	C	8.25 (0.50)	4.13 (0.38)	0.00 (0.00)	2.13 (0.63)
		VE	6.88 (0.63)	2.50 (0.75)	0.00 (0.00)	2.63 (0.38)
	25/4/96	C	9.00 (0.00)	3.00 (0.50)	1.75 (0.25)	2.00 (0.00)
		V	7.25 (0.25)	0.75 (0.25)	1.75 (0.25)	3.25 (1.25)
		E	6.50 (0.00)	1.50 (0.50)	1.75 (0.25)	2.00 (0.00)
	Rainfed	VE	8.25 (0.25)	1.25 (0.25)	0.75 (0.25)	3.25 (1.25)
		C	6.75 (0.25)	1.50 (0.00)	1.00 (0.00)	2.50 (0.50)
		V	7.00 (0.50)	1.75 (0.25)	2.00 (0.00)	0.75 (0.25)
	Water stress V	E	7.25 (1.25)	1.50 (1.00)	1.25 (0.25)	3.00 (0.50)
		VE	7.75 (0.25)	1.50 (0.00)	1.50 (0.50)	2.25 (0.25)
		C	6.75 (0.25)	2.25 (0.25)	1.00 (0.50)	1.50 (0.50)
	Water stress VE	V	7.00 (1.00)	2.50 (0.50)	0.50 (0.50)	2.25 (0.25)
		C	7.00 (0.00)	2.00 (0.00)	1.75 (0.25)	1.50 (0.50)
		VE	7.50 (1.00)	2.00 (1.00)	1.25 (0.25)	2.75 (0.25)
	12/6/96	C	8.13 (0.13)	1.75 (0.75)	2.13 (0.13)	2.63 (0.38)
		V	10.00 (0.25)	2.50 (0.75)	1.50 (0.25)	3.75 (0.50)
		VE	8.63 (0.13)	1.13 (0.13)	1.13 (0.13)	3.25 (0.25)
	Rainfed	C	7.63 (0.50)	1.63 (0.25)	1.50 (0.50)	2.88 (0.13)
		V	8.63 (0.88)	1.88 (0.63)	1.13 (0.63)	3.50 (0.50)
		VE	8.50 (0.00)	2.50 (0.25)	1.38 (0.63)	2.88 (0.63)
	Water stress V	C	8.25 (0.50)	1.13 (0.38)	1.38 (0.13)	3.13 (0.13)
		V	8.50 (1.00)	1.75 (0.25)	1.00 (0.75)	3.63 (1.13)

(Continued on page 156)

Table 3. Continued.

Dates	Treatments		TN	DT	MAB	DDB
	Water levels	Defoliation				
30/7/96	Water stress VE	C	7.88 (0.38)	2.00 (0.50)	1.63 (0.13)	2.50 (0.25)
		VE	9.38 (0.88)	3.13 (1.13)	1.00 (0.00)	2.00 (0.50)
	Irrigation	C	8.00 (0.00)	1.38 (0.88)	1.75 (0.00)	3.38 (0.63)
		V	8.25 (0.00)	1.75 (0.75)	1.25 (0.00)	3.38 (0.38)
		VE	7.63 (0.38)	2.25 (0.25)	1.13 (0.38)	2.00 (0.25)
	Rainfed	C	8.25 (0.75)	2.50 (0.00)	0.88 (0.13)	2.13 (0.88)
		V	8.88 (0.63)	2.75 (1.00)	1.25 (0.25)	2.50 (1.00)
		VE	8.25 (1.00)	1.88 (0.63)	0.75 (0.50)	4.13 (0.88)
	Water stress V	C	8.00 (0.00)	2.25 (0.00)	0.88 (0.63)	3.13 (0.63)
		V	7.63 (0.13)	1.88 (0.38)	1.13 (0.88)	3.00 (1.25)
21/9/96	Water stress VE	C	9.25 (1.25)	2.50 (1.00)	1.00 (0.25)	4.25 (0.00)
		VE	8.25 (0.50)	2.63 (0.63)	1.38 (0.13)	2.13 (0.13)
	Irrigation	C	8.13 (0.63)	1.50 (0.75)	0.38 (0.13)	3.88 (0.88)
		E	8.13 (0.38)	1.88 (0.88)	0.38 (0.13)	3.63 (1.38)
		VE	8.00 (0.25)	2.88 (0.13)	0.25 (0.25)	2.38 (0.13)
	Rainfed	C	8.75 (0.25)	3.13 (0.13)	0.13 (0.13)	3.25 (0.25)
		E	8.13 (0.13)	1.88 (0.13)	0.25 (0.25)	2.25 (1.25)
		VE	8.88 (0.13)	2.38 (0.13)	0.63 (0.63)	3.63 (0.63)
	Water stress E	C	9.63 (0.63)	3.38 (0.88)	1.13 (0.13)	2.13 (0.38)
		E	8.25 (0.25)	2.38 (0.13)	0.63 (0.63)	2.75 (1.00)
30/10/96	Water stress VE	C	8.88 (0.13)	2.75 (1.25)	1.13 (0.63)	1.63 (0.63)
		VE	7.88 (0.38)	2.13 (0.63)	0.75 (0.25)	3.13 (0.63)
	Irrigation	C	7.88 (0.13)	1.38 (0.13)	0.00 (0.00)	4.50 (0.00)
		V	8.63 (0.63)	2.00 (0.75)	0.38 (0.13)	4.25 (1.00)
		E	—	—	—	—
		VE	7.75 (0.50)	2.25 (0.50)	0.00 (0.00)	3.13 (0.63)
	Rainfed	C	7.88 (0.13)	2.25 (0.25)	0.00 (0.00)	3.75 (0.00)
		V	7.50 (0.25)	2.13 (0.13)	0.13 (0.13)	2.38 (0.63)
		E	8.50 (0.75)	1.63 (0.88)	0.38 (0.38)	4.00 (1.00)
		VE	9.63 (0.38)	2.63 (0.13)	0.13 (0.13)	4.75 (0.00)
	Water stress V	C	7.63 (0.38)	2.00 (0.50)	0.00 (0.00)	3.50 (0.00)
		V	8.63 (0.13)	4.38 (0.38)	0.25 (0.00)	2.00 (0.50)
7/1/97	Water stress VE	C	8.25 (0.00)	2.13 (0.13)	0.75 (0.25)	4.00 (0.75)
		VE	8.63 (0.38)	2.13 (1.13)	0.13 (0.13)	4.88 (1.38)
	Irrigation	C	6.88 (0.13)	2.13 (0.13)	0.00 (0.00)	2.88 (0.13)
		V	6.38 (0.13)	2.13 (0.63)	0.00 (0.00)	2.13 (0.63)
		E	6.50 (0.50)	1.25 (0.25)	0.00 (0.00)	2.25 (0.00)
		VE	6.75 (0.25)	1.50 (0.00)	0.13 (0.13)	2.63 (0.13)
	Rainfed	C	6.75 (0.75)	2.00 (0.25)	0.13 (0.13)	2.50 (0.75)
		V	7.63 (0.63)	2.63 (0.13)	0.00 (0.00)	2.75 (0.75)
		E	6.88 (0.88)	0.88 (0.13)	0.00 (0.00)	4.00 (0.50)
		VE	6.75 (0.75)	1.50 (1.00)	0.13 (0.13)	3.50 (0.25)
	Water stress V	C	6.63 (0.88)	1.63 (0.38)	0.00 (0.00)	3.00 (1.00)
		V	6.25 (0.25)	2.38 (0.13)	0.25 (0.25)	1.63 (0.38)
12/3/97	Water Stress E	C	7.25 (0.25)	2.00 (0.25)	0.00 (0.00)	2.50 (0.25)
		E	8.13 (1.38)	2.13 (0.63)	0.13 (0.13)	3.25 (1.00)
	Water stress VE	C	9.46 (1.21)	3.04 (0.29)	0.29 (0.04)	1.96 (0.29)
		VE	9.09 (0.58)	2.50 (0.50)	0.00 (0.00)	3.54 (0.21)
	Irrigation	C	7.13 (0.38)	3.38 (1.13)	0.00 (0.00)	1.75 (0.25)
		V	6.75 (0.00)	1.88 (0.13)	0.00 (0.00)	2.50 (0.00)
		E	6.96 (0.29)	2.00 (0.00)	0.25 (0.25)	1.71 (0.04)
		VE	6.63 (0.38)	2.25 (0.00)	0.13 (0.13)	1.38 (1.13)
	Rainfed	C	6.13 (0.13)	2.13 (0.63)	0.13 (0.13)	1.50 (1.00)
		V	6.88 (0.63)	1.75 (0.25)	0.63 (0.38)	2.00 (0.25)
		E	7.00 (0.75)	2.13 (0.63)	0.13 (0.13)	2.13 (0.13)
		VE	6.25 (0.25)	1.63 (0.38)	0.25 (0.25)	1.88 (0.13)
	Water stress V	C	6.25 (0.25)	2.63 (0.13)	0.25 (0.25)	1.38 (0.13)
		V	7.38 (0.13)	2.75 (0.25)	0.00 (0.00)	2.25 (0.75)
	Water stress E	C	6.63 (0.13)	2.25 (0.25)	0.00 (0.00)	2.00 (0.50)
		E	7.50 (0.50)	2.00 (0.50)	0.13 (0.13)	3.13 (0.88)
	Water stress VE	C	7.38 (0.38)	3.00 (0.00)	0.13 (0.13)	1.75 (0.25)
		VE	7.50 (0.75)	2.75 (1.25)	0.00 (0.00)	2.25 (0.50)

water potentials were lower ($p < 0.05$) than those in the irrigated plots in 1995, and higher ($p < 0.05$) than those in the water-stressed plots in 1996 (Tables 1 and 2). This was very likely due to the lower annual rainfall in 1995 (447.2 mm) than in 1996 (621.3 mm) (Fig. 1).

In 1995, leaf water potential on average for all treatments was similar ($p > 0.25$) among species, except in April when this variable was higher ($p < 0.05$) in *S. clarazii* than in *S. tenuis*. Plants of the desirable species had higher ($p < 0.05$) leaf water potentials than *S. gynerioides* in mid-August, September, and December in 1996 (Tables 1 and 2).

Bud metabolic activity and axillary bud outgrowth

On average for each date and species, between 62 and 82% of the total number of nodes had daughter tillers, metabolically active buds or dormant or dead buds on parent tillers. This indicates that not all leaves possess axillary buds which is similar to results of Mueller and Richards (1986) and Hendrickson and Briske (1997) on other perennial grasses.

Numbers of total nodes, daughter tillers, and metabolically active or dormant or dead buds were similar ($p > 0.10$) between defoliation treatments and water levels during 1995, 1996, and early 1997 on parent tillers of *S. gynerioides* (Table 3). This implies that neither axillary bud activation nor initial outgrowth would contribute to explain the observed release from competition of *S. gynerioides* after selective defoliation of *S. clarazii* (Moretto and Distel 1999) and *S. clarazii* and *S. tenuis* (Flemmer 2000). These results also show the lack of sensitivity of axillary buds in *S. gynerioides* to water stress, a common abiotic factor to which plants are exposed in the temperate, central semiarid rangelands of Argentina (Busso 1997, Fernández and Busso 1999). Axillary buds of this species, however, are susceptible to fire (Distel and Bóo 1996, Peláez 2000).

Total node number, and numbers of daughter tillers, and metabolically active or dormant or dead buds were also similar ($p > 0.25$) in all water level and defoliation treatments on parent tillers of *S. tenuis* during 1995 (Table 4). These results indicate that the degree of metabolic activity and outgrowth capacity of axillary buds are maintained on parent tillers of this species after a one-year-exposure to the combined or separate influence of water stress and defoliation. Similar results ($p > 0.25$) were obtained for most sampling dates in 1996 (Table 4).

Table 4. Number of total nodes (TN), buds which originated daughter tillers (DT), and metabolically active (MAB) and dead and dormant (DDB) buds on parent tillers of *S. tenuis* at the different treatments in 1995, 1996 and early 1997. I: Irrigation, R: Rainfed, WS: Water stress, C: Undeveloped controls, and defoliation at the vegetative (V), internode elongation (E) or both phenological stages (VE). Each value is the mean (+/-SE) of n=2. Values without SE come from n=1.

Dates	Treatments		TN	DT	MAB	DDB
	Water levels	Defoliation				
23/5/95	Irrigation	C	7.25 (0.25)	2.75 (1.75)	2.25 (1.25)	0.25 (0.25)
		V	7.00 (1.00)	3.00 (0.00)	1.75 (0.25)	0.50 (0.50)
		VE	6.00 (0.00)	2.00 (0.00)	1.50 (0.00)	1.00 (0.00)
	Rainfed	C	7.00 (0.00)	5.00 (0.00)	0.00 (0.00)	0.50 (0.00)
		V	7.00 (0.50)	3.00 (0.50)	1.25 (0.75)	0.75 (0.25)
		VE	5.00 (1.00)	2.50 (0.50)	0.50 (0.50)	1.00 (1.00)
	Water stress V	C	10.00 (1.00)	4.00 (1.00)	3.50 (1.50)	0.00 (0.00)
		V	5.25 (0.25)	3.25 (0.25)	0.50 (0.50)	0.00 (0.00)
	Water stress VE	C	6.75 (0.25)	3.25 (0.75)	0.00 (0.00)	1.00 (1.00)
		VE	7.00 (2.00)	1.50 (0.50)	1.75 (0.25)	0.50 (0.50)
7/9/95	Irrigation	C	9.00 (1.25)	2.88 (1.38)	1.50 (1.00)	2.13 (0.63)
		V	8.71 (1.04)	3.92 (0.58)	1.50 (0.50)	1.75 (0.25)
		VE	8.00 (1.25)	3.25 (0.50)	1.75 (1.50)	1.50 (0.00)
	Rainfed	C	8.00 (2.00)	4.50 (1.50)	1.13 (0.13)	0.38 (0.38)
		V	7.13 (0.88)	3.38 (0.63)	2.25 (0.75)	0.42 (0.08)
		VE	7.46 (0.79)	2.50 (0.50)	2.38 (0.38)	1.29 (0.04)
	Water stress V	C	9.25 (0.25)	3.88 (1.63)	3.25 (1.25)	0.50 (0.00)
		V	7.33 (1.00)	3.17 (1.17)	1.00 (0.67)	1.17 (0.83)
	Water stress VE	C	7.21 (0.54)	2.33 (0.33)	2.21 (1.54)	1.46 (1.21)
		VE	8.04 (1.71)	3.58 (0.08)	1.58 (0.92)	1.04 (0.71)
27/9/95	Irrigation	C	10.13 (0.88)	3.38 (1.38)	1.75 (0.25)	3.38 (0.88)
		E	9.83 (0.83)	3.79 (0.46)	1.58 (1.08)	1.08 (0.42)
		VE	10.00 (1.00)	3.63 (0.13)	2.50 (1.00)	2.25 (0.50)
	Rainfed	C	8.75 (1.25)	2.75 (1.00)	2.88 (0.63)	1.25 (0.50)
		E	9.75 (1.00)	4.50 (0.25)	2.13 (0.38)	1.88 (1.13)
		VE	8.88 (1.63)	3.25 (0.25)	2.50 (1.25)	1.38 (0.38)
	Water stress E	C	9.00 (1.75)	4.25 (0.50)	1.38 (0.63)	2.00 (1.75)
		E	8.88 (0.63)	3.25 (0.25)	3.00 (0.50)	1.25 (0.75)
	Water stress VE	C	8.75 (0.25)	3.88 (0.13)	1.50 (0.00)	1.50 (0.50)
		VE	9.75 (1.00)	2.75 (0.50)	3.75 (0.25)	2.00 (0.25)
14/12/95	Irrigation	C	8.75 (0.25)	3.63 (0.88)	1.00 (0.50)	2.63 (0.63)
		E	7.50 (2.50)	1.75 (1.00)	1.00 (0.75)	2.88 (2.13)
		VE	9.00 (1.75)	3.50 (0.25)	0.63 (0.13)	3.63 (1.63)
	Rainfed	C	8.63 (0.88)	3.88 (1.38)	2.00 (0.00)	1.50 (0.50)
		E	8.25 (3.00)	3.88 (2.38)	1.00 (0.25)	2.00 (0.75)
		VE	9.63 (0.88)	4.25 (0.25)	0.75 (0.25)	2.88 (1.38)
	Water Stress E	C	8.75 (0.75)	4.25 (0.50)	0.63 (0.13)	2.38 (0.13)
		E	9.25 (0.75)	4.38 (0.38)	1.25 (1.00)	2.00 (0.75)
	Water stress VE	C	8.25 (1.00)	3.88 (0.13)	1.50 (1.00)	1.25 (0.75)
		VE	9.38 (1.38)	3.63 (0.38)	0.25 (0.25)	4.00 (1.50)
25/4/96	Irrigation	C	6.50 (0.00)	2.75 (0.75)	0.75 (0.75)	1.25 (1.25)
		V	9.50 (0.50)	3.50 (1.50)	1.75 (0.75)	3.00 (0.00)
		E	6.00 (0.50)	1.50 (0.00)	1.75 (0.25)	0.75 (0.75)
		VE	7.00 (0.00)	0.00 (0.00)	3.00 (0.00)	2.00 (0.00)
	Rainfed	C	8.00 (1.00)	3.25 (0.75)	1.00 (0.50)	1.25 (1.25)
		V	7.50 (1.50)	3.25 (0.75)	0.25 (0.25)	1.50 (1.50)
		E	7.00 (0.00)	2.75 (0.75)	1.25 (1.25)	0.50 (0.50)
		VE	7.00 (2.00)	3.75 (0.75)	1.75 (1.75)	0.25 (0.25)
	Water stress V	C	9.25 (1.25)	4.00 (0.00)	1.25 (0.75)	1.25 (1.25)
		V	7.50 (0.00)	3.75 (0.75)	2.00 (0.50)	0.25 (0.25)
	Water stress E	C	7.50 (1.00)	2.25 (0.25)	3.25 (1.25)	0.50 (0.50)
		E	7.25 (2.25)	2.75 (1.25)	2.00 (0.50)	0.25 (0.25)
	Water stress VE	C	8.75 (0.25)	3.00 (2.00)	3.25 (1.25)	0.50 (0.50)
		VE	8.00 (0.00)	2.75 (1.25)	1.50 (1.00)	2.00 (1.50)

(Continued on page 158)

However, defoliation affected bud metabolic activity of *S. tenuis* independently of plant water status in June 1996 (before defoliation at V). While defoliated and undeveloped plants of this species had a similar ($p > 0.25$) total bud number, numbers of metabolically active buds were lower ($p < 0.05$) and those of dormant or dead buds were higher ($p < 0.05$) on plants defoliated at the vegetative and vegetative + early internode elongation stages in the previous year than on undeveloped controls under all water levels (Table 4). Despite this lower degree of metabolic activity, defoliated and undeveloped plants of *S. tenuis* had a similar ($p \geq 0.10$) number of daughter tillers. Busso et al. (1989) also reported a reduction in the number of metabolically active buds on plants of *Agropyron spicatum* (Pursh) Scribn. and Smith (Syn: *Pseudoroegneria spicata* (Pursh) A. Löve ssp. *spicata*) under the simultaneous influence of defoliation and water stress during 2 consecutive years. At the same time in June 1996, daughter tiller production (DT) was greater ($p < 0.05$) on plants defoliated twice than on those defoliated at the vegetative stage under rainfed and irrigated conditions in *S. tenuis*; this was associated with a lower ($p < 0.01$) number of metabolically active buds. A greater defoliation frequency has increased daughter tiller production in other perennial grasses by modifying both light quantity and quality at stem bases (Deregibus et al. 1983, Casal et al. 1985, Gautier et al. 1999).

In June 1996, plants of *S. tenuis*, whether defoliated or not during the previous year, had a greater ($p < 0.05$) number of daughter tillers and total nodes after exposure to water stress in the vegetative+early internode elongation than in the vegetative stage. It is likely that accumulation of total nonstructural carbohydrates in the stem bases increased as the period of exposure to water stress also increased. Since this species remains dormant during dry summers (Distel and Fernández 1986), these carbohydrates may be utilized for rapid regrowth during the next growing season. Various studies have reported that accumulation of total nonstructural carbohydrates in the stem bases of perennial grasses during periods of water stress resulted in greater tillering responses (Busso et al. 1990, Fulkerson and Slack 1995, Volaire 1995, Oosthuizen and Snyman 1999). Also by mid-year 1996, numbers of dormant or dead buds were greater ($p < 0.01$) under irrigated than under rainfed or water stress conditions on plants of *S. tenuis* which had been defoliated

Table 4 Continued.

Dates	Treatments		TN	DT	MAB	DDB
	Water levels	Defoliation				
12/6/96	Irrigation	C	11.50 (0.25)	4.75 (0.25)	4.38 (0.38)	0.25 (0.25)
		V	11.00 (0.00)	3.25 (0.00)	2.00 (0.00)	4.00 (0.00)
		VE	10.00 (0.00)	5.63 (0.38)	0.50 (0.00)	2.38 (0.13)
	Rainfed	C	8.88 (0.88)	3.88 (0.38)	3.38 (0.63)	0.38 (0.13)
		V	9.75 (1.50)	4.13 (0.13)	1.38 (0.38)	1.38 (0.13)
		VE	10.75 (0.00)	5.25 (1.50)	0.88 (0.88)	2.75 (0.50)
	Water stress V	C	8.25 (0.00)	3.63 (0.63)	2.63 (0.13)	0.25 (0.00)
		V	8.88 (0.38)	4.13 (0.38)	1.00 (0.50)	2.00 (0.50)
	Water stress VE	C	10.50 (0.00)	4.50 (0.00)	4.25 (0.00)	0.25 (0.00)
		VE	10.92 (0.58)	5.96 (0.29)	0.46 (0.21)	2.96 (0.29)
30/7/96	Irrigation	C	9.88 (0.38)	3.25 (0.75)	1.88 (1.38)	2.75 (2.25)
		V	10.63 (1.88)	5.38 (0.63)	2.75 (2.25)	1.25 (0.75)
		VE	12.25 (0.75)	3.50 (0.50)	5.00 (1.00)	2.13 (1.13)
	Rainfed	C	10.00 (1.00)	5.00 (2.25)	1.88 (1.38)	1.25 (0.75)
		V	9.50 (1.00)	3.38 (0.88)	1.50 (1.50)	2.75 (2.25)
		VE	11.00 (0.00)	4.75 (0.25)	2.13 (1.63)	1.63 (1.13)
	Water stress V	C	8.63 (0.13)	4.00 (0.00)	2.00 (0.25)	0.63 (0.13)
		V	9.25 (0.00)	3.38 (0.13)	0.75 (0.75)	2.25 (1.25)
	Water stress VE	C	7.25 (0.00)	3.00 (0.00)	3.25 (0.00)	0.00 (0.00)
		VE	9.25 (0.00)	3.63 (0.13)	2.50 (1.50)	1.63 (1.63)
21/9/96	Irrigation	C	9.88 (0.38)	4.00 (0.75)	2.25 (0.25)	1.88 (1.13)
		E	10.63 (0.13)	5.13 (1.13)	2.50 (1.75)	1.50 (1.25)
		VE	10.50 (1.50)	4.00 (0.25)	1.38 (1.38)	3.38 (0.63)
	Rainfed	C	12.00 (1.50)	5.25 (2.00)	0.63 (0.38)	4.38 (0.38)
		E	10.63 (1.38)	4.38 (0.13)	0.75 (0.75)	3.63 (2.13)
		VE	9.50 (1.00)	4.63 (0.63)	0.00 (0.00)	3.00 (0.50)
	Water stress E	C	10.75 (0.25)	6.00 (0.25)	1.13 (0.63)	2.00 (0.25)
		E	9.88 (0.38)	4.75 (0.50)	2.25 (0.75)	1.13 (1.13)
	Water stress VE	C	10.00 (0.00)	5.75 (0.00)	2.25 (0.00)	0.75 (0.00)
		VE	9.63 (0.88)	4.25 (1.50)	0.38 (0.38)	2.25 (0.00)
30/10/96	Irrigation	C	9.88 (0.13)	5.00 (0.25)	0.88 (0.38)	2.00 (0.00)
		V	8.38 (0.88)	3.13 (0.13)	1.13 (0.88)	2.25 (0.50)
		E	--	--	--	--
		VE	11.50 (1.50)	5.50 (0.75)	1.00 (1.00)	3.00 (0.25)
	Rainfed	C	8.88 (0.63)	4.25 (1.25)	0.00 (0.00)	2.88 (1.38)
		V	9.63 (0.13)	4.75 (0.75)	0.13 (0.13)	3.13 (0.63)
		E	9.50 (0.25)	4.00 (0.25)	0.50 (0.50)	3.38 (0.13)
		VE	8.75 (1.25)	3.38 (1.63)	0.83 (0.13)	3.50 (0.50)
	Water stress V	C	10.75 (0.25)	5.88 (0.38)	0.38 (0.13)	2.50 (0.00)
		V	10.50 (0.75)	4.88 (0.63)	0.25 (0.25)	3.63 (0.38)
	Water stress E	C	10.50 (0.50)	6.13 (0.38)	0.13 (0.13)	2.25 (0.00)
		E	10.00 (2.00)	3.75 (1.75)	1.63 (0.63)	2.50 (0.00)
	Water stress VE	C	11.67 (0.00)	4.33 (0.00)	0.33 (0.00)	6.00 (0.00)
		VE	10.25 (0.75)	3.75 (0.25)	1.88 (1.88)	3.50 (2.50)
7/1/97	Irrigation	C	9.63 (0.13)	4.25 (1.25)	0.50 (0.50)	2.25 (0.25)
		V	9.25 --	2.75 --	2.00 --	1.25 --
		E	10.00 --	4.50 --	0.00 --	3.00 --
		VE	10.17 (0.83)	2.75 (0.75)	0.83 (0.17)	3.96 (0.29)
	Rainfed	C	10.63 (0.13)	5.75 (0.75)	1.25 (0.75)	2.13 (0.13)
		V	10.50 (0.00)	5.25 (0.50)	1.00 (0.75)	2.63 (0.13)
		E	7.00 --	3.00 --	0.75 --	1.25 --
		VE	11.25 (2.50)	3.88 (2.13)	1.38 (0.88)	3.88 (1.13)
	Water stress V	C	9.50 (0.25)	3.75 (1.00)	0.13 (0.13)	2.63 (0.13)
		V	9.88 (1.63)	3.75 (0.00)	0.13 (0.13)	3.38 (0.88)
	Water stress E	C	8.63 (2.63)	3.25 (1.75)	1.38 (0.88)	0.75 (0.75)
		E	8.00 (1.50)	3.13 (0.38)	0.50 (0.25)	2.25 (0.50)
	Water stress VE	C	11.00 --	6.50 --	0.50 --	2.00 --
		VE	6.50 --	1.25 --	0.00 --	3.25 --

(Continued on page 159)

ed at the vegetative stage the previous year, although numbers of daughter tillers were similar ($p > 0.25$) among water levels.

Axillary bud activation and outgrowth in *S. tenuis* were not affected by any treatment ($p > 0.25$) after defoliation at the vegetative stage in July 1996 (Table 4). Numbers of total nodes in this species, however, were on average lower ($p < 0.01$) under water stress than under better moisture levels. Reduction of leaf production (equal to number of TN) is a common response in plants of perennial grasses exposed to water stress (Brown 1995, Busso and Richards 1995, Volaire 1995).

At the end of the 1996 growing cycle, total bud number was similar ($p > 0.15$) among treatments. However, numbers of dormant or dead buds in *S. tenuis* were greater ($p < 0.05$) on plants defoliated twice under rainfed or irrigated conditions, and on those defoliated once or twice under water stress, than on undefoliated controls (Table 4). Defoliation under water stress also lowered metabolic activity on buds of *A. spicatum* (Busso et al. 1989). The observed response resulted in a lower number of daughter tillers on plants defoliated twice than on undefoliated controls under all water levels, although differences were not significant ($p > 0.25$). At the same time, numbers of dormant or dead buds were greater ($p < 0.05$) when defoliated and undefoliated plants of *S. tenuis* were exposed to water stress at the vegetative or vegetative+early internode elongation than at the early internode elongation stage. This indicates that early (i.e., at V) or prolonged (i.e., at VE) water stress can be more detrimental on the degree of bud metabolic activity than late water stress (i.e., at E) in *S. tenuis*.

By early September 1995, responses in *S. clarazii* differed among water levels depending on whether plants were defoliated or not. Numbers of daughter tillers were 50% greater ($p < 0.05$) under rainfed than under irrigated or water stress conditions on undefoliated plants of this species (Table 5). When plants were defoliated, however, numbers of daughter tillers were on average 50% greater ($p < 0.01$) in the water stress than in the other water availability treatments. In comparison to values obtained before defoliation at the vegetative stage, subsequent responses can be explained, at least partially, through a greater bud activation and outgrowth on undefoliated, rainfed plants; a greater suppression of bud activation on defoliated, irrigated plants, and a greater bud outgrowth on plants defoliated at the vegetative stage under water stress.

Table 4 Continued.

Dates	Treatments		TN	DT	MAB	DDB
	Water levels	Defoliation				
12/3/97	Irrigation	C	7.00 –	3.33 –	0.00 –	1.00 –
		V	9.00 –	4.00 –	0.50 –	2.00 –
		E	0 –	0 –	0 –	0 –
		VE	5.00 –	3.00 –	0.00 –	0.00 –
	Rainfed	C	7.25 –	3.00 –	0.00 –	2.75 –
		V	6.50 (0.00)	3.50 (0.00)	0.00 (0.00)	1.13 (0.38)
		E	6.50 –	3.00 –	0.25 –	0.75 –
		VE	10.13 (3.88)	5.63 (2.38)	0.50 (0.50)	0.63 (0.63)
	Water stress V	C	6.88 (0.63)	3.13 (1.13)	0.25 (0.25)	1.75 (0.75)
		V	6.75 –	3.75 –	0.00 –	0.75 –
	Water stress E	C	6.50 (0.75)	3.50 (0.00)	0.25 (0.25)	0.63 (0.38)
		E	6.88 (0.13)	3.63 (0.38)	0.00 (0.00)	0.75 (0.25)
	Water stress VE	C	9.50 –	6.00 –	0.00 –	1.00 –
		VE	7.63 (1.63)	3.00 (2.00)	0.13 (0.13)	3.00 (1.00)

With a few exceptions, all studied variables showed similar ($p > 0.10$) values in all defoliation and water level treatments at each sampling date in 1996 on parent tillers of *S. clarazii* (Table 5). Early in 1996, variations observed on numbers of daughter tillers in response to treatments were associated with variations on numbers of dormant or dead buds. This means that treatment effects on investigated variables were observed earlier in *S. clarazii*

than in *S. tenuis* after the first year of treatment application. Numbers of daughter tillers were greater ($p < 0.05$) and those of dormant or dead buds were lower ($p < 0.05$) on *S. clarazii* plants defoliated twice than on those defoliated at the vegetative stage or nondefoliated during the previous year under rainfed conditions (Table 5). Increases in defoliation frequency have stimulated tillering through changes in light quality and/or quantity reaching stem

bases in perennial grasses (Deregibus et al. 1983, Casal et al. 1985, Gautier et al. 1999). However, numbers of dormant or dead buds were greater ($p < 0.05$) on plants defoliated twice than on undefoliated controls under irrigation in *S. clarazii* (Table 5); this contributed to a lower number of daughter tillers, although differences were not significant ($p > 0.10$). At the same time, numbers of daughter tillers were greater ($p < 0.05$) on plants defoliated at the vegetative than at the early internode elongation or vegetative + early internode elongation stage in *S. clarazii* under irrigated conditions. Defoliated plants of this species, however, had a lower ($p < 0.05$) number of daughter tillers than undefoliated controls under water stress; this was associated with a greater number of dormant or dead buds, although differences were not significant ($p > 0.12$). Late or frequent defoliations have reduced daughter tiller production on several perennial grass species exposed to irrigated or water stress conditions (Busso et al. 1989, Simoes and Baruch 1991). This response has been associated with direct effects of defoliation in suppressing bud activation or to a low remaining photosynthetic leaf surface area after defoliation

Fig. 3. Number of total nodes (TN), buds which originated daughter tillers (DT), and metabolically active (MAB) and dead and dormant (DDB) buds on average for all parent tillers of *S. clarazii* (Sc), *S. gynerioides* (Sg), and *S. tenuis* (St) observed at each date during the study period. Each symbol is an average of $n=29-112$. Vertical bars represent one S.E.M.

Table 5. Number of total nodes (TN), buds which originated daughter tillers (DT), and metabolically active (MAB) and dead and dormant (DDB) buds on parent tillers of *S. clarazii* at the different treatments in 1995, 1996 and early 1997. I: Irrigation, R: Rainfed, WS: Water stress, C: Undeveloped controls, and defoliation at the vegetative (V), internode elongation (E) or both phenological stages (VE). Each value is the mean (+/-SE) of n=2.

Dates	Treatments		TN	DT	MAB	DDB	
	Water levels	Defoliation					
------(number)-----							
23/5/95	Irrigation	C	7.25 (0.25)	2.50 (0.00)	2.00 (0.50)	0.50 (0.50)	
		V	7.00 (0.50)	1.25 (0.25)	2.75 (1.75)	0.00 (0.00)	
		VE	8.50 (0.00)	2.50 (0.00)	2.50 (0.00)	0.00 (0.00)	
	Rainfed	C	8.00 (0.00)	2.00 (0.00)	1.50 (0.00)	1.00 (0.00)	
		V	7.25 (0.75)	3.00 (1.50)	1.75 (0.25)	0.25 (0.25)	
		VE	6.25 (1.75)	2.25 (0.75)	1.75 (0.25)	0.25 (0.25)	
	Water stress V	C	7.25 (0.75)	2.00 (1.00)	1.50 (0.50)	0.25 (0.25)	
		V	8.50 (0.50)	3.25 (0.25)	2.75 (0.25)	0.00 (0.00)	
	Water stress VE	C	6.25 (0.25)	2.25 (1.25)	2.25 (0.75)	0.25 (0.25)	
		VE	7.50 (1.50)	4.00 (2.00)	1.00 (0.00)	0.50 (0.50)	
7/9/95	Irrigation	C	9.25 (1.00)	2.75 (0.25)	2.38 (0.13)	0.83 (0.13)	
		V	7.67 (0.33)	1.25 (0.75)	3.08 (0.58)	1.00 (1.00)	
		VE	7.63 (0.13)	1.63 (0.38)	3.00 (0.25)	0.75 (0.25)	
	Rainfed	C	8.50 (0.00)	4.50 (0.00)	2.50 (0.00)	0.00 (0.00)	
		V	7.88(1.38)	2.13 (0.13)	2.25 (0.50)	0.50 (0.00)	
		VE	7.13 (0.13)	2.13 (1.13)	2.75 (0.25)	0.38 (0.13)	
	Water stress V	C	7.25 (0.25)	2.13 (0.38)	2.00 (0.25)	0.88 (0.13)	
		V	8.75 (1.00)	4.25 (0.50)	1.38 (0.13)	0.50 (0.50)	
	Water stress VE	C	6.83 (0.17)	1.79 (0.54)	2.46 (0.79)	0.33 (0.33)	
		VE	8.63 (0.63)	4.38 (0.38)	1.25 (0.25)	0.75 (0.75)	
	27/9/95	Irrigation	C	9.25 (1.50)	3.75 (0.50)	2.50 (1.50)	0.50 (0.25)
			E	9.42 (1.92)	3.04 (0.71)	3.33 (1.33)	1.25 (0.75)
			VE	8.13 (0.38)	1.88 (0.13)	3.50 (0.25)	0.25 (0.00)
		Rainfed	C	11.25 (1.75)	3.42 (0.08)	2.71 (0.96)	1.88 (0.13)
E			8.21 (0.46)	1.88 (0.13)	3.46 (0.21)	0.29 (0.04)	
VE			8.63 (0.13)	2.88 (1.13)	2.88 (1.38)	0.38 (0.13)	
Water stress E		C	9.04 (0.29)	4.17 (0.17)	1.54 (0.21)	0.63 (0.38)	
		E	10.38 (0.38)	3.13 (0.38)	2.63 (0.38)	1.38 (0.38)	
Water stress VE		C	9.25 (0.75)	4.63 (0.88)	1.88 (0.38)	0.50 (0.50)	
		VE	9.25 (0.50)	3.75 (1.00)	3.00 (1.50)	0.75 (0.50)	
14/12/95	Irrigation	C	7.38 (2.13)	2.50 (0.25)	0.63 (0.38)	1.25 (1.00)	
		E	9.38 (0.38)	4.38 (0.63)	0.25 (0.25)	1.13 (0.13)	
		VE	8.63 (0.13)	1.75 (0.25)	2.13 (0.88)	2.50 (0.50)	
	Rainfed	C	9.25 (0.75)	3.88 (0.13)	0.63 (0.38)	1.92 (0.58)	
		E	8.75 (1.75)	3.13 (0.63)	2.25 (0.75)	0.88 (0.13)	
		VE	8.50 (0.75)	3.00 (1.00)	0.75 (0.75)	2.38 (0.88)	
	Water stress E	C	8.00 (0.25)	4.38 (1.38)	0.25 (0.00)	0.88 (0.63)	
		E	10.25 (1.50)	3.88 (0.63)	1.63 (0.88)	2.13 (1.13)	
	Water stress VE	C	8.88 (1.13)	4.25 (0.75)	0.38 (0.13)	2.00 (0.00)	
		VE	9.88 (0.13)	4.88 (0.63)	0.25 (0.00)	2.38 (0.63)	
25/4/96	Irrigation	C	7.25 (0.25)	1.75 (0.25)	2.50 (0.50)	0.25 (0.25)	
		V	7.50 (0.00)	2.25 (0.25)	2.75 (0.75)	1.25 (0.75)	
		E	5.75 (1.25)	0.50 (0.50)	2.75 (0.25)	0.50 (0.00)	
		VE	8.00 (0.00)	0.75 (0.25)	2.75 (1.25)	2.00 (1.00)	
	Rainfed	C	8.75 (2.25)	1.00 (0.50)	2.00 (0.00)	2.75 (0.75)	
		V	11.25 (1.75)	1.25 (0.75)	5.25 (2.75)	2.50 (0.50)	
		E	8.50 (0.50)	2.00 (0.00)	2.25 (0.25)	1.50 (0.50)	
		VE	8.75 (0.25)	2.75 (0.75)	4.25 (0.75)	0.50 (0.00)	
	Water stress V	C	7.50 (0.00)	3.50 (0.50)	1.50 (0.00)	0.25 (0.25)	
		V	7.75 (0.25)	1.75 (0.25)	4.00 (1.00)	0.50 (0.50)	
	Water stress E	C	8.50 (1.00)	1.50 (0.50)	4.00 (1.00)	1.25 (0.75)	
		E	8.25 (0.25)	1.25 (0.25)	3.25 (0.25)	2.50 (0.50)	
	Water stress VE	C	8.75 (0.75)	2.00 (1.00)	2.75 (0.25)	2.00 (0.00)	
		VE	9.00 (1.00)	1.25 (0.25)	2.25 (0.75)	2.75 (0.75)	
12/6/96	Irrigation	C	9.13 (0.38)	2.00 (0.75)	4.00 (0.75)	0.25 (0.25)	
		V	9.25 (1.25)	2.50 (0.50)	2.38 (0.13)	1.38 (1.13)	
		VE	9.00 (1.50)	2.13 (0.63)	3.50 (0.25)	0.63 (0.13)	

(Continued on page 161)

which is insufficient to maintain a high degree of bud metabolic activity under different levels of soil water availability (Busso et al. 1989). As mentioned previously, the opposite response was observed under rainfed conditions. Photosynthetically active radiation at crown level of the desirable grasses under irrigation was 70% of that under rainfed conditions (Flemmer 2000). Greater shading effects by *S. gynerioides* under higher soil water availability levels, and greater leaf water potentials in the rainfed than in the water stress treatment (Tables 1 and 2), may help explain the greater number of daughter tillers and the lower number of dormant or dead buds on defoliated than on undefoliated plants under rainfed than under irrigated or water stress conditions.

At the beginning of 1996, defoliated and undefoliated plants of *S. clarazii* had more daughter tillers ($p < 0.05$) and fewer dormant or dead buds ($p < 0.01$) after exposure to water stress at the vegetative than at the early internode elongation or vegetative + internode elongation stage. Contrary to that found in *S. tenuis*, water stress had a less detrimental impact on the degree of bud metabolic activity and subsequent outgrowth in *S. clarazii* when it occurred early (i.e., at V) than when it was present late (i.e., at E), or was prolonged (i.e., VE) during the growing season. Jamieson et al. (1995) reported a lower leaf senescence associated with a higher light interception on plants exposed to early rather than late water stress.

In October 1996, numbers of total nodes were lower ($p < 0.05$) on plants of *S. clarazii* defoliated at either the early internode elongation stage under water stress, or at the vegetative and vegetative+early internode elongation stages under irrigation than on undefoliated controls (Table 5). At the same time, however, plants of this species showed a greater ($p < 0.01$) number of total nodes under water stress when they were defoliated at the vegetative + early internode elongation stage than when they remained undefoliated. Reduction of transpiratory leaf surface areas after defoliation may have reduced detrimental effects of water stress on plant growth in comparison to undefoliated controls (Mohammad et al. 1982, Simoes and Baruch 1991).

At the end of the 1996 growing cycle, the greatest ($p < 0.05$) number of total nodes in *S. clarazii* was observed on defoliated and undefoliated plants which had been exposed to water stress at the vegetative+early internode elongation stage (Table 5). The amount of rainfall from the

Table 5. Continued.

Dates	Treatments		TN	DT	MAB	DDB	
	Water levels	Defoliation					
------(number)-----							
30/7/96	Rainfed	C	9.00 (1.00)	2.13 (0.63)	3.50 (0.50)	1.50 (0.00)	
		V	9.63 (0.38)	2.75 (0.50)	3.50 (0.25)	1.00 (0.00)	
		VE	9.50 (0.25)	2.63 (0.38)	2.88 (0.88)	1.63 (0.13)	
	Water stress V	C	9.13 (0.63)	3.75 (0.50)	2.38 (0.38)	1.13 (0.88)	
		V	8.75 (0.00)	2.75 (1.00)	1.75 (1.25)	1.38 (1.38)	
	Water stress VE	C	9.38 (0.13)	3.50 (0.25)	3.38 (0.13)	0.63 (0.38)	
		VE	9.75 (0.00)	2.63 (0.13)	3.25 (0.25)	2.63 (0.13)	
	Irrigation	C	10.38 (1.38)	4.25 (0.25)	2.13 (0.13)	0.13 (0.13)	
		V	9.13 (0.63)	2.88 (0.13)	2.75 (0.50)	1.38 (0.88)	
		VE	10.00 (0.25)	3.75 (1.00)	1.13 (0.88)	1.63 (1.38)	
	Rainfed	C	8.88 (0.63)	1.50 (0.25)	2.13 (0.63)	2.38 (0.13)	
		V	9.88 (0.63)	3.75 (1.00)	3.38 (0.13)	1.13 (1.13)	
		VE	9.50 (0.50)	3.75 (0.00)	1.38 (1.13)	1.63 (0.38)	
	Water stress V	C	9.00 (0.50)	3.25 (0.50)	2.38 (0.88)	1.13 (0.88)	
		V	9.00 (0.75)	3.00 (0.00)	2.50 (0.50)	1.88 (0.63)	
	Water stress VE	C	9.13 (1.63)	2.88 (0.13)	2.38 (0.13)	1.50 (1.25)	
		VE	9.25 (1.00)	3.00 (0.75)	2.63 (0.38)	1.50 (0.50)	
	21/9/96	Irrigation	C	9.50 (0.00)	5.13 (1.13)	1.13 (0.38)	0.88 (0.88)
E			10.25 (1.00)	3.63 (0.38)	1.25 (0.00)	2.00 (0.25)	
VE			9.75 (1.00)	4.00 (1.00)	0.88 (0.13)	2.13 (0.13)	
Rainfed		C	8.38 (0.88)	2.25 (0.50)	1.63 (1.13)	2.00 (1.50)	
		E	8.88 (1.63)	3.25 (0.50)	0.25 (0.25)	2.25 (0.50)	
		VE	10.75 (0.50)	3.00 (0.75)	0.63 (0.38)	4.25 (1.75)	
30/10/96	Water stress E	C	11.00 (1.25)	4.00 (1.00)	1.25 (1.00)	1.38 (0.38)	
		E	8.25 (0.50)	3.00 (0.25)	1.38 (0.63)	1.13 (0.38)	
	Water stress VE	C	11.88 (1.38)	4.13 (0.38)	3.38 (1.13)	2.00 (0.75)	
		VE	9.25 (1.00)	2.00 (0.00)	2.38 (0.13)	2.50 (0.75)	
	Irrigation	C	10.50 (1.25)	3.50 (0.00)	0.38 (0.13)	1.75 (0.25)	
		V	7.75 (0.25)	3.63 (0.63)	0.75 (0.00)	0.38 (0.13)	
		E	—	—	—	—	
		VE	8.00 (0.50)	3.50 (0.25)	0.38 (0.13)	0.88 (0.38)	
	Rainfed	C	8.75 (0.50)	3.50 (0.50)	0.13 (0.13)	1.75 (0.25)	
		V	8.50 (0.50)	2.25 (0.00)	0.38 (0.38)	3.13 (0.38)	
		E	9.13 (0.38)	3.88 (1.88)	1.88 (0.88)	1.00 (0.25)	
		VE	9.38 (0.13)	3.25 (0.00)	0.13 (0.13)	3.25 (0.50)	
	Water stress V	C	8.50 (0.25)	4.13 (0.88)	0.13 (0.13)	1.50 (0.75)	
		V	9.38 (0.63)	4.00 (0.75)	0.63 (0.38)	1.75 (0.25)	
	Water stress E	C	10.75 (0.25)	4.25 (0.25)	0.75 (0.75)	2.25 (2.00)	
		E	8.88 (0.13)	3.50 (0.50)	0.63 (0.13)	2.38 (0.38)	
	7/1/97	Water stress VE	C	8.38 (0.38)	2.63 (0.13)	1.38 (0.38)	1.88 (0.88)
			VE	12.63 (0.13)	3.75 (0.50)	2.13 (1.38)	4.25 (0.50)
Irrigation		C	7.63 (0.88)	2.88 (1.63)	0.13 (0.13)	1.50 (0.25)	
		V	7.63 (1.38)	3.13 (0.88)	0.25 (0.00)	0.63 (0.38)	
		E	6.75 (0.50)	1.75 (0.25)	0.88 (0.38)	1.00 (0.25)	
		VE	7.38 (1.38)	2.38 (0.88)	0.25 (0.25)	1.38 (0.63)	
Rainfed		C	7.13 (1.38)	2.38 (1.13)	0.38 (0.13)	1.13 (0.38)	
		V	8.00 (0.50)	2.38 (0.13)	0.63 (0.13)	1.00 (0.75)	
		E	10.13 (0.63)	3.88 (1.38)	0.88 (0.63)	2.25 (0.75)	
		VE	8.88 (0.88)	3.00 (1.00)	0.13 (0.13)	2.63 (0.13)	
Water stress V		C	7.63 (0.13)	2.63 (0.38)	0.25 (0.25)	0.88 (0.13)	
		V	7.00 (0.50)	2.50 (0.25)	0.13 (0.13)	0.63 (0.13)	
Water stress E		C	8.13 (0.13)	3.75 (0.25)	0.25 (0.25)	0.75 (0.25)	
		E	7.50 (0.75)	2.63 (1.63)	0.88 (0.63)	1.88 (1.13)	
Water stress VE		C	10.88 (1.13)	5.13 (0.63)	0.50 (0.50)	3.13 (0.13)	
		VE	11.38 (1.38)	3.75 (1.00)	1.75 (0.25)	3.63 (0.63)	
12/3/97		Irrigation	C	6.13 (0.63)	1.75 (0.25)	0.00 (0.00)	1.75 (0.25)
			V	7.13 (0.38)	2.50 (0.00)	0.50 (0.25)	1.88 (0.63)
	E		7.75 —	1.75 —	0.25 —	2.00 —	
	VE		7.63 (0.63)	1.63 (0.63)	0.50 (0.00)	2.63 (0.13)	

(Continued on page 162)

end of the water stress treatment at the vegetative + early internode elongation stage to sampling at the end of the growing cycle in 1996 was high (221 mm). This and total nonstructural carbohydrates which may have accumulated during the long water stress period (i.e., VE) may have resulted in such a high number of total nodes at the end of the second year of successive treatments. Numbers of dormant or dead buds, however, were greater ($p < 0.01$) on plants exposed to water stress at the vegetative + early internode elongation than at the vegetative or early internode elongation stage. Similar to that found in other perennial grasses (Busso et al. 1989), prolonged water stress stimulated suppression of bud activation in *S. clarazii*.

At the beginning of 1997, after 2 years of successive treatments, numbers of total nodes and bud metabolic activity and outgrowth were similar ($p > 0.25$) between defoliation treatments or water levels on parent tillers of *S. clarazii* and *S. tenuis* (Tables 4 and 5). A similar response was reported on *S. tenuis* and *P. napostaense*: these species did not modify their potential regrowth capacity after rainfed plants were defoliated at different phenological stages during 2 consecutive years (Becker et al. 1997). The degree of metabolic activity and outgrowth of axillary buds has also been similar on perennial grass plants coming from sites with very different grazing histories (Hendrickson and Briske 1997). Potential regrowth capacity of *S. tenuis*, *P. napostaense* and *S. gynerioides*, however, is reduced by fire (Peláez et al. 1997, Peláez 2000).

Numbers of total nodes, daughter tillers, and metabolically active buds tended to be similar or greater on the desirable than on the undesirable species when averaging values for all parent tillers within each species and sampling date (Fig. 3). Numbers of daughter tillers tended to be greater in *S. tenuis* than in *S. clarazii* during 1996. On the other hand, *S. gynerioides* appeared to have a greater number of dormant or dead buds than *S. clarazii* in 1995, and than both desirable species in 1996 (Fig. 3). Early in 1997, greatest numbers of metabolically active buds and daughter tillers were observed on parent tillers of *S. clarazii* and *S. tenuis*, respectively. Thus, *S. clarazii* showed a greater potential regrowth capacity than *S. tenuis*, whereas *S. tenuis* was able to activate a greater bud number and produce more new tillers than *S. clarazii* after 2 years of treatment. Recent studies have indicated a greater competitive ability and tolerance to defoli-

Table 5. Continued.

Treatments						
Dates	Water levels	Defoliation	TN	DT	MAB	DDB
			----- (number) -----			
	Rainfed	C	7.50 (0.50)	1.75 (0.25)	0.50 (0.25)	1.75 (0.25)
		V	8.88 (1.63)	2.38 (1.13)	1.25 (1.25)	2.25 (1.75)
		E	6.63 (0.13)	1.38 (0.38)	0.63 (0.63)	1.63 (0.13)
		VE	8.21 (1.46)	1.38 (0.63)	2.29 (1.04)	2.13 (0.13)
	Water stress V	C	7.63 (0.88)	1.25 (0.25)	2.25 (1.25)	1.63 (1.38)
		V	8.00 (0.25)	0.75 (0.50)	0.50 (0.00)	3.13 (0.13)
	Water stress E	C	6.88 (1.13)	1.38 (0.38)	0.75 (0.50)	1.13 (0.88)
		E	7.13 (0.13)	0.88 (0.38)	0.88 (0.13)	2.50 (0.00)
	Water stress VE	C	9.13 (1.38)	2.38 (1.13)	0.88 (0.38)	3.38 (0.13)
		VE	11.50 (4.25)	2.75 (1.50)	1.00 (0.50)	4.63 (2.38)

ation in *S. clarazii* than in *S. tenuis* (Saint Pierre et al. 2000a, 2000b). Our results show that plant traits which make *S. clarazii* a superior competitor and more tolerant to defoliation are not linked to producing more daughter tillers.

As the growing season progressed in 1995 and 1996, numbers of metabolically active buds decreased and those of dormant or dead buds increased on parent tillers of the 3 species (Fig. 3). Bud senescence or necrosis may increase suppression of bud activation towards the end of a growing season in perennial grasses (Mitchell 1953). With the advancement of the growing season, however, signs of bud senescence were minor with most buds looking viable in *A. desertorum* and *A. spicatum* (Mueller and Richards 1986). Low percentages of metabolically active buds at the end of 1996 were confirmed early in 1997 indicating a decreased potential regrowth capacity in all 3 species in comparison to previous years, probably because of cumulative treatment effects.

During 1995 in all 3 species and *S. clarazii* and *S. tenuis* in 1996, approximately 50-60% of the entire bud pool (DT+MAB+DDB) was able to grow out and produce new tillers. However, less than 41% of all buds grew out into daughter tillers on parent tillers of *S. gynerioides* in 1996. Percentage of buds which grew out and produced tillers from the entire bud pool is greater than that reported for other perennial grasses of semiarid regions (Mueller and Richards 1986, Busso et al. 1989, Hendrickson and Briske 1997).

Despite some transitory effects of defoliation on axillary bud dynamics, rapid photosynthetic canopy reestablishment after defoliation under all water levels was not limited by availability and/or regrowth capacity of axillary buds in *S. clarazii* and *S. tenuis*. These results do not support hypothesis 2. The only exception, and in

agreement with this hypothesis, was observed after defoliation at the vegetative stage in 1995 on parent tillers of *S. clarazii*: these tillers had a greater number of daughter tillers after being defoliated than remaining undefoliated under water stress. At the same time, however, numbers of daughter tillers were lower on defoliated than on undefoliated plants of this species when exposed to rainfed or irrigated conditions. Lack of consistent responses to defoliation have been attributed, at least partially, to the complexity of physiological mechanisms (i.e., see Murphy and Briske 1992) and the great number of potentially intervening factors (i.e., abiotic variables, phenological stage of development, and frequency and intensity of defoliation) which can regulate bud metabolic activity and subsequent regrowth in perennial grasses (Briske and Richards 1995). In our study, responses were specific to the species, imposed treatments, sampling times, and cumulative treatment effects. This makes prediction of plant responses under natural conditions difficult, a conclusion similar to that reported by Haferkamp and Karl (1999) or Allen et al. (1989) after studying the effects of defoliation on plant growth of an annual brome grass or the degree of colonization of perennial grass roots by arbuscular-vesicular mycorrhiza, respectively.

Literature Cited

- Allen, M.F., J.H. Richards and C.A. Busso. 1989. Influence of clipping and soil water status on vesicular-arbuscular mycorrhizae of two semi-arid tussock grasses. *Biol. Fert. Soils* 8: 285-289.
- Anderson, V.J. and D.D. Briske. 1995. Herbivore-induced species replacement in grasslands: Is it driven by herbivory tolerance or avoidance?. *Ecol. Appl.* 5: 1014-1024.

- Becker, G.F., C.A. Busso, and T. Montani. 1997. Effects of defoliating *Stipa tenuis* and *Piptochaetium napostaense* at different phenological stages: axillary bud viability and growth. *J. Arid Environ.* 35: 233-250.
- Briske, D.D. 1991. Developmental morphology and physiology of grasses. In: R.K. Heitschmidt and J.W. Stuth (eds) *Grazing Management: an ecological perspective*. pp.85-108. Timber Press, Portland, Ore.
- Briske, D.D. and V.J. Anderson. 1990. Competitive ability of the bunchgrass *Schizachyrium scoparium* as affected by grazing history and defoliation. *Vegetatio* 103:41-49.
- Briske, D.D. and J.R. Hendrickson. 1998. Does selective defoliation mediate competitive interactions in a semiarid savanna? A demographic evaluation. *J. Veg. Sci.* 9: 611-622.
- Briske, D.D. and J.H. Richards. 1995. Plant responses to defoliation: a physiological, morphological and demographic evaluation. In: D.J. Bedunah and R.E. Sosebee (eds) *Wildland Plants: Physiological Ecology and Developmental Morphology*. pp. 635-710. Soc. for Range Manage., Denver, Colo.
- Brown, R.W. 1995. The water relations of range plants: adaptations to water deficits. In: D.J. Bedunah and R.E. Sosebee (eds) *Wildland Plants: Physiological Ecology and Developmental Morphology*. pp. 291-413. Soc. for Range Manage., Denver, Colo.
- Bullock, J.M., B. Clear Hill, and J. Silvertown. 1994. Tiller dynamics of two grasses - responses to grazing, density and weather. *J. Ecol.* 82: 331-340.
- Busso, C.A. 1997. Towards an increased and sustainable production in semiarid rangelands of Central Argentina: Two decades of research. *J. Arid Environ.* 36: 197-210.
- Busso, C.A. and J.H. Richards. 1993. Leaf extension rate in two tussock grasses: effects of water stress and clipping. *Acta Oecol.* 14: 3-15.
- Busso, C.A. and J.H. Richards. 1995. Drought and clipping effects on tiller demography and growth of two bunch grasses in Utah. *J. Arid Environ.* 29: 239-251.
- Busso, C.A., R.M. Bóo, and D.V. Peláez. 1993. Fire effects on bud viability and growth of *Stipa tenuis* in semiarid Argentina. *Ann. Bot.* 71:377-381.
- Busso, C.A., R.J. Mueller, and J.H. Richards. 1989. Effects of drought and defoliation on bud viability in two caespitose grasses. *Ann. Bot.* 63: 477-485.
- Busso, C.A., J.H. Richards, and N.J. Chatterton. 1990. Nonstructural carbohydrates and spring regrowth of two cool-season grasses: Interaction of drought and clipping. *J. Range Manage.* 43: 336-343.
- Cano, E. 1988. Pastizales Naturales de La Pampa. Descripción de las especies más importantes. Tomo I. Convenio AACREA-Provincia de La Pampa, Capital Federal, Buenos Aires.
- Casal, J.J., V.A. Deregibus, and R.A. Sánchez. 1985. Variation in tiller dynamics and morphology in *Lolium multiflorum* Lam. vegetative and reproductive plants as affect-

- ed by differences in red far-red irradiation. *Ann. Bot.* 56: 553–559.
- Casal, J.J., R.A. Sánchez, and V.A. Deregibus. 1986.** The effect of plant density on tillering: the involvement of R/FR ratio and the proportion of radiation intercepted per plant. *Environ. Exp. Bot.* 26: 365–371.
- Deregibus, V.A. and M.J. Trlica. 1990.** Influence of defoliation upon tiller structure and demography in two warm-season grasses. *Acta Oecol.* 11: 693–699.
- Deregibus, V.A., R.A. Sánchez, and J.J. Casal. 1983.** Effects of light quality on tiller production in *Lolium* spp. *Plant Physiol.* 72: 900–902.
- Devkota, N.R., P.D. Kemp, and J. Hodgson. 1997.** Screening pasture species for shade tolerance. *Proc. Agron. Soc. of New Zealand* 27:119–128.
- Distel, R.A. and R.M. Bóo. 1996.** Vegetation States and Transitions in Temperate Semiarid Rangelands of Argentina. In: N.E. West (ed) *Rangelands in a Sustainable Biosphere*, Proc. Symp. Vth Internat. Rangeland Congr., 23–28 July. pp. 117–118. Salt Lake City, Utah
- Distel, R.A. and O.A. Fernández. 1986.** Productivity of *Stipa tenuis* Phil. and *Piptochaetium napostaense* (Speg.) Hack in semi-arid Argentina. *J. Arid Environ.* 11: 93–96.
- Flemmer, A.C. 2000.** Influencia simultánea del estrés hídrico y la defoliación en distintos momentos del desarrollo de *Stipa clarazii* y *Stipa tenuis* en competencia con *Stipa gynerioides*. MSc Thesis, Departamento de Agronomía, Universidad Nacional del Sur, Bahía Blanca, Argentina.
- Fernández, O.A. and C.A. Busso. 1999.** Arid and semi-arid rangelands: two thirds of Argentina. In: O. Arnalds and S. Archer (eds) *Case Studies of Rangeland Desertification*, Proc. Internat. Workshop. Agr. Res. Institute, 16–19 September 1997. pp. 41–60. Reykjavik, Iceland.
- Font Quer, P. 1982.** Diccionario de Botánica. Labor S.A., Barcelona.
- Fulkerson, W.J. and K. Slack. 1995.** Leaf number as a criterion for determining defoliation time for *Lolium perenne*: 2. Effect of defoliation frequency and height. *Grass Forage Sci.* 50:16–20.
- Gautier, H., C. Varlet-Grancher, and L. Hazard. 1999.** Tillering responses to the light environment and defoliation in populations of perennial ryegrass (*Lolium perenne* L.) selected for contrasting leaf length. *Ann. Bot.* 83:423–429.
- Giorgetti, H.D., Z. Manuel, O.A. Montenegro, G.D. Rodríguez, and C.A. Busso. 2000.** Phenology of some herbaceous and woody species in central, semiarid Argentina. *Phyton* 69:91–108.
- Haferkamp, M.R. and M.G. Karl. 1999.** Clipping effects on growth dynamics of Japanese brome. *J. Range Manage.* 52:339–345.
- Hendrickson, J.R. and D.D. Briske. 1997.** Axillary bud banks of two semiarid perennial grasses: occurrence, longevity, and contribution to population persistence. *Oecologia* 110:584–591.
- Jamieson, P.D., R.J. Martin, GS Francis, and D.R. Wilson. 1995.** Drought effects on biomass production and radiation-use efficiency in barley. *Field Crops Res.* 43:77–86.
- Jewis, O.R. 1972.** Tillering in grasses - its significance and control. *J. British Grass. Soc.* 27: 65–82.
- McNaughton, S.J. 1992.** Laboratory-simulated grazing: interactive effects of defoliation and canopy closure on Serengeti grasses. *Ecol.* 73:170–182.
- Mitchell, K.J. 1953.** Influence of light and temperature on the growth of ryegrass (*Lolium* sp.) II. The control of lateral bud development. *Physiol. Plant.* 6: 425–43.
- Mohammad, N., D.D. Dwyer, and F.E. Busby. 1982.** Responses of crested wheatgrass and Russian wildrye to water stress and defoliation. *J. Range Manage.* 35:227–320.
- Moretto, A.S. and R.A. Distel. 1997.** Competitive interactions between palatable and unpalatable grasses native to a temperate semi-arid grassland of Argentina. *Plant Ecol.* 130:155–161.
- Moretto, A.S. and R.A. Distel. 1999.** Effects of selective defoliation on the competitive interaction between palatable and unpalatable grasses native to a temperate semi-arid grassland of Argentina. *J. Arid Environ.* 42:167–175.
- Mueggler, W.F. 1972.** Influence of competition on the response of bluebunch wheatgrass to clipping. *J. Range Manage.* 25: 88–92.
- Mueller, R.J. and J.H. Richards. 1986.** Morphological analysis of tillering in *Agropyron spicatum* and *Agropyron desertorum*. *Ann. Bot.* 58:911–921.
- Murphy, J.S. and D.D. Briske. 1992.** Regulation of tillering by apical dominance: Chronology, interpretive value, and current perspectives. *J. Range Manage.* 45:419–429.
- Olson, B.E. and J.H. Richards. 1988.** Tussock regrowth after grazing: intercalary meristem and axillary bud activity of tillers of *Agropyron desertorum*. *Oikos* 51:374–382.
- Oosthuizen, I.B. and H.A. Snyman. 1999.** The influence of water stress on the growth reserves of *Themeda triandra* Forssk. in the semi-arid grasslands of South Africa. In: D. Eldridge and D. Freudenberger (eds) *People and Rangelands Building the Future*, Proc. Symp. VIth Internatio. Rangeland Congress, 19–23 July. pp. 209. Townsville, Australia.
- Peláez, D.V. 2000.** Respuesta de gramíneas perennes nativas del Caldenal a distintas intensidades de fuego. PhD Thesis, Departamento de Agronomía, Universidad Nacional del Sur, Bahía Blanca, Argentina.
- Peláez, D.V., R.M. Bóo, O.R. Elía, and M.D. Mayor. 1997.** Effect of fire intensity on bud viability of three grass species native to central semi-arid Argentina. *J. Arid Environ.* 37: 309–317.
- Saint Pierre, C., C.A. Busso, O.A. Montenegro, G.D. Rodríguez, H.D. Giorgetti, and T. Montani. 2000a.** Producción de materia seca en especies de gramíneas perennes nativas del centro de Argentina. XVI Reunión Latinoamericana de Producción Animal, III Congreso Uruguayo de Producción Animal. Montevideo, Uruguay. Available on CD-ROM.
- Saint Pierre, C., C.A. Busso, O.A. Montenegro, G.D. Rodríguez, H.D. Giorgetti, and T. Montani. 2000b.** Demografía y crecimiento en especies de gramíneas nativas del Sur de la Provincia Fitogeográfica del Monte. XVI Reunión Latinoamericana de Producción Animal, III Congreso Uruguayo de Producción Animal. Montevideo, Uruguay. Available on CD-ROM.
- Simoes, M. and Z. Baruch. 1991.** Responses to simulated herbivory and water stress in two tropical C₄ grasses. *Oecologia* 88:173–180.
- Smith, M. 1992.** CROPWAT-A computer program for irrigation planning and management. FAO Irrigation and Drainage Paper No. 46. FAO, Rome.
- Smith, M. 1993.** CLIMWAT for CROPWAT - A climatic database for irrigation planning and management. FAO Irrigation and Drainage Paper No. 49. FAO, Rome.
- Steel, R.G.D. and J.H. Torrie. 1985.** Bio Estadística: principios y procedimientos. McGraw-Hill.
- Turner, N.C. 1987.** The use of the pressure chamber in studies of plant water status. *Proceedings International Conference on Measurements of Soil and Plant Water Status*. pp. 13–24. Logan, Utah.
- Volaire, F. 1995.** Growth, carbohydrate reserves and drought survival strategies of contrasting *Dactylis glomerata* populations in a Mediterranean environment. *J. Appl. Ecol.* 32:56–66.
- Waring, R.H. and B.D. Cleary. 1967.** Plant moisture stress: evaluation by pressure bomb. *Science* 155:1248–1254.
- Williams, K.J., B.J. Wilsey, S.J. McNaughton, and F.F. Banyikwa. 1998.** Temporally variable rainfall does not limit yields of Serengeti grasses. *Oikos* 81:463–470.

Northern dry mixed prairie responses to summer wildlife and drought

CATHERINE ERICHSEN-ARYCHUK, EDWARD W. BORK, AND ARTHUR W. BAILEY

Authors are former Range Management Specialist, Alberta Agriculture, Food and Rural Development, Hanna, Alberta, Canada, T0J 1P0; and Assistant Professor and Professor emeritus, Department of Agricultural, Food & Nutritional Science, University of Alberta, Edmonton, Alberta, Canada, T6G 2P5.

Abstract

In August 1994, wildfire burned 6,500 ha of native Dry Mixed Prairie in southeastern Alberta. The following year, a study was initiated to monitor the recovery of major plant communities. Burning was followed by 3 successive years of drought, reducing total vegetative cover by 10%. Exposed soil increased to a high of 23%, three years after the fire. Litter and grass production were reduced through 1997, with the greatest decline in 1995 when grass production on burned and unburned areas averaged 890 and 1,468 kg ha⁻¹, respectively. Of the major forage species, *Stipa* spp. and *Koeleria macrantha* (Ledeb. J.A. Schultes f.) were affected for a single year and *Agropyron* spp. 2 years by burning. Both *Agropyron* and *Stipa* abundance displayed interactions with topographic position in response to fire. In 1995, *Agropyron* increased on uplands with burning from 90 to 143 kg ha⁻¹, but decreased on lowlands from 383 to 238 kg ha⁻¹, a pattern repeated in 1996. In contrast, *Stipa* declined at both positions, but only for a single year. Where livestock grazing occurred after the fire, forage removal was greater on burned areas. Drought conditions, in combination with summer wildfire, reduced Dry Mixed Prairie range productivity and ground cover for several years and intensified livestock grazing, highlighting the need for changes in rangeland management under these conditions.

Key Words: composition, forage, litter, preference, production, topography

In August 1994, a late summer wildfire burned through approximately 6,500 ha of native northern Dry Mixed Prairie in southeastern Alberta. Although a number of studies have looked at fire effects in the more mesic northern Mixed Prairie and Fescue Grasslands of the Aspen Parkland in western Canada (e.g. Coupland 1973, Bailey and Anderson 1978, Anderson and Bailey 1980, Redmann et al. 1993, Gerling et al. 1995), relatively little is known of the response of Dry Mixed Prairie vegetation to fire in the Canadian Great Plains. In the single documented study of fire within this region (Clarke et al. 1947), fire was examined during the spring and fall under prescribed conditions rather than as wildfire during the late summer dry period. Wildfires, because they tend to occur during the driest part of the year, are likely to cause greater damage within rangeland ecosystems (Wright 1974b).

Authors wish to thank Lorne Cole, Range Management Specialist for Special Areas District, Hanna, Alberta, for his assistance with data collection, and 2 anonymous reviewers for their comments on earlier versions of the manuscript.

Manuscript accepted 8 Jul. 01.

Resumen

En Agosto de 1994, un fuego natural quemó 6,500 ha de Pradera Seca Mixta del sudeste de Alberta. En el año siguiente se inicio un estudio para monitorear la recuperación de las principales comunidades vegetales. La quema fue seguida de tres años consecutivos de sequía reduciendo la cubierta vegetal total en un 10%, y tres años después del fuego, el suelo expuesto se incrementó a un máximo de 23%. El mantillo y la producción de zacates se redujo desde el incendio hasta 1997, registrándose la mayor disminución en 1995, cuando la producción de zacate de áreas quemadas y no quemadas promedio 890 and 1468 kg.ha⁻¹, respectivamente. De las principales especies forrajeras, *Stipa* spp. y *Koeleria macrantha* fueron afectadas por la quema solo un año y *Agropyron* spp. por dos años. La abundancia de *Agropyron* y *Stipa* mostraron interacciones con la posición topográfica en respuesta al fuego. En 1995, en las tierras altas, el *Agropyron* aumento con el fuego de 90 a 143 kg.ha⁻¹, pero disminuyo en las tierras bajas de 383 a 238 kg.ha⁻¹, este patrón se repitió en 1996. En contraste, el *Stipa* disminuyó en ambas posiciones, pero solo un año. Cuando el ganado apacento después del fuego la remoción de forraje fue mayor en las áreas quemadas. Las condiciones de sequía, en combinación con los fuegos no prescritos de verano redujeron la productividad de la Pradera Seca Mixta y la cobertura del suelo por varios años, e intensifican el apacentamiento del ganado, resaltando la necesidad de cambios en el manejo de los pastizales bajo estas condiciones.

Rangeland plant communities of the northern Mixed Prairie are generally thought to be well-adapted to wildfire, as this type of disturbance was an important part of these ecosystems prior to European settlement (Bailey 1978). Wright and Bailey (1982) estimate a natural historical fire frequency of 5 to 10 years in the Northern Great Plains. Lightning and aboriginal people were the probable cause of many fires (Nelson and England 1971).

Bailey and Anderson (1978) found that single prescribed burns in spring or fall had little effect on total herbage production in northern Fescue Prairie. In more water-limited environments, rangeland productivity is typically reduced by fire (Redmann 1978, Engle and Bultsma 1984). Fire removes litter, increasing soil temperatures and moisture loss (De Jong and MacDonald 1975, Facelli and Pickett 1991).

Burning can affect the species composition of northern Great Plains rangelands. Burning Fescue Prairie, particularly in fall, reduced *Festuca hallii* (Vasey) Piper¹ (Anderson and Bailey 1980, Gerling et al. 1995). Coupland (1973) found *Agropyron*

¹Nomenclature follows Moss (1992).

smithii Rydb. and *Koeleria macrantha* (Ledeb.) J.A. Schultes f. declined the year after burning, while *Carex* spp. and *Stipa viridula* Trin. increased. Clarke et al. (1947) found *Stipa-Bouteloua gracilis* (HBK.) Lag. communities to be more tolerant of fire than *Agropyron* communities in southern Alberta.

Grazing management also influences the recovery of burned rangelands because burning may increase subsequent livestock utilization (Daubenmire 1968, Wright 1974b, Willms et al. 1980). Burned and grazed Mixed Prairie pastures recover more slowly than areas protected from grazing (Clarke et al. 1947). Both Hopkins et al. (1948) and Launchbaugh (1964) found similar results in Shortgrass Prairie.

Although several studies have examined fire impacts on Alberta grasslands, most involve prescribed burning during spring or fall, and have been limited to regions with favorable precipitation. As a result, this study was initiated to examine the effects of the 1994 August wildfire on northern Dry Mixed Prairie ground cover, herbage production and species composition over 3 subsequent years. A second component of the study examined utilization by cattle for 2 years after the fire on adjacent burned and unburned rangeland to assess livestock foraging preferences.

Methods

Study Area

The study area is located in the Special Areas administrative district south of Buffalo, Alberta, Canada (50°44' N, 110°38' W), within the Dry Mixed Grass Ecoregion (Strong and Leggat 1992). Average summer temperatures for the region are 16.2°C, and annual precipitation averages 272 mm, with significant moisture deficits during July and August (Strong and Leggat 1992). The landscape of the area is moderately undulating, with soils typically medium-textured, well to moderately well-drained Brown Chernozems (Haploxerolls).

The 1994 wildfire burned over 6,500 ha of Dry Mixed Prairie rangeland, which included an entire grazing lease and approximately 5% of a local community pasture before being brought under control. Range condition throughout the study area was good to excellent prior to the fire (assessed as per Wroe et al. 1988). Within the community pasture, cattle were free to graze selectively on burned and unburned areas during the course of the study beginning in 1995, at a stocking rate of 0.64 AUM·ha⁻¹.

Vegetation within the study area consisted of predominantly cool-season (C3) plants. Available water and soil nutrients severely limit forage production in the region (Strong and Leggat 1992), with plant growth typically complete by mid-summer. Dominant plant species include *Stipa comata* Trin. & Rupr., *Stipa curtisetata* (A.S. Hitchc.) Barkworth, *Bouteloua gracilis*, *Agropyron dasystachyum* (Hook.) Scribn. and *smithii*, as well as *Koeleria macrantha*, with their representation in plant communities heavily dependent on site conditions (Willms and Jefferson 1993). Table 1 shows the relative abundance of major plant species within burned and unburned areas of both upland and lowland topographic positions. Unburned data indicate that the upland and lowland areas are indicative of the *Stipa-Bouteloua-Agropyron* (S-B-A) and *Stipa-Agropyron* (S-A) faciations, respectively (Coupland 1961). *Artemisia frigida* Willd. was a common half-shrub throughout the area, with *Symphoricarpos occidentalis* Hook. present on lowlands as well (Table 1).

Vegetation Sampling and Assessment

Sample sites were situated within dominant range sites (upland and lowland topography) in May 1995 on the grazing lease. Transects were randomly situated in pairs along the fire-line, on both burned and adjacent unburned areas. Six transects were positioned on lowland sites and 8 on upland sites. Each transect was 20 meters long, randomly positioned and permanently marked.

A variation of the weight-estimate technique was used to estimate forage yield. On each transect, six previously unsampled 0.25 m² quadrats at stratified intervals were assessed in 1995, 1996, and 1997, with lowlands sampled a fourth time in 1998. Yearly vegetation assessments were done at peak standing phytomass (late July to early August), providing a reliable estimate of total forage production (Redmann et al. 1993).

The grazing lease was rested from livestock grazing in 1995 and 1996 to facilitate range recovery. Although pronghorn antelope could not be excluded from the area, forage utilization by this species was estimated to be negligible on the burned area in both years. In 1997 and 1998, 1 m² cages were used to prevent livestock grazing on all sample quadrats. Cattle use of the area around the transects remained light to moderate, with use never exceeding an estimated 30%.

Data collection on each quadrat was conducted as described in Wroe et al. (1988). For each quadrat, the percent groundcover of total (live and dead) vegetation, bare soil and *Selaginella densa* Rydb. was estimated using cover classes (Daubenmire 1959). All plant species present were identified and the percentage contribution of each to total yield, based on dry matter weight, visually estimated. Estimates were later checked by clipping and weighing herbage of each species present within other representative quadrats.

After the cover assessment was complete, all litter and vegetation present in the 0.25 m² quadrat was harvested. All

Table 1. Average species composition (% weight estimate) of the dominant plant species (minimum 1%) at Buffalo, Alberta, within the burned and unburned areas at each topographic position. Data are pooled over all years (1995–1997).

Species:	Upland (S-B-A)		Lowland (S-A)	
	Burned	Unburned	Burned	Unburned
	(% weight)			
Grasses:				
<i>Agropyron smithii</i> & <i>dasystachyum</i>	11.3	7.6	13.7	15.2
<i>Bouteloua gracilis</i>	6.2	8.4	2.1	3.2
<i>Carex</i> spp.	8.5	6.3	14.0	13.4
<i>Koeleria macrantha</i>	19.8	12.8	13.2	5.6
<i>Poa sandbergii</i>	7.3	2.4	3.3	1.7
<i>Stipa comata</i> & <i>spartea</i> var. <i>curtiseta</i>	37.7	39.8	50.9	52.9
Forbs:				
<i>Anemone patens</i>	0.4	0.2	0.7	1.3
<i>Artemisia frigida</i>	1.3	17.4	0.8	3.4
<i>Comandra pallida</i>	1.0	1.0	0.2	0.4
<i>Sphaeralcea coccinea</i>	2.2	1.6	1.2	0.9
<i>Vicia americana</i>	0	0	0	2.1
<i>Zygadenus gramineus</i>	0	0	0.6	1.4
Shrubs:				
<i>Artemisia cana</i>	0.9	0.3	1.0	0
<i>Rosa arkansana</i>	0	0	1.1	0.3
<i>Symphoricarpos occidentalis</i>	0	0	6.4	6.8

standing phytomass was clipped at ground level and sorted into dead material, as well as live graminoid, forb and shrub species. Shrubs were combined with forbs due to their limited abundance. Fallen litter was carefully raked from the soil surface and added to standing dead material, with the sum of these components collectively referred to as litter. Lichens, *Selaginella densa* and *Phlox hoodii* Richards. were not harvested. Each component was bagged separately by quadrat, dried to constant mass, and weighed, followed by conversion to kg ha⁻¹ to provide standing crop values. The production of each species per quadrat was determined by multiplying the average proportions estimated for each species by composited dry matter (kg ha⁻¹) harvested by growth form.

On the adjoining Buffalo-Atlee Community Pasture, 4 additional upland sites were randomly selected to assess cattle utilization on burned and unburned Dry Mixed Prairie in 1995 and 1996. Eight cages, each 1 m², were used to obtain ungrazed herbage production, with 4 cages on each of the burned and unburned areas. At each cage, 0.25 m² paired quadrats from both inside and outside the cage were assessed using the procedure described previously. Cages were not moved to avoid confounding yield data with localized site heterogeneity; instead, clipped quadrats within cages were rotated to avoid re-sampling in subsequent years. Actual herbage and litter utilization was calculated for each cage as the difference between ungrazed and grazed quadrats.

Analysis

Statistical analysis was done using Proc GLM in SAS (SAS 1990). All data were evaluated in each of the 3 postfire monitoring years with a 2 x 2 factorial model for the effects of burning, topographic position (lowland vs upland) and their interaction (e.g., Burn x Position). Only the Burn and Burn x Position results are presented here as fire was the factor of interest in this study, with any significant interactions used to aid interpretation of the main effect. Dependent variables included the estimated standing crop of major forage species, actual grass, forb, and litter weights, as well as the ground cover of total vegetation, bare soil and *Selaginella*. All comparisons across the fire boundary occurred within randomly selected but internally uniform range sites. In addition, sample sites were all located where the fire-line was man-made (i.e., grader-bladed), negating the risk of site confoundment across the fire boundary.

Table 2. Seasonal and total precipitation data for the nearest weather station at Brooks, Alberta, from 1993 to 1999, inclusive.

Year:	Season ¹				Total	Deviation ²
	Winter	Spring	Summer	Fall		
	(mm precipitation)					— (%) —
1993	26.5	141.2	126.2	48.5	342.4	0.4
1994	62.9	136.6	52.6 ³	36.6	288.7	-15.4
1995	12.6	97.9	126.2	51.6	288.3	-15.4
1996	12	74.2	124.6	78.6	289.4	-15.1
1997	56.8	94.8	63.0	20.4	235.0	-31.1
1998	77.8	143.4	63.2	28.1	312.5	-8.3
1999	22.8	192.9	159.8	19.7	395.2	15.9
7 Year Mean	36.6	138.1	99.0	41.3	315.1	-7.6
St. Dev.	23.3	47.3	36.8	17.5	48.3	
30 Year Mean	47.0	131.7	113.2	49.0	340.9	

¹Winter, spring, summer, and fall, represent the inclusive periods Jan. - March, April - June, July - Sept., and Oct. - Dec., respectively.

²Represents deviation from 30 year mean.

³Coincides with time of wildfire.

Cattle utilization data were evaluated only for differences between burn treatments, as all sampling sites were situated on upland topography. For all data sets, each year was analyzed separately in an attempt to assess the specific duration of fire effects. Variables were considered significantly different when $p < 0.05$.

Results and Discussion

Growing Conditions

Precipitation in 1994 at Brooks, the nearest weather station approximately 85 km southwest of the study area, was 289 mm, 15% below the 30 year mean of 341 mm (Table 2). During the summer of 1994, only 53 mm of precipitation fell at Brooks: this value is 54% below the long-term mean and likely provided ideal conditions for the August wildfire. Notably, precipitation for the 15 months leading up to the fire were at or above normal, and may have ensured an adequate supply of fuel through favorable vegetation growth

in the summer of 1993 and spring of 1994. Precipitation levels for 4 subsequent years following the fire were indicative of prolonged drought, however, ranging from 31% below average in 1997 to 8% below in 1998. (Table 2). Thus, post-fire drought was an influential factor on vegetation recovery.

Ground Cover Response

Although burned areas were lower in mean total vegetation cover in each of the 3 years after the fire, significant differences ($p < 0.05$) were limited to 1996 (Table 3). The delayed response may be linked to the extended below-normal levels of precipitation during the post-burn period. Sustained drought would impose an additive stress on plant communities, further affecting their inherent resilience.

The August 1994 wildfire significantly increased bare soil on burned areas for 3 subsequent years (Table 3). Increased bare soil likely reduced available moisture by increasing soil temperatures and surface evaporation, while reducing water infiltration.

Table 3. Effect of burning on mean cover (SE) of key ground components, including *Selaginella densa*, bare soil, and total live vegetation, within the study area during each of the first 3 years after wildfire.

Variable:	Year	Signif. Tests:		Burned ¹	Unburned ¹
		Burn	Burn x Pos.		
		----- p-values -----		----- (% cover) -----	
<i>Selaginella densa</i>	1995	NS	NS	26 (6)	28 (9)
	1996	NS	NS	30 (9)	31 (10)
	1997	NS	NS	53 (11)	41 (12)
Bare Soil	1995	p < 0.01	NS	21 (8)	2 (0.4)
	1996	p < 0.01	NS	11 (2)	2 (0.4)
	1997	p < 0.01	NS	23 (5)	7 (3)
Total Vegetation	1995	NS	NS	74 (6)	84 (6)
	1996	p < 0.05	NS	74 (6)	84 (6)
	1997	NS	NS	82 (6)	92 (3)

¹Only main effects are presented as no interactions met the 5% minimum level of significance.

Table 4. Effect of burning on mean (SE) grass and forb production, as well as accumulated litter (including standing dead) within the study area, during each of the first 3 years after wildfire. Interaction means are provided only for significant Burn x Position interactions.

Variable:	Year	Signif. Tests:		Burned			Unburned		
		Burn	Burn x Pos.	Upland	Lowland	Total	Upland	Lowland	Total
		p-values		(kg·ha ⁻¹)					
Grass	1995	p<0.01	NS	810 (83)	1050 (55)	890 (69)	1120 (212)	2166 (308)	1468 (239)
	1996	NS	NS	n/a	n/a	1053 (161)	n/a	n/a	1263 (233)
	1997	p<0.05	p<0.05	791 (50)	1288 (119)	1004 (113)	756 (70)	1838 (225)	1220 (238)
Forb	1995	NS	NS	n/a	n/a	106 (33)	n/a	n/a	151 (29)
	1996	NS	NS	n/a	n/a	70 (34)	n/a	n/a	169 (60)
	1997	NS	NS	n/a	n/a	85 (40)	n/a	n/a	180 (53)
Litter	1995	p<0.01	p<0.05	29 (29)	9 (9)	22 (19)	400 (124)	1159 (449)	653 (198)
	1997	p<0.01	NS	n/a	n/a	572 (165)	n/a	n/a	1464 (452)

tion (De Jong and MacDonald 1975, Facelli and Pickett 1991), thereby amplifying the magnitude of drought effects for 4 years. Defosse and Robberecht (1996) found soil temperatures after burning were 12 to 15°C greater due to increased absorption of solar radiation. Burning and loss of litter may also increase plant water stress through reduced snow trapping (Trlica and Schuster 1969, Redmann 1978).

In contrast to soil and vegetation, *Selaginella* cover was not affected by burning (Table 3), although some of this species was observed to die following the fire. These results contrast those of Dix (1960), who found *Selaginella* may be killed by fire.

Standing Crop Response

Graminoid production was reduced by the fire in 1995 and 1997, the first and third growing seasons, respectively (Table 4). Furthermore, the interaction between burning and topographic position was significant in 1997. While uplands recovered by 1997, grass production on lowlands remained 30% lower within burned areas, indicating wildfire reduced grass production to a greater extent and for a longer period on these areas. Lowlands were reassessed in 1998 and 4 years after the fire, grass production had recovered and was statistically similar between burned (1,380 kg·ha⁻¹, SE ± 97) and unburned (1,660 kg·ha⁻¹, SE ± 292) areas ($p > 0.10$).

These results are consistent with other studies that have found fire reduces grassland herbage production for 1 to 3 growing seasons (Dix 1960, Coupland 1973, Wright 1974a, Redmann 1978, Whisenant and Uresk 1989, Defosse and Robberecht 1996). In the study by Coupland (1973) on mesic Mixed Prairie in Saskatchewan, annual herbage production on burned areas remained 27 to 31% lower than unburned areas even after 3 years. Spring prescribed burning of Dry Mixed Prairie

in southern Alberta reduced forage yield 50% the first year and 15% the second year, with full recovery by the third (Clarke et al. 1947).

Much of the production loss may result from the removal of litter. Litter was significantly lower in the burned area throughout the monitoring period, and in 1997, remained 61% lower than the unburned area (Table 4). These findings are consistent with White and Currie (1983) and Engle and Bultsma (1984) indicating litter requires considerable time to re-accumulate in semi-arid areas. In western North Dakota, 4 growing seasons were needed for a *Stipa comata* community to recover after an August fire (Dix 1960). Full litter recovery in more northern temperate grasslands may take even longer (Redmann et al. 1993).

Litter acts as a physical barrier to heat and water flow at the soil surface (Weaver and Rowland 1952), thereby conserving soil moisture via reduced evaporation (Naeth et al. 1991). The physical removal of standing dead and surface litter over 1 to 3 years on northern Dry Mixed Prairie reduces herbage production by 25 to 56% (Willms et al. 1986, Willms et al. 1993). By removing litter, burning reduces production over an extended period in this semi-arid environment, and may increase the likelihood of yield losses during drought. The significant reduction in grass yield in 1997 may result from the loss of litter coupled with lower spring and summer precipitation that year (Table 2). Given that litter is slow to accumulate within northern Dry Mixed Prairie, management following fire should strive to enhance litter accumulation through measures such as reduced livestock stocking rates.

The variation in vegetation response to fire observed between uplands and lowlands are consistent with those of Clarke et al. (1947) who found *Stipa-Bouteloua* uplands were more resilient to prescribed burning than moister areas dominated by *Agropyron* plant communities. Similarly,

Coupland (1973) found a 3 year consecutive decline in annual herbage production of mesic *Agropyron* range in Saskatchewan after an August wildfire. Generally, lowland vegetation is expected to be more resilient than that on uplands due to a more favorable moisture regime, as lowlands accumulate snow, surface runoff and groundwater. The results found here, however, contrast the notion of enhanced resilience.

There are a number of possible explanations for the landscape-based differences in production between burned and unburned areas. One possibility is that greater fuel loads within lowlands caused greater fire intensities, which in turn led to greater damage to plants, thus offsetting any resilience to wildfire. Another explanation is that drought from 1994 to 1997 may have accentuated subsequent fire impacts by modifying local moisture regimes, further stressing vegetation. The loss of greater quantities of litter from lowlands during the fire may have played a role in further limiting subsequent herbage production. A third possibility is that carbohydrate reserve and/or morphological differences between upland and lowland vegetation resulted in differential tolerances to fire.

Carbohydrate reserves are, among other factors, a function of basic plant phenology, stresses such as fire and defoliation, and the type of plant species (White 1973). In some cases (e.g., big bluestem in Tallgrass Prairie), burning has been found to increase the carbohydrate content of plants (Rains et al. 1975), possibly due to the stimulating effect of mulch removal on regrowth (Ehrenreich 1959). Despite this, little is known about the specific response of carbohydrate levels within cool-season grasses exposed to fire. Species such as *Agropyron smithii* are considered susceptible to defoliation because of an extended V-shaped carbohydrate cycle (Menke and Trlica 1981), with heavy defoliation capable of reducing carbohydrates (Buwai and Trlica 1977).

Table 5. Effect of burning on the mean (SE) biomass of *Agropyron*, *Stipa*, and *Koeleria*, the 3 dominant graminoid components within the study area, during each of the first 3 years after wildfire. Interaction means are provided only for significant Burn x Position interactions.

Variable:	Year	Signif. Tests:		Burned			Unburned		
		Burn	Burn x Pos.	Upland	Lowland	Total	Upland	Lowland	Total
		p-values		(kg.ha ⁻¹)					
Grass	1995	p<0.01	NS1	810 (83)	1050 (55)	890 (69)	1120 (212)	2166 (308)	1468 (239)
<i>Agropyron</i> spp.	1995	NS	p<0.05	143 (21)	238 (54)	184 (30)	90 (30)	383 (34)	216 (63)
	1996	p<0.05	p<0.01	88 (43)	62 (11)	77 (24)	58 (31)	249 (25)	140 (43)
	1997	NS	NS	n/a	n/a	103 (31)	n/a	n/a	341 (227)
<i>Stipa</i> spp.	1995	p<0.01	p<0.01	164 (47)	326 (14)	233 (42)	288 (47)	966 (55)	578 (150)
	1996	NS	NS	n/a	n/a	489 (120)	n/a	n/a	608 (207)
	1997	NS	NS	n/a	n/a	378 (87)	n/a	n/a	482 (137)
<i>Koeleria</i>	1995	p<0.05	NS	178 (50)	146 (44)	164 (32)	114 (37)	24 (13)	75 (27)
<i>macrantha</i>	1996	NS	NS	141 (62)	138 (86)	140 (46)	141 (30)	48 (39)	101 (29)

Although the burned area was ungrazed in 1994 following the fire, lowland vegetation may have been more detrimentally affected by an August burn because it was more likely to be actively growing at the time of the fire, as well as more likely to regrow following burning. Throughout the fall of 1994 after the fire, visual estimates of vegetation regrowth were 2 to 4 cm and 7 to 10 cm on uplands and lowlands, respectively (Lorne Cole - Special Areas Range Manager, pers. observation). The greater regrowth on lowlands, followed by winter dormancy, would likely deplete both carbohydrate reserves and available lateral buds with minimal opportunity for replenishment, further damaging vegetation at this topographic position and effecting recovery. In contrast, low soil moisture during the summer drought of 1994 would make upland vegetation more likely to remain dormant after fire, minimizing carbohydrate loss and lateral bud death.

In contrast to grasses, wildfire did not significantly reduce peak forb production in any year (Table 4). These results are similar to Redmann et al. (1993) who found burning had little effect on forb phytomass within Mixed Prairie in Saskatchewan. In contrast, Bailey and Anderson (1978) found perennial forb cover in Fescue Prairie increased after burning, as did Engle et al. (1998) on burned mid-successional Tallgrass Prairie. Collectively, these studies suggest that forbs respond favorably to fire, but only in regions where moisture is relatively abundant.

The response of rangeland production to burning partly depends on the timing of fire. Clarke et al. (1947) found fall burning of *Stipa* rangeland reduced herbage production by 30% only in the following year, while spring burning resulted in a 50% decline the first year and a 15% decrease the second year. The 3 year response documented here on vegetation recovery is evidence of either the intense severity of this wildfire, the impact of

drought, or most likely, the interaction between wildfire and subsequent drought. Gerling et al. (1995) observed the same pattern with grass yields in Fescue Prairie, with late spring burning causing the greatest reductions, likely due to a combination of active plant growth coupled with declining soil moisture. These results indicate that although the August 1994 fire may have been detrimental to northern Dry Mixed Prairie rangeland, the impact may have been even more severe had upland plants not completed their annual growth prior to the fire.

Response of Dominant Grasses

Fire affected the amount of *Agropyron* spp. in 1995 and 1996 (Table 5), with both years showing a significant interaction between fire and topographic position. Burning reduced *Agropyron* production on lowlands while increasing it on uplands, producing a response similar to that found by other researchers (Wright 1974b, White and Currie 1983).

Agropyron spp. are normally quite resistant to fire as they have less flammable litter concentrated at the base of the plant near the meristematic tissues, and can regrow from rhizomes (Wright and Bailey 1982). These species may even be favored over others by fall burning (Wright 1974b, White and Currie 1983). The poor response observed at Buffalo, particularly in 1996, may be caused more by moisture stress, as *Agropyron* spp. frequently decrease during drought (Willms and Jefferson 1993). Although Launchbaugh and Owensby (1978) documented a decline in *Agropyron* with burning in Kansas, that fire occurred during spring when these species would have been actively growing and thus, more susceptible to fire damage.

Fire also reduced the production of *Stipa* spp. in 1995 (Table 5), with a significant

interaction of fire and topographic position again evident. Burning had a more negative effect within lowlands, but unlike the *Agropyron* spp., *Stipa* recovered by the second growing season. The shorter-term decline was unexpected as large bunch grasses have a concentration of dead material at their bases, typically resulting in relatively high temperatures for long periods when burned (Wright 1971). The decline in *Stipa* observed here is similar to those from other studies indicating fire can harm bunch grasses like *Stipa comata* (Dix 1960, Wright and Klemmedson 1965, Wright 1971). The timing of fire may also influence the magnitude and extent of *Stipa* decline. For example, Engle and Bulsma (1984) found Mixed Prairie burned in spring reduced *Stipa*, but only in the year of the burn, while in southern Idaho, *Stipa comata* was reduced by burning in June or July, but had more resistance to August fires (Wright and Klemmedson 1965). In contrast, Whisenant and Uresk (1989) found fire in either April or October reduced *Stipa comata* for up to 3 growing seasons. Based on these studies, it is apparent that even greater decreases in *Stipa* may have occurred had the wildfire taken place when vegetation was actively growing during spring or fall.

Fire significantly increased *Koeleria* production in the year following the wildfire (Table 5). The short, tufted habit of this species appears to be more resilient to burning in August than larger bunch grasses. The overall abundance of *Poa sandbergii* Vasey also appeared to increase after burning (Table 1). Short bunch grasses typically recover quickly after fire (Wright and Klemmedson 1965, Wright and Bailey 1982) as they accumulate less litter and experience lower fire intensities. Although *Bouteloua gracilis*, a warm season perennial, has been found to decrease following summer burning (Dix 1960,

Launchbaugh 1964), no notable difference was found in this species between burned and unburned areas (Table 1).

Burning also appeared to reduce the overall abundance of *Artemisia frigida* (Table 1). Several studies have documented prominent declines in sage with burning, including those by Dix (1960), Coupland (1973), and Bailey and Anderson (1978). The apparent reduction suggests that fire may have the potential for the control of this undesirable species on northern Dry Mixed Prairie rangelands.

Cattle Preference

Cattle utilized significantly more grass on burned uplands than their unburned counterparts in 1995, but not 1996 (Table 6). Burning typically increases forage preference and utilization (Barker and Erickson 1971, Willms et al. 1980).

Mixed Prairie may need 3 to 5 years to recover compared to one to three years for burned pastures that remain ungrazed. As a result, grazing management should be adjusted to account for livestock preferences, with burned areas either grazed separately from unburned areas to facilitate more uniform range use, or unburned areas within a pasture burned off to promote uniform grazing (Launchbaugh and Owensby 1978).

Conclusion

The August 1994 wildfire in northern Dry Mixed Prairie at Buffalo, Alberta, increased bare soil while reducing grass production and litter for several growing seasons. Rangeland recovery was likely impaired by 3 consecutive years of

Table 6. Evaluation of the Burn x Grazing interaction on year end mean standing crop (SE) on burned and unburned sites within the Atlee Community Pasture grazed during 1995 and 1996, the first 2 growing seasons after wildfire.

Year	Variable:	Burn x Grazing		Burned		Unburned	
		F-Value	Probability	Grazed	Ungrazed	Grazed	Ungrazed
----- (kg ha ⁻¹) -----							
1995	Grass	6.72	p<0.05	686 (128)	1206 (82)	1842 (82)	1678 (200)
	Forb	0.08	NS	247 (114)	229 (101)	288 (147)	205 (98)
	Litter	0.04	NS	0 (0)	0 (0)	826 (269)	736 (356)
1996	Grass	2.39	NS	910 (129)	2080 (460)	1400 (279)	1670 (183)
	Forb	0.95	NS	220 (194)	120 (63)	230 (106)	600 (424)
	Litter	0.26	NS	340 (128)	1070 (267)	1880 (423)	2080 (909)

Burned areas are preferred because forage is younger, more palatable, and more accessible (Coleman and Barth 1973, Wright 1974b). Post-burn vegetation can be higher in protein and lower in crude fiber (Allen et al. 1976, Willms et al. 1981). Burning also increases utilization simply by removing standing dead litter that acts as a barrier to grazing (Willms et al. 1980).

Grazing inhibits the short-term recovery of desirable forage species and slows the accumulation of litter on burned rangeland, potentially by up to several years (Dix 1960), thereby preventing the stabilization of soils and restoration of normal rangeland hydrologic functions. Many Mixed Prairie species such as *Agropyron* are strongly affected by defoliation during the growing season (Kowalenko and Romo 1998), and need more than two years rest before attaining full recovery. Given the established preference of cattle for burned areas, the findings of this study lend support to the conclusion of Clarke et al. (1947), that burned and grazed Dry

drought. Fire and subsequent drought conditions had the longest lasting impact on lowlands. Cattle preferred to forage on burned areas 1 year after the fire, which may further inhibit rangeland recovery, necessitating changes to grazing management to facilitate recovery. Given animal preferences for burned areas, as well as the reduction and slow recovery in vegetation characteristics within the study area, subsequent grazing management, including stocking rates, should be adjusted to facilitate range recovery, particularly when accompanied by extended drought.

Literature Cited

- Allen, L.J., L.H. Harbers, R.R. Schalles, C.E. Owensby and E.F. Smith. 1976. Range burning and fertilizing related to nutritive value of bluestem grass. *J. Range Manage.* 29:306-308.
- Anderson, H.G. and A.W. Bailey. 1980. Effects of annual burning on grassland in the Aspen Parkland of east-central Alberta. *Can. J. Bot.* 58:985-996.
- Bailey, A.W. 1978. Use of fire to manage grasslands of the Great Plains: Northern Great Plains and adjacent forests. pp. 691-693. *In:* D.N. Hyder (ed.). *Proc. of the First Internat. Rangeland Congress. Soc. for Range Manage.*, Denver, Colo.
- Bailey, A.W., and M.L. Anderson. 1978. Prescribed burning of a *Festuca-Stipa* grassland. *J. Range Manage.* 31:446-449.
- Barker, W.T. and D.O. Erickson. 1971. The effects of burning and mowing on utilization. *J. Anim. Sci.* 39:985.
- Buwai, M. and M.J. Trlica. 1977. Multiple defoliation effects on herbage yield, vigor, and total nonstructural carbohydrates of fire range species. *J. Range Manage.* 30:164-171.
- Clarke, S.E., E.W. Tisdale and N.A. Skoglund. 1947. The effects of climate and grazing practices on short-grass prairie vegetation in southern Alberta and southwestern Saskatchewan. *Can. Dep. Agr. Tech. Bull.* 46. 53 pp.
- Coleman, S.W. and K.M. Barth. 1973. Quality of diets selected by grazing animals and its relation to quality of available forage and species composition of pastures. *J. Anim. Sci.* 36:754-761.
- Coupland, R.T. 1961. A reconsideration of grassland classification in the Northern Great Plains of North America. *J. Ecol.* 49:135-167.
- Coupland, R.T. 1973. Producers: I. Dynamics of above-ground standing crop. *Matador Project. Canadian IBP Prog. Tech. Rep. No.* 27. Saskatoon, SK.
- Daubenmire, R. 1968. Ecology of fire in grasslands. pp. 209-266. *In:* *Advances in Ecological Research No. 5.* Academic Press, New York.
- Daubenmire, R.F. 1959. A canopy-coverage method of vegetational analysis. *Northw. Sci.* 33:43-64.
- De Jong, E. and K.B. MacDonald. 1975. The soil moisture regime under native grassland. *Geoderma* 14:207-221.
- Defosse, G.E. and R. Robberecht. 1996. Effects of competition on the postfire recovery of two bunchgrass species. *J. Range Manage.* 49:137-142.
- Dix, R.L. 1960. The effects of burning on the mulch structure and species composition of grasslands in western North Dakota. *Ecol.* 41:49-56.
- Ehrenreich, J.A. 1959. Effect of burning and clipping on growth of native prairie in Iowa. *J. Range Manage.* 12:133-137.
- Engle, D.M. and P.M. Bultsma. 1984. Burning of northern mixed prairie during drought. *J. Range Manage.* 37:398-401.
- Engle, D.M., R.L. Mitchell, and R.L. Stevens. 1998. Late growing-season fire effects in mid-successional tall-grass prairies. *J. Range Manage.* 51:115-121.

- Facelli, J.M. and S.T.A. Pickett. 1991.** Plant litter: Its dynamics and effects on plant community structure. *Bot. Rev.* 57:1-32.
- Gerling, H.S., A.W. Bailey and W.D. Willms. 1995.** The effects of burning on *Festuca hal-lii* in the parklands of central Alberta. *Can. J. Bot.* 73:937-942.
- Hopkins, H., F.W. Albertson and A. Riegel. 1948.** Some effects of burning upon a prairie in west-central Kansas. *Kansas Acad. of Sci. Trans.* 51:131-141.
- Kowalenko, B.L. and J.T. Romo. 1998.** Regrowth and rest requirements of northern wheatgrass following defoliation. *J. Range Manage.* 51:73-78.
- Launchbaugh, J.L. 1964.** Effects of early spring burning on yields of native vegetation. *J. Range Manage.* 17:5-6.
- Launchbaugh, J.L. and C.E. Owensby. 1978.** Kansas rangelands: their management based on a half century of research. *Kansas Agr. Exp. Sta. Bull.* 622.
- Menke, J.W. and M.J. Trlica. 1981.** Carbohydrate reserve, phenology, and growth cycles of nine Colorado species. *J. Range Manage.* 34:269-277.
- Moss, E.H. 1992.** *Flora of Alberta* 2nd Ed. University of Toronto Press, Toronto, Ontario. 687 pp.
- Naeth, M.A., A.W. Bailey, D.S. Chanasyk and D.J. Pluth. 1991.** Water holding capacity of litter and soil organic matter in mixed prairie and fescue grassland ecosystems of Alberta. *J. Range Manage.* 44:13-17.
- Nelson, J.C. and R.E. England. 1971.** Some comments on the causes and effects of fire in the northern grasslands area of Canada and the nearby United States, ca. 1750-1900. *Can. Geogr.* 15:295-306.
- Rains, J.R., C.E. Owensby, and K.E. Kemp. 1975.** Effects of nitrogen fertilization, burning, and grazing on reserve constituents of big bluestem. *J. Range Manage.* 28: 358-362.
- Redmann, R.E. 1978.** Plant and soil water potentials following fire in a northern mixed grassland. *J. Range Manage.* 31:443-445.
- Redmann, R.E., J.T. Romo, and B. Pylypec. 1993.** Impacts of burning on primary productivity of *Festuca* and *Stipa-Agropyron* grasslands in central Saskatchewan. *Amer. Midl. Nat.* 130:262-273.
- SAS (Statistical Analysis System). 1990.** SAS/STAT User's Guide. SAS Institute, Inc., Cary, N.C.
- Strong, W.L. and K.R. Leggat. 1992.** Ecoregions of Alberta. Alberta Forestry, Lands and Wildlife, Edmonton, Alberta. 59 pp. plus map.
- Trlica, M.J. and J.L. Schuster. 1969.** Effects of fire on grasses of the Texas high plains. *J. Range Manage.* 22:329-333.
- Weaver, J.E. and N.W. Rowland. 1952.** Effects of natural mulch on development, yield, and structure of native grassland. *Bot. Gazette* 114:1-19.
- Whisenant, S.G. and E.W. Uresk. 1989.** Burning upland mixed prairie in Badlands National Park. *Prairie Nat.* 21:221-227.
- White, L.M. 1973.** Carbohydrate reserves of grasses: a review. *J. Range Manage.* 26:13-18.
- White, R.S. and P.O. Currie. 1983.** Prescribed burning in the Northern Great Plains: yield and cover responses of three forage species in the mixed grass prairie. *J. Range Manage.* 36:179-183.
- Willms, W.D. and P.G. Jefferson. 1993.** Production characteristics of the mixed prairie: constraints and potential. *Can. J. An. Sci.* 73:765-778.
- Willms, W.D., S.M. McGinn and J.F. Dormaar. 1993.** Influence of litter on herbage production in the mixed prairie. *J. Range Manage.* 46:320-324.
- Willms, W.D., S. Smoliak, and A.W. Bailey. 1986.** Herbage production following litter removal on Alberta native grasslands. *J. Range Manage.* 39:536-540.
- Willms, W., A.W. Bailey and A. McLean. 1980.** Effect of burning or clipping *Agropyron spicatum* in the autumn on the spring foraging behavior of mule deer and cattle. *J. Appl. Ecol.* 17:69-84.
- Willms, W., A.W. Bailey, A. McLean, and C. Kalnin. 1981.** Effects of fall clipping or burning on the distribution of chemical constituents in bluebunch wheatgrass in spring. *J. Range Manage.* 34:267-269.
- Wright, H.A. 1971.** Why squirreltail is more tolerant to burning than needle-and-thread. *J. Range Manage.* 24:277-284.
- Wright, H.A. 1974a.** Effect of fire on southern mixed prairie grasses. *J. Range Manage.* 27:417-419.
- Wright, H.A. 1974b.** Range burning. *J. Range Manage.* 27:5-11.
- Wright, H.A. and A.W. Bailey. 1982.** *Fire ecology United States and Southern Canada.* John Wiley and Sons, Inc. Toronto, ON. 501 pp.
- Wright, H.A. and J.O. Klemmedson. 1965.** Effects of fire on bunchgrasses of the sagebrush-grass region in southern Idaho. *Ecol.* 46:680-688.
- Wroe, R.A., S. Smoliak, B.W. Adams, W.D. Willms and M.L. Anderson. 1988.** Guide to range condition and stocking rates for Alberta grasslands. Alberta Forestry, Lands and Wildlife, Public Lands, Edmonton, AB.

Vegetation responses following wildfire on grazed and ungrazed sagebrush semi-desert

NEIL E. WEST AND TERENCE P. YORKS

Authors are Professor and Research Associate, respectively, Department of Rangeland Resources, Utah State University, Logan, Utah 84322-5230.

Abstract

A 20-year set of cover data on sagebrush semi-desert plant communities responding to wildfire and livestock grazing near Mills in central Utah provided an opportunity to compare the assumptions and adaptability of classical and state-and-transition models for describing secondary succession. Cover data were organized and analyzed by plant species, growth forms, and other ground cover classes. Graphical analysis, ordination (employing semi-strong hybrid multi-dimensional scaling), regression, and analysis-of-variance were used to determine whether the patterns observed were best described as community change (tightly linked species) or individualistic change (each species acting independently). Distinct differences in total plant cover, growth form, and species composition were found between burned (both grazed and ungrazed) and the unburned and grazed treatments. Conventional graphical and statistical analyses of burned and ungrazed plots showed greater and earlier expansion of perennial grasses and then relatively less cover-weighted compositional change in recent years compared to the other treatments. Vegetation on none of the treatments appears to have stabilized toward either the pre-burn sagebrush semi-desert, a new state or the potential natural community for the site involved. Pathways of change reflected in the ordinations have been complex in all treatments. The only obvious trends in responses of individual species were to fire and the inverse relationship of cheatgrass to total perennial vegetational cover. All this evidence points to few tight linkages between species or growth form groups and thus favors viewing these patterns individually. While the state-and-transition model allows greater flexibility than the classical model in the depiction of plant community/individual species changes consequent to any management action, it doesn't apply readily everywhere, as exemplified by this case study.

Key Words: community dynamics, Clementsian model, state-and-transition model, ordination, trend, condition

Resumen

Un juego de datos de 20 años sobre cambios de la cobertura vegetal de comunidades semidesérticas de "Sagebrush" en respuesta a fuegos naturales y apacentamiento de ganado de áreas cerca de Mills, en la parte central de Utah, dieron una oportunidad para comparar los supuestos y la adaptabilidad de los modelos clásicos y los de estado y transición para describir la sucesión secundaria. Los datos de cobertura fueron organizados y analizados por especies de plantas, formas de crecimiento y otras clases de cobertura de suelo. El análisis gráfico, la ordenación (empleando un híbrido semi-fuerte de escalamiento multidimensional), el análisis de varianza y regresión se utilizaron para determinar si los patrones observados fueron los mejores para describir como cambia la comunidad (especies fuertemente ligadas) y los cambios individualísticos (cada especie actuando individualmente). Se encontraron distintas diferencias entre los tratamientos de quema (ambos, apacentados y sin apacentar) y los sin quema y apacentados, diferencias respecto a la cobertura vegetal total, la forma de crecimiento y la composición de especies. Los análisis gráficos y estadísticos convencionales de las parcelas quemadas y sin apacentar mostraron una expansión mayor y mas temprana de los zacates perennes y por lo tanto un cambio relativamente menor de composición ponderada por cobertura en los años recientes comparado con otros tratamientos. En ninguno de los tratamientos la vegetación parece haberse estabilizado hacia las condiciones previas a la quema del "Sagebrush" semidesértico, un nuevo estado o la comunidad natural potencial del sitio involucrado. Las rutas de cambio reflejadas en los ordenamientos han sido complejas en todos los tratamientos. Las unicas tendencias obvias en las respuestas de las especies individuales fueron al fuego y la relación inversa del "Cheatgrass" con la cobertura vegetal total perenne. Toda esta evidencia apunta a unos pocos vínculos fuertes entre grupos de especies o formas de crecimiento y de este modo favorece el ver estos patrones en forma individual. Mientras el modelo de estado y transición permite una mayor flexibilidad que el modelo clásico en la representación de los cambios de especies individuales o comunidades en consecuencia de cualquier acción de manejo, este no aplica fácilmente en todas partes, como se ejemplifica en este caso.

Research was funded by the Utah Agricultural Experiment Station of which this journal is Paper No. 7289. This research would have not been possible without permission from previous landowners as well as the current land owner, Ben Gambino. Also, a long list of students and the West family helped in annually collecting the data. All data and ancillary records are deposited in the Archive Section of the Merrill Library at Utah State University. Special thanks go to Susan Durham and Jim Haefner for advice on analysis methods.

Manuscript accepted 13 Apr. 01.

Basic ecologists, beginning about 1958, have rejected the linear, gradual, deterministic and reversible model of succession to climax (called the "classic" model here) associated with F.E. Clements (Burrows 1990). Rangeland ecologists slowly accepted this situation and have been searching for a replacement theory (Lauenroth and Laycock 1989) and a more modern means to

monitor rangeland trend and judge condition (West and Smith 1997). Some (e.g. Laycock 1991, 1995) think that the state-and-transition model (Westoby et al. 1989a) will be that replacement. Joyce (1993), however, cautions the profession not to abandon older ways of applying successional theory to the monitoring of trend and assessment of condition until we have adequate means of operating within a new theoretical framework. Scarnecchia (1995) persuasively argues that theory and methods should not be intimately linked if the profession is to mature. Both theory and methods will continue to evolve independently anyway.

The classic successional model is based on a mechanical metaphor (Botkin 1990), the static concept of stability (lack of change unless disturbed), and an ability to return to the previously defined single state of constancy (climax) after disturbance (Joyce 1993). The classic model assumes tight linkages between species and positive feedback of plants in changing microclimate and soils (facilitation) and advocates steady, unidirectional change toward climax. The state-and-transition model (Westoby et al. 1989a, 1989b) implies that plant community composition makes dramatic changes only during times of unusual environmental influences. Furthermore, the species composition of differing plant communities in particular states, on a particular ecological site, fluctuate within defined limits (Treshow and Allan 1985), which can also be expressed as several domains of attraction, or boundedness (Lewontin 1969, Friedel 1991, Crowley 1992), depending on the degree of responses to disturbance.

Most modern observers consider the longer-term, directional differences between species presence and abundances within stands of vegetation occupying the same ecological sites and enduring similar treatments to indicate individualistic change (uncoordinated temporal changes by individual plant species in a particular community). While the state-and-transition model is capable of depicting either individualistic or co-ordinated compositional change, an examination of data in light of the manager's needs should indicate the favored perspective in particular circumstances.

How is a rangeland technician/manager to go about monitoring with this swirl of scientific and technological change about him or her? Rather than just considering these needs abstractly, we find it useful to work with case studies and analyze data in alternative ways. The following reviews

how a 20-year interannual set of data on plant community and soil surface exposure in a sagebrush semi-desert area changed after wildfire. Some of the plots were subsequently grazed, but other plots were protected from livestock grazing. We will compare the responses in these differing treatments with competing theoretical and analytical frameworks.

Our objective was to opportunistically examine changes in vegetation cover and bare soil in a Utah instance and compare the assumptions and adaptability of classical and newer models of secondary succession. In particular, we wished to compare data organized by plant species, growth forms and other ground cover classes, analyzed by statistical, graphical and ordination techniques. The literature led us to expect that alternate stable states would be created by wildfire, particularly when followed by livestock grazing. Detection of the several putative stable states was expected to be most easily discerned by ordination. We also expected that there would be evidence of tight rather than loose or no connections between species and growth forms as they replaced each other over time.

Materials and Methods

The study site is located on privately-owned land 7.9 km west of the village of Mills, Juab Co. in central Utah (39° 29' N, 112° 7' W) on a dissected fan remnant or

ballena (Peterson 1981) on the northeastern flank of the Canyon Mountains. Slopes are 1 to 2% east-facing, with elevations ranging between 1,617 and 1,622 meters (5,305 to 5,320 ft). Mean annual precipitation is about 300 mm and is, on average, concentrated from October to April. The mean annual air temperature is about 8° C (Trickler and Hall 1984).

Soils in the study area were mapped as Borvant cobbly loam, 2–8% slopes (Trickler and Hall 1984). Profiles are mostly shallow, with less than 50 cm of calcareous, gravelly to very gravelly loam above a petrocalcic horizon, which overlies stratified layers of gravelly loam and calcium carbonate-cemented material (Boettinger et al. 1997). These soils are classified as loamy-skeletal, carbonatic, mesic shallow Petrocalcic Paleoxerolls. The designated ecological site is Upland Shallow Loam (Juniper-Pinyon) with a potential natural community composed of 40% perennial grasses, 10% perennial forbs and 50% shrubs (by relative contribution to peak new growth phytomass) (Trickler and Hall 1984).

Vegetation at the study site immediately pre-burn and during the first 3 years of recovery following the wildfire of 26 July 1981 have been previously reported (West and Hassan 1985). This earlier paper also has further details about the fire. Since these responses to the pulse treatment of the fire were likely transitory (Tilman 1988), subsequent vegetational change was of continuing interest. Table 1 lists

Table 1. The 3 plant species contributing the greatest average cover in each of 5 lifeform classes at our study site.

Lifeform	Rank 1	Rank 2	Rank 3
Perennial grasses	bluebunch wheatgrass <i>Pseudoroegneria spicata</i> (Pursh) A. Löve ssp. <i>spicata</i>	Indian ricegrass <i>Achnatherum hymenoides</i> (Roemer & J.A. Schultes) Barkworth	Sandberg bluegrass <i>Poa secunda</i> J. Presl
Annual grasses	cheatgrass <i>Bromus tectorum</i> L.		
Shrubs	Wyoming big sagebrush <i>Artemisia tridentata</i> Nutt. ssp. <i>wyomingensis</i> Beetle & Young	Nevada jointfir (or Mormon tea) <i>Ephedra nevadensis</i> S. Wats.)	yellow rabbitbrush <i>Chrysothamnus viscidiflorus</i> (Hook.) Nutt.
Annual forbs	Russian thistle <i>Salsola kali</i> L.	northern tansymustard <i>Descurainia sophioides</i> (Fisch. ex Hook.) O.E. Schulz	prickly lettuce <i>Lactuca serriola</i> L.
Half-shrubs	broom snakeweed <i>Gutierrezia sarothrae</i> (Pursh) Britt. & Rusby	granite prickly phlox <i>Leptodactylon pungens</i> (Torr.) Torr. ex Nutt.	phlox <i>Phlox longifolia</i> Nutt.
Perennial forbs	mountain pepperweed <i>Lepidium montanum</i> Nutt.	sandwort <i>Arenaria fendleri</i> Gray	fleabane <i>Erigeron argentatus</i> Gray

Plant name source: USDA, NRCS 1999. The PLANTS database (<http://plants.usda.gov/plants>).

Fig. 1. Summarization of disturbance history for the various treatments.

the 3 most important plant species (in terms of average cover) in each of the life-form categories used.

The history of the treatments is summarized in Figure 1. Pre-fire vegetational and ground surface data were collected in 1981 within 4 original macro-plots used for another study (Hassan and West 1986). Establishment of a new well following the fire made a previously unwatered and lightly grazed portion of the 4,700 ha pasture, of which the study site is in the northwestern corner, accessible to cattle grazing. In order to opportunistically observe the changes in vegetation after fire, with and without the concomitant press-type (Tilman 1988) effect of livestock grazing, the 4 original macro-plots were separately fenced and 2 storage gauges for crop-year (1 September to 30 June) precipitation were established within 2 of the 4 exclosures within the burned and ungrazed treatment (Fig. 1).

Additional macro-plots were established outside of the exclosures on the same ecological site to conduct an ad hoc "experiment" on vegetation dynamics in burned and unburned patches under grazed conditions (Fig. 1). Large enough unburned patches on the same ecological site were, unfortunately, unavailable to also fence and thus balance the design. Monitoring to support adaptive resource management will, however, require compromises between the scientists' need for experimental rigor with managers' needs for timely decision making (Szaro 1999, Thomas and Birchfield 2000).

All available treatments were replicated (Fig. 1), although numbers of replicates varied with the opportunities available. The study area had probably been lightly grazed in winter by sheep several decades before the wildfire event. The owners during the early part of our study period, however, leased the land only for cattle

use. Neither the owner or leasee were willing to provide specifics of the grazing arrangement. We, therefore, can provide only qualitative impressions that there were usually "moderate" levels of grazing on the areas outside the fenced exclosures. Livestock grazing prior to collection of data would have a negative impact on the amount of plant cover remaining in the unfenced plots. Also there were some years late in the time series when cattle had not used the areas around the exclosures at all. These less frequent circumstances will be pointed out in the discussion of results. The pre-burn rangeland at this site was considered to be in "high good" (late seral) condition in 1981 by conventional methods (West and Hassan 1985).

The 4 exclosures (burned and ungrazed) and the unfenced, burned and grazed plots measured 20 m by 50 m. Four exclosures (each 20 m by 50 m in size) were fenced during the fall of 1981 on comparable segments of the largely burned ballena. These constituted the 4 replicates of the burned and ungrazed treatment. Four other areas of 20 m by 50 m size in adjacent locations on similar terrain were also marked out at that time. These involved the burned and grazed treatment. Both of these treatments constituted subsamples of the larger available burned areas. The rarer unburned and grazed patches had to be sampled by three, 20 m by 20 m macro-plots and occupy most of the "islands" left within the mostly burned ballena. Five years following initiation of the study, some of the area outside the fenced exclosures was chained by the owner to topple scattered, fire-killed juniper snags. This activity seriously altered 1 of the unburned and grazed replicates and further sampling was not done there.

A second wildfire occurred on a subset of the original plots before the 1987 data collection. However, because of a drought (Fig. 2) and consequent lack of continuous fine fuel, the effects of that fire were very patchy. From yearly photographs taken at permanent points and field journal notes, it appeared that Exclosures #2 and #3 were partially impacted, Exclosure #1 escaped entirely, and Exclosure #4 was completely reburned. Effects of the second fire on the vegetation were no longer either visually or statistically discernable the year following its occurrence in early July 1987. None of the grazed plots were impacted by the 1987 fire. In 1996, shortly after data collection, 1 of the unburned and grazed plots was burned, and so lost for further comparisons.

Fig. 2. Total crop-year (Sept. 1-June 30) precipitation (mm) at the study area, 1981–2000. Average of two storage gauges, except 1981–3 and 1988 when gauges were vandalized and an estimate was made by correlation with the Scipio station located 26 km to the SSE at 1,615 m elevation, $r^2 = 0.67$.

Both cover and end-of-growing season aboveground plant standing crop data were collected in 1982 (West and Hassart 1985). The latter was time-consuming, and if repeated annually, would have severely altered the vegetation on these relatively small macro-plots. Thus, only the cover in the topmost layer in the sward was estimated after 1982 in all plots. Canopy cover data are also more easily related to remotely-sensed imagery than phytomass. Canopy cover data were rapidly and non-destructively collected, using a gimbaled point technique (Winkworth and Goodall 1962), near the end of each growing season (third week of July). One hundred stations, from random starting points for 4 stepped off transects, were visited per macro-plot, and readings interpreted as percentage canopy cover of the current year's plant growth. Bare soil, gravel, rock, microphytes (moss + lichen), standing dead and litter were also enumerated where no live plants occurred directly above a point (sampling station). These sample numbers were considered adequate to detect changes in total community cover and cover classes greater than 3%, through duplicate sampling 1 day apart in 1993 (Hosten 1995). Treshow and Allan (1985) employed similar numbers of subsamples for comparable vegetation.

In addition to graphing cover over time for total live and dead cover, growth form groups and species composition in each plot, ordination diagrams were used to discern temporal trends in total canopy cover-weighted plant community species composition within each replicate of each

treatment. Semi-Strong Hybrid (SSH) Multi-Dimensional Scaling (Faith et al. 1987) was the chosen indirect ordination tool using the PATN (Belbin 1992) software package. The continuous form of the Kulczynski Similarity Index (Belbin 1992) was used as input. Judging the similarities/dissimilarities of ordinations is difficult just by visual inspection. In order to judge "tightness" and similarity/dissimilarity of the successional trajectories between treatments, we calculated mean distances between sequential points in

time, total lengths of the time trajectories, numbers of crossovers, and directions of the yearly segments from the centroid. The SSH multi-dimensional scaling was chosen because it produces a measure of adequacy of fit to the scattergram termed "stress" (Faith et al. 1987). "Stress" is analogous to distances of points from the regression line in a least squares sense (Dillon and Goldstein 1984, p. 129). The values of "stress" potentially range from 0 to 1.0, but points with "stress" values above 0.2 are considered unreliable (Dillon and Goldstein 1984) and thus not discussed here. Discrete clusters of points in different quadrants of ordination space would be taken as evidence of alternate stable states. Closely clustered points [separated by distances shorter than those expected by a combination of sampling error and those due to climatic fluctuation (Rabotnov 1974)] would be taken as evidence of no ecologically significant change in species or lifeform composition.

Data bearing on the classical static notion of stability could be gathered only on the burned and ungrazed treatment because the chronic impact of livestock grazing occurred outside these 4 exclosures. The degree of return to pre-fire plant community composition was ascertained from both graphs of cover by lifeforms and from ordination diagrams by visually comparing the placement of ordination points against a background representing ordination of all plots during all years including 1981. Comparison of vegetation change between all of the treat-

Fig. 3. Total and growth form canopy cover due to live plants within the burned and ungrazed exclosures, 1981–2000.

Fig. 4. Total and growth form canopy cover due to live plants within the burned and grazed macro-plots, 1982–2000

ments could be legitimately done with 1982 and older data because ordination space is flexible and relational, changing as data are added or subtracted (Dillon and Goldstein 1984). The placement of data points representing plots outside the exclosures, where cattle usually grazed, were compared to those inside the exclosures to determine possible additive effects of grazing and the interactions between burning and grazing.

While the graphical and ordination approaches helped us to visualize the important changes in vegetation within these plots over time, we also needed a means of deciding whether the differences observed had statistical significance. Accordingly, commercial statistical software packages were used; JMP® was the basis for regression, and SYSTAT® for testing ANOVA models. To address the possibility of lack of independence between years (serial correlation), we used a general linear mixed model for longitudinal data incorporating each macroplot as a block (accommodating variability among them) and explicitly accounting for the covariance among repeated measures within a macroplot (Verbeke 1997). A 5% probability for false separation among least square means was the chosen level of statistical significance.

Results and Discussion

Mean Total Cover

Mean total cover due to living plants within the four burned and ungrazed exclosures averaged 57%, but varied between 37% and 79% over the 20 years

of available data (Fig. 3). Live plant cover appeared to increase during wet periods and decline during droughts (Figs. 2 and 3). The correlation of total live cover to total precipitation received during the preceding crop year was, however, only 0.42 ($p = 0.07$), indicating lagged soil moisture effects and other influences on plant cover were also probably operative.

Mean total live plant cover within the 3 burned and grazed plots (Fig. 4) followed the same trends as the burned and ungrazed macro-plots, except that the average cover was 46%, and minima (22%) and maxima (73%), each of which were less than on the burned and ungrazed treatment even though no cattle grazing took place on these unfenced macro-plots

in 1997, 1999, and 2000.

Mean total live cover in the unburned and grazed plots (Fig. 5) followed similar trends with the average cover (47%) and maxima similar (68%, in 2 different years), whereas the minimum was greater (37%) than the other grazed treatment.

Shrub Cover

Prior to the fire of 1981, shrubs, which were mostly Wyoming big sagebrush (West and Hassan 1985), constituted 32% of live plant cover on the 4 burned and ungrazed macro-plots (Fig. 3). The unburned and grazed remnants had 22 to 26% relative shrub cover for the first 3 years following the 1981 fire (Fig. 5). That proportion increased only slightly over the next 17 years (Fig. 5). The shrub cover increase on the burned areas was mainly due to Mormon tea. This shrub has shown several periods of growth (sometimes exceeding its pre-burn cover about two-fold) and diminishment that were not always synchronous in the 3 treatments (Fig. 6). *Artemisia* has been slow to reestablish at our burned locations. The return of sagebrush at this sagebrush semi-desert (West 1983) site is much slower following fires than in sagebrush steppe (Bunting 1984, Britton and Clark 1984, West 2000). As Treshow and Allen (1985) found for another sagebrush semi-desert site in Utah, shrub cover varied little during the period of study on the unburned but grazed plots (Fig. 5). The dominant Wyoming big sagebrush is a deep rooted evergreen known not to vary as much as herbaceous species in response to drought (Passey et al. 1982).

Fig. 5. Total and growth form canopy cover due to live plants within the unburned and grazed macro-plots, 1982–2000.

Fig. 6. Mean total canopy cover due to Mormon tea observed in the three treatments from 1982–2000.

Perennial Grass Cover

Perennial grasses constituted about 32% cover (55% of the relative live cover) in 1981 before the first fire (Fig. 3). After an initial large reduction due to the fire, relative cover of the perennial grasses in the burned and ungrazed treatment increased steadily until 1994 when the second drought during the study period began (Fig. 2). Absolute cover of perennial grasses also increased until 1994 in this treatment (Fig. 3). Since 1994 perennial grass cover has fluctuated and other perennial life forms (half-shrubs, forbs) have increased, both in relative and absolute senses.

Perennial grass cover on the burned and grazed plots increased during the first 5 years following the 1981 fire and then fluctuated greatly (Fig. 4), apparently mainly due to variations in both precipitation (Fig. 2) and grazing. No apparent cattle grazing occurred here in 1997, 1999, and 2000. Moderate levels of utilization were qualitatively observed until 1996 when the heaviest degree of cattle grazing was noted.

Perennial grass cover in the unburned and grazed macro-plots has varied the least of any growth form over time (Fig. 5), never exceeding 30% absolute cover or 50% of relative live cover. This is apparently a result of the continuing control of the micro-environment in these patches by sagebrush (Pierson and Wight 1991, Treshow and Allan 1985).

Annual Grass Cover

Annual grasses were the major cover component on all burned macro-plots from 1982 to 1984 (Figs. 3 and 4). Their

absolute and relative contributions to live cover decreased nearly to 0 from 1989 to 1993 (Hosten and West 1994) on all treatments during the greatest drought occurring during the study period (Fig. 2). Annual grasses, however, increased in

both absolute and relative senses on all treatments in the generally wetter period since 1993 (Fig. 2), until 2000, when precipitation was again below the long term mean (Figs. 2, 3, 4, and 5).

Ordinations

Although copies of full tabular data showing cover composition by individual species (besides Mormon tea, Fig. 6) under the 3 treatments over 20 years are available from the authors, their demand for printed space precludes their publication here. Accordingly, we have chosen to graphically show the overall changes in plant community composition through ordination of data from the 3 treatments (Fig. 7). Ordination is a dimension-reducing, pattern-seeking, relational technique. That is, the dimensions of covers of all individual species or growth form categories are reduced to 2 dimensions (axes) so the results of the multivariate analyses can be viewed on paper.

To test the sensitivity of ordination to differences in data input, we compared the SSH ordinations of the burned, ungrazed treatment with and without the 1981 pre-burn data. This created trajectories which started and stopped in differing quadrants

Fig. 7. Ordination of mean cover-weighted plant species composition in the three treatments from 1982–2000. The gray area represents the overall area within which points were found through ordinations of individual macro-plots.

Table 2. Characteristics of ordination pathways. Mean values for each of three treatments. Lengths are relative units, positive degrees of change are clockwise, negative are counter clockwise, quadrant I=0-90°, II=91-179°, III=180-269°, IV=270-359°

Treatment	Mean segment length	Total path length	Number of crossovers	Net degrees of change	Frequency of Points in Quadrants			
					I	II	III	IV
Burned, Ungrazed	2.8	27	4	-287	2	7	4	6
Burned, Grazed	3.0	28	3	523	4	6	5	4
Unburned, Grazed	3.5	33	3	556	3	6	4	6

(Figs. 7a and b). The pre-burn vegetation was sagebrush dominated (West and Hassan 1985) and had a longer list of plant species present than in any other subsequent year. We, thus, confirmed the importance of only using data collected between 1982 and 2000 when comparing ordinations of data from the 3 treatments.

The comparison of 1982-2000 successional trajectories in ordination space was made with the aid of 5 enumerations (Table 2). The burned, ungrazed treatment showed the shortest total length of trajectory path and shortest average length of steps between years. Counter-clock-wise tracking canceled out most of the clockwise movement and created 4 crossovers, the most observed in any treatment. Most of the movement in the burned, ungrazed trajectory was in Quadrants II and IV (Table 7b).

The burned and grazed treatment showed an intermediate total length of pathway and mean for segment lengths between years (Table 2, Fig. 7c). The high positive net degrees of change fortifies the visual impression of a tendency for this trajectory to spiral clockwise. No particular quadrants were favored. The unburned, grazed treatment showed the longest total trajectory length and thus, also the greatest mean segment length (Table 2). This treatment also showed the strongest evidence of a clockwise twist to the time trajectory. Quadrants II and IV were favored in this treatment. The number of crossovers in the trajectories for the different treatments were very similar.

From inspections of ordinations, we found it difficult to conclude that the vegetation was stable in any of the treatments. The only consistent result was the pronounced protrusion into the second quadrant on the 2 grazed treatments during 1996, the year with the greatest degree of forage utilization by cattle. Thus, ordination did not portray secondary successional patterns in easy to interpret ways. While the literature generally favors ordination

as a way of compressing data on compositional change, this study demonstrated that where total species lists are short and temporal changes are drastic, differences in a few species with episodic occurrence (e.g. Mormon tea, cheatgrass) can result in very different pathways of secondary succession being expressed.

Regression Analyses

Another, simpler way to make comparisons of vegetational changes over time between treatments is to graph scatter plots, visually compare, and regress the time courses of life form cover by treatment. While we did this for all life form groups, the most notable patterns were observed for total perennials (Fig. 8) and perennial grasses (Fig. 9). This was true regardless of whether all the data in a treatment were combined (Figs. 8 and 9) or analyzed replication by replication (not shown). Both the linear regressions and statistical analysis of their slopes (Underwood 1997) showed there has been a significantly ($p < .05$) faster increase of perennials in the burned and ungrazed than the other 2 treatments. No significant change in perennial cover was detected in either type of grazed treatment. The drought of 1986-92 (Fig. 2) had no consistent effect on these patterns. Perennial grasses were the major contributors to the total perennial cover in the burned treatments, thus, when they were considered alone (Fig. 9), it was no surprise that the burned and ungrazed treatment showed perennial grass cover increased at the most rapid rate and sustained the greatest average cover of these plants at the end of the study.

Another interesting feature of the regression analyses was that while there was no evidence from linear fits that either total perennial (Fig. 8) or perennial grass (Fig. 9) cover had yet reached the maximum in the burned and ungrazed treatment, many nonlinear fits were tried but a

4th order nonlinear fit of the combined data did increase the R^2 about 50% and indicated a leveling off since about 1993. This asymptotic response is to be expected in ungrazed vegetation of this region (Passey et al. 1982, Sneva and Britton 1983). We also analyzed these data with each replicate as a data point. These results showed a similar pattern, with an increased variance, but are too visually cluttered to reproduce effectively here.

The drought period of 1986-92 (Fig. 2) did not reduce the cover of perennial grasses, but did reduce the cover of annual grasses, regardless of treatment (Fig. 3, 4, and 5). Annual grasses, however, have rebounded comparatively more since the drought on the burned plots, both grazed and ungrazed (Figs. 3 and 4). This conclusion is further supported by plotting the relationship of perennial grass cover to annual grass cover by treatment over all years, irrespective of the time course (Fig. 10). In the ungrazed macro-plots, there was a clear tradeoff of more perennial grass as annual grasses declined and vice versa, a situation not found in either the burned and grazed or unburned and grazed macro-plots ($p < .05$) (Fig 10).

Analysis of Variance (ANOVA)

Another common way to compare the effects of treatments is through ANOVA (Underwood 1997). Total perennial cover, (Fig. 11a), was similar in the exclosures (burned and ungrazed) and the unburned and grazed treatment, but lower ($p < .01$) in the burned and grazed treatment. Annual grass cover (Fig. 12b) was significantly ($p < 0.05$) lower in the unburned and grazed treatment. The largest separation among life form groups was for perennial grasses (Fig. 11c), where the repeated measures ANOVA confirmed that the burned and ungrazed treatment had significantly higher cover ($p < .001$). This result supports the earlier discussion of the temporal pattern of increases in the perennial grass component (Fig. 3 and 9).

Conclusions

This long-term study has found several results that are counter to the expectations derived from earlier, and mostly shorter-term investigations reported in the literature (West and Young 2000). First of all, once cheatgrass came to dominate in the first few years following the 1981 wildfire, we expected this widespread invader grass to stay abundant thereafter. Instead, the perennial grasses recovered vegeta-

Fig. 8. Regressions of mean total perennial canopy cover observed in the three treatments from 1982-2000, plus 1981 mean pre-fire cover for the burned and ungrazed exclosures. Poly = fourth order polynomial fit.

Fig. 9. Regressions of mean total perennial grass canopy cover observed for each of the three treatments from 1982-2000, plus 1981 mean pre-fire cover for the burned and ungrazed exclosures. Poly = fourth order polynomial fit.

Fig. 10. Cover of perennial grasses in relation to cover of annual grasses by treatment over all years.

tively and came to dominate plant cover ever since, especially in the ungrazed macro-plots. Furthermore, cheatgrass and other annuals almost became locally

absent from 1989–1992, during the longest and most profound drought experienced during the study. This means that the threshold (Stringham et al., in press) to

a new annual-dominated state, as has occurred often elsewhere (West and Young 2000), has not been crossed at the site studied here.

The reinvasion of sagebrush and juniper following the wildfire was unexpectedly slow. Although several surges of Mormon tea recovery and subsequent dieback were detected, that species also recovered vegetatively. Wyoming big sagebrush and Utah juniper must return through seed dispersal. Even though unburned patches with mature sagebrush and juniper have persisted nearby (less than 50 m away), sagebrush seedlings are few, and juniper seedlings undetected, so far, in the burned macro-plots. This would support the conclusion that bunchgrasses were probably more dominant in the past (Trickler and Hall 1984) before the fire regime was altered (West 2000). The potential natural community for this site, however, is expected (Trickler and Hall 1984) to have about 50% cover by woody species.

Looking at the results of our analyses in total, not just by species or growth form groups, suggests that permanent changes in state have not yet occurred here, regardless of treatment. We are, however, using the definitions of Stringham et al. (in press), where changes in state are what happens when thresholds of permanent change in the abiotic environment occur, usually following accelerated soil erosion. Except for the obvious negative interactions between annuals, particularly cheatgrass, and all perennials, primarily the bunchgrasses, we see only loose linkages between species and life form groups in vegetational recovery following fire and subsequent sporadic cattle grazing of the unfenced plots.

We expected ordination to be the most revealing method for interpreting species-oriented vegetation change. We found, however, that the type of ordination we used is very sensitive to changes in the input data, low species numbers and the dramatic shifts in this vegetation over time. Graphic analysis was more easily interpretable than ordination. Regression and ANOVA also had some utility in distinguishing between treatments with known statistical significance. All the different methods of analysis used showed unique and partial views of results that complement one another.

The owner of the privately-held land upon which we conducted this study expects to continue to derive some income from livestock grazing. Thus, to him, the vegetation in the exclosures is not the reference condition or what he expects to see

Literature Cited

Fig. 11. Least square means and standard error bars for (a) total perennial cover, (b) perennial grass and, (c) annual grass cover in the three treatments. Differing lower case letters over the bars indicate statistical significant differences at $p < 0.05$. Different treatments designated by same code as used in Figure 1.

across all portions of the pasture where the Upland Shallow Loam (Juniper-Pinyon) Ecological Site occurs. On the nearby federally owned (BLM) land with the same ecological site, livestock production is not necessarily the sole or primary objective. Soil protection and wildlife interests rank higher there. In those circumstances, the vegetation within the exclosures have higher value as references for judging condition (Szaro 1999).

It should be noted that our study area is not typical of most sagebrush semidesert (West 1983) sites in the eastern Great Basin. The ballena on which the data were taken is a remnant of an alluvial fan that has undergone considerable dissection (Peterson 1981). In other words, the land upon which the plots occur is very old. This is shown by the continuous accumulation of the petrocalcic layer (Boettinger et al. 1997) with only a shallow surface horizon above. Thus, because of this great age of the soil, most of the nutrients have probably either long ago left the site or are occluded on the calcium carbonate (phosphorus in particular).

In 1981, we found sagebrush dominated vegetation with remnants of herbaceous perennials. The wildfire destroyed the sagebrush and widely scattered juniper over most of the ballena. While cheatgrass dominated in the first few years following the fire, the perennial grasses recovered vegetatively and have come to dominate since, especially in the ungrazed exclosures. We speculate that such an unexpected result (the transitive role of cheatgrass) can only be expected on sites with low stores of and capacities to fix nitrogen and other critical elements to plant growth.

In summary, we have found the collection and analysis of interannual vegetational data aggregated and analyzed in various ways in this opportunistic "experiment" to be illuminating of the issues involved in modernization of our approaches to applying ecology to determine rangeland condition and trend. While our specific results apply only to 1 ecological site, we feel we have demonstrated with minimal effort (4 person days per year of field work), the usefulness of long-term data sets in guiding acceptance or rejection of some of the general suggestions in the literature as to how to organize data for and interpret the results of monitoring to guide management decisions. We recommend that others look for similar opportunities elsewhere.

- Belbin, L. 1992.** PATN: Pattern analysis package users guide. Commonw. Scientific and Indust. Res. Organ., Div. of Wildlife and Rangelands Res., Canberra, ACT, Australia.
- Boettinger, J.L., J.A. Doolittle, N.E. West, E.W. Bork and E.W. Schupp. 1997.** Nondestructive assessment of rangeland soil depth to petrocalcic horizon using electromagnetic induction. *Arid Soil Res. and Rehabilitation* 11:375-390.
- Botkin, D.B. 1990.** *Discordant harmonies*. Oxford University Press, New York, N.Y.
- Bunting, S.C. 1984.** Fires in sagebrush-grass ecosystems: successional changes, p. 7-11. *In: K. Sanders and J. Durham (eds.) Rangeland fire effects: a symposium*. U.S. Dept. Interior Bureau of Land Manage., Boise, Ida.
- Britton, C.M. and R.G. Clark 1984.** Effects of fire on sagebrush and bitterbrush, p. 22-26. *In: K. Sanders and J. Durham (eds.) Rangeland fire effects: a symposium*. U.S. Dept. Interior, Bureau of Land Manage., Boise, Ida.
- Burrows, C.J. 1990.** *Processes of vegetation change*. Unwin Hyman, London.
- Crowley, P.H. 1992.** Density dependence, boundedness, and attraction: Detecting stability in stochastic systems. *Oecologia* 90:246-254.
- Dillon, W.R. and M. Goldstein. 1984.** *Multivariate analysis: methods and applications*. John Wiley and Sons, New York N.Y.
- Faith, D.P., P.R. Minchin, and L. Belbin. 1987.** Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* 69:57-68.
- Friedel, M.H. 1991.** Range condition assessment and the concept of thresholds: a viewpoint. *J. Range Manage.* 44:422-426.
- Hassan, M.A. and N.E. West. 1986.** Dynamics of soil seed pools in burned and unburned sagebrush semi-deserts. *Ecol.* 76:269-272.
- Hosten, P.E. 1995.** Assessing the relative utility of models of vegetation dynamics for the management of sagebrush steppe rangelands. Ph.D. Diss., Utah State Univ., Logan, Ut.
- Hosten, P.E. and N.E. West. 1994.** Cheatgrass dynamics following wildfire on a sagebrush semidesert site in central Utah, p. 56-62. *In: S.B. Monsen, and S.G. Kitchen (compilers), Proc. Symposium Ecology And Management Annual Rangelands*, U.S. Dept. Agr. Forest Service, Intermountain Res. Sta., Gen. Tech. Rep. INT-GTR-313, Ogden, Ut.
- Joyce, L.A. 1993.** The life cycle of the range condition concept. *J. Range Manage.* 46:132-138.
- Lauenroth, W.K. and W.A. Laycock (eds.) 1989.** *Secondary succession and the evaluation of rangeland condition*. Westview Press, Boulder, Colo.
- Laycock, W.A. 1991.** Stable states and thresholds of range condition on North American rangelands—A viewpoint. *J. Range Manage.* 44:427-433

- Laycock, W.A. 1995.** New perspectives on ecological condition of rangelands: can state and transition or other models better define conditions and diversity, p. 140–164. *In:* L. Montes and G.E. Olivia (eds.) *Proceedings International Workshop on Plant Genetic Resources Desertification and Sustainability*. Centro Regional Patagonia Sur, INTA-EEA, Rio Gallegos, Santa Cruz, Argentina.
- Lewontin, R.C. 1969.** The meaning of stability, p. 13–22. *In:* G.M. Woodwell and H.H. Smith (eds.), *Diversity and stability in ecological systems*. Brookhaven Sym. Biology 22. Brookhaven National Laboratory, Upton, N.Y.
- Passey, H.B., V.K. Hugie, E.W. Williams, and D.E. Ball. 1982.** Relationships between soil, plant community, and climate on rangelands of the Intermountain West. U.S. Dept. Agr. Soil Cons. Serv., Tech. Bull. 1669.
- Pierson, F.B. and J.R. Wight. 1991.** Variability of near surface temperature on sagebrush rangeland. *J. Range Manage.* 44:491–497.
- Peterson, F.F. 1981.** Landforms of the Basin and Range Province defined for soil survey. Nevada Agr. Exp. Sta. Tech. Bull. 28, Univ. Nevada, Reno, Nev.
- Rabotnov, T.A. 1974.** Differences between fluctuations and succession, p. 21–21. *In:* R. Knapp (ed.) *Vegetation Dynamics. Handbook of Vegetation Science*. Vol 8. W. Junk Publ., The Hague, Netherlands.
- Scarnecchia, D.L. 1995.** Viewpoint: The rangeland condition concept and range sciences search for identity: A system viewpoint. *J. Range Manage.* 48:181–186.
- Sneva, F. and C.M. Britton. 1983.** Adjusting and forecasting herbage yields in the Intermountain Big Sagebrush Region of the Steppe Province. Oregon Agr. Exp. Sta. Bull. 659. Oregon State Univ., Corvallis, Ore.
- Stringham, T.K., W.C. Krueger, P.J. Meiman and P. Shaver, in press.** States, transitions, and thresholds: Further refinement for rangeland applications. Addendum to National Range and Pasture Handb. Natural Resources Cons. Service, Grazing Lands Tech. Institute, Fort Worth, TX.
- Szaro, R. 1999.** Monitoring and evaluation, 223–230. *In:* N.C. Johnson, A.J. Malk, R.C. Szaro, and W.T. Sexton (eds.), *Ecological stewardship*, Vol. I, Elsevier, Amsterdam.
- Tilman, D. 1988.** Plant strategies and the dynamics and structure of plant communities. Princeton Univ. Press, Princeton, N.J.
- Thomas, J.W. and J. Birchfield. 2000.** Science, politics and land management. *Rangelands* 22 :45–51.
- Treshow, M. and J. Allan. 1985.** Uncertainties associated with the assessment of vegetation. *Environ. Manage.* 9:471–478.
- Trickler, D.L. and D.T. Hall. 1984.** Soil survey of Fairfield-Nephi area Utah. U.S. Dept. Agr. Soil Conservation Service, Salt Lake City, Ut.
- Underwood, A.J. 1997.** Experiments in ecology. Cambridge Univ. Press, Cambridge, U.K.
- Verbeke, G. 1997.** Linear mixed models for longitudinal data, 63–155. *In:* G. Verbeke and G. Molenberghs (eds.), *Linear Mixed Models in Practice: A SAS-oriented approach*. Lecture Notes in Statistics. No. 126, Springer-Verlag, New York.
- West, N.E. 1983.** Great Basin-Colorado Plateau Sagebrush Semi-desert, p. 331–349. *In:* N.E. West (ed.) *Temperate deserts and semi-deserts*. Elsevier Sci. Publ., Amsterdam, Netherlands.
- West, N.E. 2000.** Synecology and disturbance regimes of sagebrush steppe ecosystems, p. 15–26. *In:* P.G. Entwistle et al., compilers, *Proceedings: Sagebrush Steppe Ecosystems Symposium*, Bureau of Land Management Publication No. BLM/ID/PT-001001+150 Boise, ID.
- West, N.E. and M.A. Hassan. 1985.** Recovery of sagebrush-grass vegetation following wildfire. *J. Range Manage.* 38:131–134.
- West, N.E. and E.L. Smith. 1997.** Improving the monitoring of rangelands. *Rangelands* 19:9–14.
- West, N.E. and J.A. Young. 2000.** Intermountain valleys and lower mountain slopes, p. 255–284. *In:* M.A. Barbour and W.D. Billings (eds.), *North American Terrestrial Vegetation*, 2nd ed. Cambridge Univ. Press, New York.
- Westoby, M., B. Walker and I. Noy-Meir. 1989a.** Opportunistic management for rangelands not at equilibrium. *J. Range Manage.* 42:266–274.
- Westoby, M., B. Walker and I. Noy-Meir. 1989b.** Range management on the basis of a model which does not seek to establish equilibrium. *J. Arid Environ.* 17:235–239.
- Winkworth, R.E. and D.W. Goodall. 1962.** A crosswire sighting tube for point quadrat analyses. *Ecol.* 43:342–343.

Seasonal dynamics of prairie sandreed rhizome development

PATRICK E. REECE, JENNIFER S. NIXON, LOWELL E. MOSER, AND STEVEN S. WALLER

Authors are Professor, University of Nebraska, Panhandle Research and Extension Center, 4502 Avenue Scottsbluff, Nebr. 69361; Extension Educator, Sioux County Extension, 325 Main, Harrison, Nebr. 69346; Professor, Dept. of Agronomy, 352 Keim Hall, University of Nebraska, Lincoln, Nebr. 68583; Associate Dean, 103 Agricultural Hall, University of Nebraska, Lincoln, Nebr. 68583.

Abstract

Multiple generations of rhizome-connected tillers stabilize soils and produce measurable amounts of herbage on sandy rangeland throughout the world. However, little is known about the dynamics of rhizome development in these clonal plant species. Seasonal relationships between foliar characteristics and rhizomes of prairie sandreed [*Calamovilfa longifolia* (Hook) Scribn.] were examined on sands range sites at 30-day intervals from May through September 1989 and 1990 at the University of Nebraska, Panhandle Experimental Range near Scottsbluff. Quadrats were excavated each year from two, 5 x 5 Latin Square macroplots in each of 2 grazing histories, long-term rest or current-year deferment. Under dry conditions in 1989, a 65% reduction in the length of new rhizomes during July preceded a 64% reduction in live tillers in August. After which, rhizome length and live tiller density were unchanged and mean tiller weight increased during September. When average precipitation occurred in 1990, a 25% reduction in live tillers and concurrent increases in new rhizome length and mean tiller weight occurred during July. Rhizome bud densities increased throughout the growing season at different but predictable rates ($R^2 \geq 0.95$) for grazing histories, regardless of precipitation. Length of new rhizomes was highly correlated ($R^2 = 0.91$) with live herbage throughout the growing season. Measurable increases in total rhizome length did not occur until live herbage of prairie sandreed exceeded a threshold of about 50 g m⁻². Maximum increase in length of new rhizomes per unit of live herbage was about 10 cm g⁻¹ near 100 g m⁻². Given its dependence on vegetative reproduction and relatively high palatability to beef cattle, periodic or repeated years of full growing season deferment may be the only reliable method of obtaining measurable increases in prairie sandreed populations.

Key Words: *Calamovilfa longifolia*, warm-season grass, clonal growth, reproduction threshold, tiller dynamics

Resumen

Generaciones múltiples de hijuelos conectados por rizomas estabilizan los suelos y producen cantidades medibles de forraje en los pastizales arenosos del mundo. Sin embargo, poco se conoce respecto a las dinámicas de desarrollo de los rizomas en estas especies vegetales clonales. Se examinaron las relaciones estacionales entre las características foliares y los rizomas del zacate "Prairie sandreed" [*Calamovilfa longifolia* (Hook) Scribn.]; el estudio se llevó a cabo en la Estación Experimental de Pastizales Panhandle de la Universidad de Nebraska, cerca de Scottsbluff, y se realizó en sitios de pastizal arenosos en intervalos de 30 días de Mayo a Septiembre de 1989 a 1990. Cada año se excavaron cuadrantes en dos macro parcelas de un Cuadro Latino 5 x 5 situadas en dos áreas con diferente historial de manejo del apacentamiento, descanso a largo plazo y diferimiento del año actual. En 1989, bajo condiciones de sequía, una reducción del 65% de la longitud de los nuevos rizomas registrada en Julio precedió a una reducción del 64% de los hijuelos vivos registrada en Agosto. Después de la cual, la longitud de los rizomas y la densidad de los hijuelos vivos permanecieron sin cambio y la media de peso de los hijuelos se incrementó durante Septiembre. En 1990, año con precipitación promedio, en Julio se observó un 25% de reducción en los hijuelos vivos e incrementos concurrentes de la longitud de los rizomas nuevos y la media de peso de los hijuelos. Las densidades de yemas de hijuelos se incrementaron a través de la estación de crecimiento a diferentes tasas (pero predecibles) ($R^2 > 0.95$) para las historias de apacentamiento, sin importar la precipitación. A lo largo de la estación de crecimiento la longitud de los nuevos rizomas estuvo altamente correlacionada ($R^2 = 0.91$) con el forraje vivo. No ocurren incrementos medibles en la longitud total de los rizomas hasta que el forraje vivo del "Prairie sandreed" excedió un umbral de aproximadamente 50 g m⁻². El máximo incremento de la longitud de los rizomas nuevos por unidad de forraje vivo fue aproximadamente de 10 cm g⁻¹ casi 100 g m⁻². Dada su dependencia en la reproducción vegetativa y su gustocidad relativamente alta para el ganado para carne, el diferimiento periódico o repetido de la estación de crecimiento completa puede ser el único método confiable para obtener incrementos medibles en poblaciones de "Prairie Sandreed".

Published as Paper 12924 Journal Series, Nebraska Agricultural Research Division. The authors wish to thank Gordon Moeller, Jay and Gretchen Lees, Myron Riggs, Mick Friemuth, Jack Alexander, Lori Williams, Maureen Skavdahl, Mollie Reece, Bill Goodwin, Hazel Fritschen, Laurie Baker, Echo Fisher, Cheryl Bolen, and Paige Wolken for the many hours they invested in excavating and processing samples. We would also like to express our appreciation to Sharon Holman for the preparation of the manuscript and to Ann Koehler for preparation of the graphics.

Manuscript accepted 20 Jul. 01.

The relative value of rhizomes in reproduction, resource acquisition, and interactions among rhizome-connected shoots has been reported for graminoid (Hartnett 1989, Jónsdóttir and Callaghan 1990, Jónsdóttir 1991, de Kroon et al. 1992, Wikberg et al. 1994, Makita 1996) and forb (Hartnett 1990, Hara and

Wakahara 1994, Schmid et al. 1995) species. However, most of this information is limited to end-of-season measurements. Field studies of grass rhizome dynamics during the growing season are rare (Brejda et al. 1989) and quantification of seasonal relationships between rhizome and shoot characteristics during the growing season has not been reported.

Networks of rhizome-connected tillers are highly effective in stabilizing sandy soils in the Nebraska Sandhills, the largest stabilized sand dune formation in the western hemisphere encompassing about 4.9 million ha. Prairie sandreed [*Calamovilfa longifolia* (Hook) Scribn.] is a co-dominant, warm-season, rhizomatous grass in mid- to late seral plant communities on all upland sites in the Sandhills and on many sandy range sites in the northern Great Plains of USA and Canada (GPFA 1986). Prairie sandreed tillers develop almost exclusively from buds at the distal end of rhizomes which are unbranched and relatively long and deep compared to other plant species in the Sandhills (Brejda et al. 1989, Nixon 1993, Hendrickson et al. 1998).

Our primary objective was to quantify seasonal relationships between prairie sandreed shoot and rhizome characteristics in natural plant communities. Excavation macroplots were also blocked by grazing history and protected from defoliation to evaluate seasonal dynamics of rhizome development after more than 14 years of rest compared to a single year of full growing season deferment. Based on preliminary field evaluations, we hypothesized that length of new rhizomes within a given soil volume increases monotonically as live herbage of prairie sandreed increases within the sample area during the growing season. We further hypothesized that the rate of change in rhizome length per unit change in herbage is independent of grazing history.

Materials and Methods

The study was conducted during 1989 and 1990 at the University of Nebraska, Panhandle Experimental Range (PER, 42° 08' N, 103° 43' W), 19 km northwest of Scottsbluff, Nebraska. Soils are Valent fine sands (Mixed Mesic Ustic Torripsamment). About 73% of annual precipitation occurs during the growing season from May to September. Long-term average annual precipitation was 340 mm with 270 mm in 1989 and 350 mm in 1990. Rangelands in mid- to late seral

stages at this location are dominated by prairie sandreed. Other abundant species include needleandthread (*Stipa comata* Trin. & Rupr.), blue grama [*Bouteloua gracilis* (HBK) Lag. ex Griffiths], and sand dropseed [*Sporobolus cryptandrus* (Torr.) A. Gray]. Sand bluestem (*Andropogon halli* Hack.) is abundant in late seral stages (GPFA 1986).

Four macroplots with uniform distribution of prairie sandreed tillers were selected in a 5.0-ha enclosure constructed in 1974 and in the pasture where the enclosure was located. The pasture had been moderately stocked at 1.0 AUM ha⁻¹ and continuously grazed from May through September since 1978. Two macroplots within each grazing history were randomly selected for excavation in each year. Fences were constructed to exclude cattle from 2 previously grazed macroplots in the pasture in April each year. A 5 x 5 grid of 0.5-m² quadrats (0.71 x 0.71 m) with 0.71-m wide alleys was marked on selected macroplots in April 1989 and 1990. Excavation dates were assigned to quadrats within rows and columns according to randomization procedures for Latin Squares. Five quadrats were excavated to a depth of 30 cm from 2 macroplots in the long-term-rested area and 2 macroplots in the current-year-deferred areas at 30-day intervals from 30 May to 30 September in 1989 and 1990. Prairie sandreed plants were separated from soil and other plant material over wire screens at the excavation site, bagged, and transported on dry ice to freezers.

Plant material was separated into live shoots, crowns, rhizome buds, new rhizomes, and old rhizomes. Initially rhizomes grow horizontally from the point of origin followed by vertical growth which culminates in the development of a shoot if the rhizome is not aborted. Rhizomes originate from buds nears the base of vertical crowns. Rhizome buds were differentiated and visually discernable shoots less than 2-cm long. Buds elongating beyond 2 cm were classified as new rhizomes. New rhizomes had numerous, light tan, intact exterior scales. Rhizomes in this category formed connections between crowns of current-year and/or prior-year shoots or they originated from a shoot and had not emerged. Old rhizomes were dark tan to black with no scales or low densities of fractured scales. Length of rhizomes was measured by hand. Intact networks of old rhizomes often connected 6 to 8 crowns. Plant components were oven dried at 50°C to a constant weight. Mean tiller weights were calculated from total weight of live

herbage and density of live tillers within each excavated area.

The average laboratory time required to separate prairie sandreed from a single 0.5-m² quadrat into plant components in 1989 was 3.5 hours. During August and September 1989, the quarter of the quadrat with the density of live prairie sandreed tillers most similar to the average for the entire 0.5 m² quadrat was excavated separately. Variances and means for quarter and full quadrat data sets were similar based on F and t-tests at $P \leq 0.05$. In 1990, the area of excavated experimental units was reduced to 35 x 35 cm, the quarter with a tiller density most similar to the original 0.5 m² quadrat.

Data were analyzed as a Latin Square using old rhizome length as a linear covariate with the General Linear Models Procedure (SAS 1986). Experimental units were individual quadrats within Latin Square macroplots, blocked by grazing history. Season and season by year interaction effects with grazing history were tested. However, comparisons of means for grazing histories were not valid without replication which was precluded by labor constraints. The Least-Squares Means Procedure within SAS was used for mean separation among excavation dates (Searle et al. 1980). Treatment effects were reported as significant at $P \leq 0.10$. Values used to compute regression equations (SAS 1986) for seasonal changes in density of differentiated rhizome buds below crowns on long-term-rested and current-year-deferred macroplots were the means of 20 excavated quadrats. Values used to compute regression equations for the relationships between the length and weight of new prairie sandreed rhizomes and between live prairie sandreed herbage and the length of new rhizomes were the means of 10 excavated quadrats.

Results and Discussion

Dormant season precipitation from 1 October to 30 April was 42% of long-term average before the 1989 growing season compared to 129% before the 1990 growing season (Fig. 1). Peak standing herbage is highly correlated with the quantity of moisture in Valent soils in mid-April (Dahl 1963). Additionally, total herbage production per unit of spring soil moisture is about 58 and 167% greater than for soil moisture received during early and late summer, respectively (Dahl 1963). While precipitation during June was only 5% of the long-term average in 1989 and 23% in

Fig. 1. Cumulative annual precipitation from 1 Oct. to 30 Sept. for the 1989 and 1990 growing seasons and the 30-year average (•—•) at the University of Nebraska, Panhandle Experimental Range near Scottsbluff, Nebr.

1990, cumulative precipitation beginning in October 1989 was similar to the 30-year average during most of the 1990 growing season because of above average precipitation during the preceding dormant season. Cumulative precipitation beginning in October 1988 was about 10 cm below the 30-year average from 1 June to 31 August 1989, the primary growing season for prairie sandreed (Fig. 1).

Tillers

Regardless of precipitation regime or grazing history, measurable declines in the density of live prairie sandreed tillers occurred during each growing season (Table 1). Densities of live tillers declined by about 64% on all macroplots during August 1989 and about 25% during July 1990 (Table 1). Similar changes in live tiller density for grazing histories in both

years indicated that mortality rates were density independent. Prairie sandreed tiller recruitment in western and central Nebraska is poorly correlated with concurrent 15 or 30 day precipitation totals (Hendrickson et al. 2000). However, in this and other studies of prairie sandreed, tiller recruitment and end-of-season tiller numbers increased as cumulative precipitation increased from the preceding October to the end of the current growing season (Cullan et al. 1999, Hendrickson et al. 2000). Epic events of tiller mortality are relatively common for rhizomatous graminoids in subarctic and temperate environments (Callaghan 1976, Kroon et al. 1992); however, they have not been observed in prairie sandreed populations 240 km east of the Panhandle Experimental Range (PER) at the University of Nebraska-Lincoln Gudmundsen Sandhills Laboratory (Cullan et al. 1999) where long-

term precipitation is 560 mm compared to 340 mm at the PER.

Mean tiller weights increased about 117% on current-year-deferred macroplots and about 175% on long-term-rested macroplots each year during the month in which measurable declines of live tiller densities occurred (Table 1). Tiller densities were unchanged and mean tiller weight continued to increase the remainder of the growing season in both years. Stable late-summer tiller densities are consistent with other studies which indicate about 80% of prairie sandreed tillers emerge by mid-June after which emergence generally remains low the remainder of the growing season (Hendrickson et al. 2000). End-of-season tiller densities increased 91% from 1989 to 1990 on current-year-deferred macroplots compared to 142% on long-term-rested macroplots (Table 1). Higher end-of-season densities and mean weights of live tillers on long-term-rested compared to current-year-deferred macroplots in 1990 are indicative of relatively high levels of plant vigor commonly observed in prairie sandreed in high seral plant communities in this area.

Rhizomes

Monthly rates of change in the density of differentiated buds that could produce rhizomes were similar for grazing histories except during July and August when bud density on long-term-rested macroplots increased by about 1.6 buds $m^{-2} day^{-1}$ compared to 0.3 buds $m^{-2} day^{-1}$ on current-year-deferred macroplots (Fig. 2). This pattern was consistent over years regardless of precipitation regime. Corresponding delays in differentiation of rhizome buds (Nixon 1993) and herbage production (Table 1) during May on long-term-rested compared to current-year-deferred macroplots indicated litter accumulation on rested sites may have reduced soil temperatures (Willms et al. 1993). Mean densities of buds for grazing histories in May 1990 were similar to densities in September 1989 indicating most of the rhizome buds in September survived into the subsequent year. End-of-season bud densities for grazing histories were similar in 1989, but 52% higher on long-term-rested than current-year-deferred macroplots in September 1990 when near average precipitation occurred (Nixon 1993).

The relationship between total weight and length of new rhizomes was highly predictable ($R^2 = 0.90$) regardless of the month or year of sampling (Fig. 3). Mean biomass ranged from 6.4 g m^{-1} with 52 cm

Table 1. Mean density and weight of live prairie sandreed tillers for grazing histories from May through September 1989 and 1990 at the University of Nebraska, Panhandle Experimental Range near Scottsbluff, Nebr.

Date	1989		1990	
	Current-year-deferred	Long-term-rested	Current-year-deferred	Long-term-rested
Tiller Density ¹ (no. m^{-2})				
May 30	169a	262a	139ab	240a
Jun 30	179a	200b	166a	258a
Jul 30	190a	248a	133b	181b
Aug 30	70b	87c	107b	186b
Sep 30	58b	69c	127b	200b
Mean Tiller Weight ² (mg)				
May 30	311cd	137d	162b	30d
Jun 30	399bc	300bc	291b	189c
Jul 30	237d	173cd	614a	527b
Aug 30	525b	467ab	492a	435b
Sep 30	681a	515a	505a	812a

¹Numbers within columns with the same letter are not significantly different, $P > 0.10$.

²The month by grazing history by year interaction for mean tiller weight was significant at $p = 0.021$.

Fig. 2. Seasonal patterns in the density of differentiated buds on vertical rhizomes below crowns of prairie sandreed that could produce new rhizomes (x = days after 30 May) from May through September on long-term-rested ($\circ$) and current-year-deferred ($\bullet$) macroplots at the University of Nebraska, Panhandle Experimental Range.

Fig. 3. The relationship between total weight and total length of new prairie sandreed rhizomes from May through Sept. 1989 ($\circ$) and 1990 ($\bullet$) at the University of Nebraska, Panhandle Experimental Range.

m^{-2} to $3.1 g m^{-2}$ with $1073 cm m^{-2}$ (Fig. 3). About 94% of the reduction in mean biomass per unit length occurred within the first 20% of the observed range in total length. Mean biomass was about $3.3 g m^{-2}$ when length of new rhizomes reached $200 cm m^{-2}$. After soil moisture deficits induced reductions in total length of new rhizomes during July 1989 (Fig. 4), mean biomass per unit length was 82% greater on current-year-deferred macroplots and 49% greater on long-term-rested macroplots (Fig. 3) indicating low-weight rhizomes may have senesced more frequently than heavy rhizomes. Additionally, remaining intact rhizomes may have received proportionately greater amounts of carbohydrates from shoots (Welch 1968) or carbohydrates may have been translocated from senescing rhizomes into intact rhizomes (Jónsdóttir and Callaghan 1990). Carbohydrate concentrations in prairie sandreed rhizomes generally increase rapidly during late summer (Welch 1968). However, little change occurred in mean biomass per unit length when rapid rhizome growth occurred during August and September 1990 (Fig. 3 and 4).

Length of old rhizomes within excavated sample volumes was a significant linear covariate in the analysis of tiller density, herbage, and density of buds that could produce rhizomes. Water and/or nutrients may be translocated from old non-assimilating tillers to connected tillers with live shoots (Jónsdóttir and Callaghan 1988). In contrast, length and weight of new rhizomes were not affected by length of old rhizomes. This contrasts with highly sig-

nificant linear relationships between preceding and current-year rhizome biomass for herbaceous species in temperate environments (de Kroon et al. 1992). However, based on the number of interconnected crowns and assuming 1 crown per year, old rhizomes may have been as much as 7 years old in our study. While crowns may produce more than 1 rhizome in a single year, only 1 crown has developed at the distal end of rhizomes per year in our preliminary field studies of plants grown in containers. Additionally, a percentage of preceding-year rhizomes may have been included in the new rhizome category if color and scale condition criteria were met. Growth of new prairie san-

dreed rhizomes after buds differentiated appeared to be primarily dependent upon resources from assimilating tillers.

The limiting effects of soil moisture deficits on length of new rhizomes in 1989 were uniformly profound regardless of grazing history (Fig. 4). Tiller weights increased from July to September (Table 1) with no change in length of new rhizomes and no difference in rhizome length between grazing histories (Fig. 4) in September. However, when average precipitation occurred in 1990, length of new rhizomes at the end of the growing season was 3.4 times greater for long-term-rested than current-year-deferred macroplots (Fig. 4). Density and mean weight of live

Fig. 4. Mean total length of new prairie sandreed rhizomes at 30-day intervals during the growing season on long-term-rested and current-year-deferred macroplots at the University of Nebraska, Panhandle Experimental Range.

Fig. 5. The relationship between total length of new rhizomes and total live herbage of prairie sandreed from May through Sept. 1989 (○) and 1990 (●) at the University of Nebraska, Panhandle Experimental Range.

tillers in late September were both about 60% higher on rested than on deferred macroplots in 1990 (Table 1) resulting in a mean of 10.7 in of new rhizomes per 1.0 m².

Lack of correlation between length of new prairie sandreed rhizomes and tiller density was similar to *Carex bigelowii* (Wikberg et al. 1994) which also exhibits epic events of tiller mortality. In contrast, live herbage of prairie sandreed accounted for 91% of the variation in new rhizome length regardless of grazing history or the year or month of sampling (Fig. 5). The relationship between total length of new rhizomes and mean tiller weight was similar to, but less predictable ($R^2 = 0.76$) compared to total live herbage (Nixon 1993). Therefore, we accept our hypothesis that the relationship between rhizome length and live herbage is not affected by grazing history. The lack of grazing history effects is consistent with studies of *Carex bigelowii* on subarctic rangeland (Jónsdóttir 1991). Strong relationships between total live herbage and length of new rhizomes have also been reported for forbs *Aster lanceolatus* and *Solidago canadensis* (Schmid et al. 1995) and *Paris tetraphylla* (Hara and Wakahara 1994).

During both years, measurable increases in total length of new rhizomes did not occur until herbage exceeded a threshold of about 50 g m⁻² (Fig. 5) which may correspond to the 4 to 5 leaf stage after which Brejda et al. (1989) reported initiation of new rhizome growth. Beyond this threshold, increases in rhizome length per unit of herbage were highest, about 10 cm g⁻¹, near 100 g m⁻² (Fig. 5). Increases in rhizome length per unit of live herbage were about 40% lower when live herbage was near 50 and 150 g m⁻¹ (Fig. 3 and 5).

Therefore we reject our hypothesis that length of new prairie sandreed rhizomes increases at a constant rate as the mass of live herbage increases.

Precipitation regime by grazing history interaction effects on herbage production were pronounced; however, the relationship between live herbage and length of new prairie sandreed rhizomes was independent of precipitation, grazing history, or excavation date indicating a wide population of inference for the results of this study. Measurable increases in rhizome length in a given year may increase the potential for herbage production if the percentage of tillers originating from relatively long rhizomes increases (White 1977 Brejda et al. 1989) and/or access to limited soil nutrients increases. Interaction between grazing history and precipitation in this study indicates availability of soil moisture will control the extent to which potential herbage production is expressed in semiarid environments.

Prairie sandreed is a mid- and late seral species capable of producing relatively large amounts of herbage critical for ecosystem functions and livestock production. Reproduction of this species is almost exclusively vegetative from crowns formed at the distal end of rhizomes (Brejda et al. 1989, Cullan et al. 1999). Clonal growth into surrounding areas without prairie sandreed and its ability to survive burial on disturbed sites are important processes in secondary succession (Weaver 1965, Maun and Perumal 1999). Consequently, the occurrence of a live-herbage threshold for rapid growth of rhizomes should be considered when developing grazing management strategies designed to increase the composition of

this species. Heavy defoliation during the growing season before threshold levels of herbage have been produced would preclude measurable increases in the composition of prairie sandreed in most years, regardless of grazing systems. The likelihood of producing enough herbage for rapid rhizome development after heavy defoliation in summer-grazed pastures, declines as the growing season progresses and/or precipitation declines (Reece et al. 1999).

Deferring grazing until seedheads have emerged in August would improve the potential for increasing the composition of prairie sandreed (Reece et al. 1996). Tillers that develop from the longest prairie sandreed rhizomes are generally the largest and most likely to produce seedheads (White 1977). Nutritive value and palatability of reproductive tillers to beef cattle decline when seedheads emerge (Reece et al. 1999). These relatively large and generally ungrazed tillers may be critically important for grazing resistance in prairie sandreed by translocating nutrients to connected vegetative tillers (Jónsdóttir and Callaghan 1990, Cullan et al. 1999) that continue to be highly palatable through the summer grazing season (Northup 1993). Given the relatively high preference by cattle for prairie sandreed (Northup 1993, Cullan et al. 1999), periodic or repeated full growing season deferment may be the only reliable method of obtaining measurable increases in prairie sandreed populations. On sites where cool-season graminoids produce 20 to 50% of the herbage, heavy grazing of cool-season species in April, before prairie sandreed tillers emerge, may enhance this species response to full growing-season deferment (Reece et al. 1999).

Literature Cited

- Brejda, J.J., L.E. Moser, and S.S. Waller. 1989. Rhizome and tiller development of three Nebraska Sandhills warm-season grasses. p. 211–215. In: T.B. Bragg and J. Stubbendieck (eds.) Proc. Eleventh North Amer. Prairie Conf Lincoln, Nebr.
- Callaghan, T.V. 1976. Growth and population dynamics of *Carex bigelowii* in an alpine environment: strategies of growth and population dynamics of tundra plants 3. Oikos 27:402–413.
- Cullan, A.P., P.E. Reece, and W.H. Schacht. 1999. Early summer grazing effects on defoliation and tiller demography of prairie sandreed. J. Range Manage. 52:447–453.
- Dahl, B.E. 1963. Soil moisture as a predictive index to forage yield for the sandhills range type. J. Range Manage. 16:128–132.

- de Kroon, H., T. Hara, and R. Kwant. 1992. Size hierarchies of shoots and clones in clonal herb monocultures: do clonal and non-clonal plants compete differently? *Oikos* 63:410–419.
- Great Plains Flora Association. 1986. Flora of the Great Plains. T.M. Barkley (ed.). University Press Kansas. Lawrence, Kan.
- Hara, T. and M. Wakahara. 1994. Variation in individual growth and the population structure of a woodland perennial herb, *Paris tetraphylla*. *J. Ecol.* 82:3–12.
- Hartnett, D.C. 1989. Density- and growth stage-dependent responses to defoliation in two rhizomatous grasses. *Oecologia* 80:414–420.
- Hartnett, D.C. 1990. Size-dependent allocation to sexual and vegetative reproduction in four clonal composites. *Oecologia* 84:254–259.
- Hendrickson, J.R., L.E. Moser, K.J. Moore, and S.S. Waller. 1998. Morphological development of 2 warm-season grasses in the Nebraska Sandhills. *J. Range Manage.* 51:456–462.
- Hendrickson, J.R., L.E. Moser, and P.E. Reece. 2000. Tiller recruitment patterns and biennial tiller production in prairie sandreed. *J. Range Manage.* 53:537–543.
- Jónsdóttir, I.S. 1991. Effects of grazing on tiller size and population dynamics in a clonal sedge *Carex bigelowii*. *Oikos* 62:177–188.
- Jónsdóttir, I.S. and T.V. Callaghan. 1988. Interrelationships between different generations of interconnected tillers of *Carex bigelowii*. *Oikos* 52:120–128.
- Jónsdóttir, I.S. and T.V. Callaghan. 1990. Intracolonial translocation of ammonium and nitrate nitrogen in *Carex bigelowii* Torr. ex Schwein. using ^{15}N and nitrate reductase assays. *New Phytol.* 114:419–428.
- Makita, A. 1996. Density regulation during the regeneration of two monocarpic bamboos: self-thinning or intracolonial regulation? *J. Vegetation Sci.* 7:281–288.
- Maun, M.A. and J. Perumal. 1999. Zonation of vegetation on lacustrine coastal dunes: effects of burial by sand. *Ecol. Letters* 2:14–18.
- Nixon, J.L. 1993. Dynamics of prairie sandreed rhizome development. M.S. Thesis. Univ. Nebraska. Lincoln, Nebr.
- Northup, B.K. 1993. Utilization of native forages of the Nebraska Sandhills by yearling cattle. Ph.D. Diss. Univ. Nebraska. Lincoln, Nebr.
- Reece, P.E., T.L. Holman, and K.J. Moore. 1999. Late-summer forage on prairie sandreed dominated rangeland after spring defoliation. *J. Range Manage.* 52:228–234.
- Reece, P.E., J.E. Brummer, R.K. Engel, B.K. Northup, and J.T. Nichols. 1996. Grazing date and frequency effects on prairie sandreed and sand bluestem. *J. Range Manage.* 49:112–116.
- SAS. 1986. SAS/STAT users guide. Release 6.03. SAS Inst., Inc., Cary, N.C.
- Schmid, B., F.A. Bazzaz, and J. Weiner. 1995. Size dependency of sexual reproduction and clonal growth in two perennial plants. *Can. J. Bot.* 73:1831–1837.
- Searle, S.R., F.M. Speed, and G.A. Milliken. 1980. Populations marginal means in the linear model: an alternative to least squares means. *Amer. Statistician* 34:216–221.
- Weaver, J.E. 1965. Native vegetation of Nebraska. Univ. Nebraska Press. Lincoln, Nebr.
- Welch, T. G. 1968. Carbohydrate reserves of sand reedgrass under different grazing intensities. *J. Range Manage.* 21:216–220.
- White, L.M. 1977. Perenniality and development of shoots of 12 forage species in Montana. *J. Range Manage.* 30:107–110.
- Wikberg, S., B.M. Svensson, and B.A. Carlsson. 1994. Fitness, population growth rate and flowering in *Carex bigelowii*, a clonal sedge. *Oikos* 70:57–64.
- Willms, W.D., S.M. McGinn, and J.F. Dormaar. 1993. Influence of litter on herbage production in the mixed prairie. *J. Range Manage.* 46:320–324.

Seed longevity and seeding strategies affect sagebrush revegetation

D. TERRANCE BOOTH

Author is Rangeland Scientist, USDA-ARS, High Plains Grassl. Res. Sta., 8408 Hildreth Road, Cheyenne, Wyo. 82009.

Abstract

Three hypotheses were tested relating to Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* (Beetle and Young) revegetation on coal-mined land in Wyoming: (1) that fourwing saltbush (*Atriplex canescens* (Pursh) Nutt.) seeded > 2.2 kg pure live seed (pls)/ha would exclude sagebrush, (2) the contrasting view that the saltbush, as a "pioneer plant", facilitated sagebrush stand development [by promoting beneficial soil microbiological activity], and (3) that sagebrush stand development would be greater on fresh-stripped, than on stored, topsoil. The hypotheses were tested by comparing stand development on field plots: 1) seeded to sagebrush in February 1992, and March 1993; 2) fallowed in 1992, and sagebrush seeded in March 1993; 3) seeded to 'Wytana' fourwing saltbush in November, 1991, with sagebrush over-seeded in March, 1993, and; 4) no seeding. The experimental design was a randomized complete block with split plots of stored and fresh-stripped topsoil and with 3 replications. New sagebrush were detected annually through 4 post-seeding spring counts. Seed efficiency was affected by seeding strategy, but efficiency, density, and height were not affected by topsoil source. Proximity to saltbush did not affect sagebrush heights. The results imply that a 'Wytana' density ≤ 5 seedlings/m² is unlikely to deter or promote development of the sagebrush stand, but it will significantly increase total-shrub seed efficiency and density. Seeding strategies, particularly pre-sowing fallow and mixed-species seedings, will likely have a greater influence on sagebrush revegetation than will topsoil source when topsoils are handled as they were in this study.

Key Words: Wyoming big sagebrush, fourwing saltbush, reclamation, fallow, early seral species, pioneer plants, ecological restoration, soil erosion

Sagebrush (*Artemisia tridentata* Nutt.) and other xerophytic shrubs are a conspicuous component of western North American

Resumen

Se probaron tres hipótesis relacionadas a la revegetación de minas de carbón en Wyoming con "Wyoming big sagebrush" (*Artemisia tridentata* Nutt. ssp. *wyomingensis* (Beetle and Young): (1) que el "Fourwing saltbush" (*Atriplex canescens* (Pursh) Nutt.) sembrado a una densidad > 2.2 kg semilla pura viable/ha excluiría al "Sagebrush", (2) El punto de vista contrastante de que el "Saltbush", como una "planta pionera", facilitaría el desarrollo de la población de "Sagebrush" (al promover la actividad microbiológica benéfica del suelo) y (3) que el desarrollo de la población "Sagebrush" sería mayor en bandas de suelo superficial recién colocado (fresco) que en suelo almacenado. Las hipótesis se probaron comparando el desarrollo de poblaciones en parcelas de campo con los siguientes tratamientos: 1) "Sagebrush" sembrado en febrero de 1992 y Marzo de 1993; 2) barbechado en 1992 y "Sagebrush" sembrado en Marzo de 1993; 3) 'Wytana' fourwing saltbush sembrado en Noviembre de 1991 y sobresembrado con "Sagebrush" en Marzo de 1993 y 4) parcelas testigo sin sembrar. El diseño experimental fue un bloques completos al azar en parcelas divididas en el que la parcela grande fue el tipo de suelo y se tuvieron 3 repeticiones. A través de 4 años después de la siembra, en los conteos anuales de primavera, se detectaron nuevas plantas de "Sagebrush". La eficiencia de la semilla fue afectada por la estrategia de siembra, pero la eficiencia, densidad y altura no fueron afectadas por la fuente de suelo. La proximidad de "Saltbush" no afectó la altura del "Sagebrush". Los resultados implican que una densidad de 'Wytana' ≤ 5 plántulas/m² es improbable que impida o promueva el desarrollo de la población de "Sagebrush", pero incrementará significativamente la eficiencia total de la semilla del arbusto y la densidad. Las estrategias de siembra, particularmente el barbecho pre-siembra y las siembras de especies mezcladas, probablemente tendrá una mayor influencia en la revegetación de "Sagebrush" que la fuente de suelo, cuando las fuentes de suelo superficial son manejadas es manejado como en este estudio.

rangelands and provide key benefits to the function and utility of the ecosystems they occupy (McKell and Goodin 1973). For that reason they are encouraged, and in Wyoming are legally mandated (Federal Register 1996), for reclamation of coal-mined rangelands.

Several approaches have been tested for improving sagebrush establishment. These include sowing sagebrush and other shrubs without competing grasses, various surface seeding techniques, topsoil management (Monsen and Meyer 1990, Skilbred 1990, Schuman et al. 1998), sowing in combination with manipulated snow catchment, mulching, and sowing shrubs first and herbaceous plants later (Stevens et al. 1981, Brock 1982, Schuman et al. 1998).

This work was supported in part by the Abandoned Coal Mine Lands Research Program at the University of Wyoming. Support was administered by the Wyoming Dept. of Environmental Quality from funds returned to Wyoming from the Office of Surface Mining of the U.S. Dept. of Interior. I thank Scott Belden, Environmental Coordinator, North Antelope Coal Mine for his cooperation and assistance; Drs. E.J. Depuit and G.E. Schuman for their part in preparing the grant proposal; Dr. G.V. Richardson who consulted on statistical design, analyses, and interpretation; L.W. Griffith, P.K. Freeman, J.R. Cockrell, C.L. Mahelona, E.M. Taylor, and M.C. Mortenson who provided technical assistance; and Drs. E.J. Depuit, E.D. McArthur, and R.D. Piper for their critical review of an earlier version of this report. Mention of trade names is for information only and does not imply an endorsement.

Manuscript accepted 7 May 01.

Two hypotheses dominated Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* (Beetle and Young) revegetation discussions when this study was begun. The “exclusion” hypothesis stated that where fourwing saltbush (*Atriplex canescens* (Pursh) Nutt.) was seeded at 2.2 kg pure live seed (pls)/ha or greater rates, monotypic stands of that shrub would develop and exclude other shrubs, particularly sagebrush. The alternative or “pioneer plant” hypothesis held that poor soil physical characteristics and low levels of mycorrhizal inoculum in mined-land soils was the reason for poor stands of climax plants such as sagebrush (Booth 1985). Fourwing saltbush was recommended as an early seral species that could “...hasten the natural successional patterns” on New Mexico mined land by Wagner et al. (1978), and Booth (1985) postulated the shrub could function in that role in Wyoming. Meyer (1990) also suggested “pioneer” shrubs prepare reclaimed sites for later seral species. Therefore, I tested the “exclusion” and “pioneer” hypotheses on fresh-stripped and stored topsoil by monitoring sagebrush stands through 4 post-seeding growing seasons.

Materials and Methods

Site Description and Preparation

The research was conducted at the North Antelope Coal Mine, about 100 km south of Gillette, in Wyoming's Powder River Basin (43° 31' 41" N, 105° 17' 04" W). Precipitation in this continental climate ranges from 250 to 330 mm annually with 70% being received April–August (Table

1). Fresh topsoil was composed of a complex of loamy and clayey calcareous, mesic, shallow, Ustic Torrorthents (Schuman et al. 1998). The study was begun in August 1990, on 1/2 ha of leveled, regraded, and deep-ripped coal-mine spoil. Topsoil, which was either fresh-stripped or from a 5-year-old stockpile (designated as “stored”), was replaced to an average depth of 30 cm, ripped, and disked (topsoil stockpiles were 10- to 15-m-high mounds seeded to native cool-season grasses) (Schuman et al. 1998).

In late April 1991, ‘Step toe’ barley (*Hordeum vulgare* L.) was seeded at 50 kg pls/ha to produce a stubble mulch over the entire study site. In mid-July the barley was mowed to remove seed heads.

Seeding Strategy

The sagebrush seeding-strategy plots were installed as follows (treatment symbols are indicated in parentheses): 1) sagebrush seeded in 1992, and in 1993 (ARTRx2), 2) fallow in 1992, sagebrush seeded in 1993 (Fallow-ARTR), 3) fourwing saltbush seeded in fall 1991, and sagebrush seeded in 1993 (ATCA-ARTR) and, 4) no seeding (Control).

The fourwing saltbush was ‘Wytana’ (*Atriplex canescens* Nutt. ssp. *aptera* (A. Nels.)), obtained from the Bridger Plant Materials Center, Bridger, Mont. The seed was harvested in 1986 and had 92.4% purity and 14% germination with a TZ test of 7% (tested 5 Oct. 1990). Total viability was counted as 14%. ‘Wytana’ has 107,900 seeds/kg (J. Sheetz, personal communication) and was drilled at 26 kg pls/ha. The rate was equal to 2.6 g pls/m² (281 live seeds/m²) and was about 12 times greater

than the 2.2 kg pls/ha suggested by some to be an upper limit above which the resulting saltbush stand would competitively exclude other shrubs (Booth 1985). However, ‘Wytana’ is a smaller shrub than most commercially available fourwing saltbush. [It is also well adapted to the extreme temperatures common to eastern Montana and Wyoming (Soil Conservation Service 1988).]

Sagebrush seed was collected locally (Powder River Basin) in December 1991. It was cleaned using a debearer (Booth et al. 1997) and a clipper cleaner as is the standard commercial practice. The purity was 52% and the germination was 74% (tag values). Sagebrush was broadcast late February 1992, at 2.4 kg pls/ha and mid-March 1993, at 2.0 kg pls/ha. Wyoming big sagebrush has 4.0 to 5.4 million seeds per kg (Meyer, In press). At 4 million seeds/kg, seeding rates would have dispersed 960 and 800 seeds/m² in 1992, and 1993, respectively. No perennial grasses were seeded on any of the plots.

Data Collection

Sampling

Shrub stand development was monitored in 1992 with 9, systematically located 1-m² quadrats in each treatment plot (Mueller-Dombois and Ellenberg 1974, p.74). Fifteen, 1-m² permanent quadrats were used in 1993 and thereafter. Shrubs were counted each spring (late April to early June). Counts were made by placing colored markers by each shrub as they were identified. The markers were counted, the plot photographed using 35mm color-print film, and the markers recollected. The camera was equipped with a

Table 1. Monthly precipitation and mean monthly temperature, North Antelope Coal Company, Gillette, Wyo., 1992–1994. The 1978–1995 precipitation average is 32.3 cm.

Month	1992		1993		1994		1995		1996	
	Precip	Temp	Precip	Temp	Precip	Temp	Precip	Temp	Precip	Temp
	(cm)	(°C)	(cm)	(°C)	(cm)	(°C)	(cm)	(°C)	(cm)	(°C)
Jan	0	-0.6	0	-7.2	0.20	-3.3	0.05	-2.2	0.03	-7.8
Feb	0.68	2.2	0.38	-7.7	0.15	-6.1	0.66	-1.6	0.23	-2.8
Mar	3.15	4.4	1.47	2.2	0.41	3.3	0.97	0.6	0.56	-2.8
Apr	0.76	7.7	6.48	5.5	2.79	6.6	2.01	3.3	1.571	6.1
May	2.26	13.2	5.94	12.7	2.87	14.9	8.94	8.3	12.171	8.9
Jun	6.43	16.5	14.15	14.3	8.36	18.2	7.21	15.0	4.421	17.8
Jul	7.75	17.6	9.70	17.1	4.93	19.8	1.68	20.0	0.711	21.1
Aug	2.95	18.2	10.13	18.2	0.81	20.9	0.03	22.8	1.42	20.6
Sep	1.75	15.4	2.29	12.1	1.22	16.0	0.23	13.9	2.24	13.3
Oct	0.41	8.8	2.36	6.1	5.49	7.2	1.96	6.1	4.111	8.9
Nov	0.89	-0.6	0.36	6.1	5.49	7.2	0.10	4.4	0.25	-2.2
Dec	<u>1.19</u>	-6.6	<u>0.10</u>	-1.7	<u>0.05</u>	-1.7	<u>0</u>	-3.3	<u>0.29</u>	-4.4
Total	28.22		53.36		27.86		23.84		28.00	

¹Data recorded at Rochelle Mine due to sensor malfunction at North Antelope site.

28mm lens and was mounted 1.5 m above the center of the plot.

The color prints were used to track seedling populations during the study period. Prints were scanned using a Hewlett-Packard ScanJet 4C color scanner, then "MapInfo Professional" software (MapInfo Corporation, Troy, N.Y.) was used to map and monitor each seedling in all 360 quadrats for the 4 years that photographs were made.

Seed Efficiency Analysis

Seed efficiency is the number of live plants/unit of seed sown. I compared shrub seed efficiency as total shrubs (1996 count)/1,000 seeds and as number of sagebrush (1996 count)/1,000 seeds. Thus, seed efficiency reflects both seedling establishment and seedling survival. For these calculations I estimated sagebrush seeds at 4.0 million/kg (Meyer In press) and used 107,900 seeds/kg for 'Wytana'.

Shrub Density and Height Analysis

Shrub density (total shrubs/m²) was compared for 1996 without regard to seeding rates. Also for fall 1996, sagebrush height was measured for all plants in 1, randomly-selected quadrat per seeding-strategy plot. Sagebrush in the ATCA-ARTR treatment were segregated according to those plants that were within, or outside, an arbitrary 7.6-cm radius of a saltbush plant.

Experimental Design and Statistical Analysis

The experimental design was a randomized complete block with split plots and with 3 replications. Main plots were fresh and stored topsoil with seeding strategies randomly assigned within topsoils. Except for cohort analysis, the several statistical analyses used the "Mixed" procedure (SAS 1988, 1996, Littell et al. 1996). The "differences" option was used to compare least-square means.

Cohort counts within strategies across years were compared with confidence limits for the proportion, cohort count over the total of all cohorts, using the normal approximation (Steel and Torrie 1980, pages 478–479).

Results and Discussion

Seed Longevity and Cohorts

New sagebrush seedlings were detected from photographic data during all 4 annual counts made after March 1993. The pho-

Table 2. Count of live sagebrush in May, 1996, by age-class and seeding strategy, and test of cohort differences. Counts for 1993 include seedlings established in 1992 and 1993. Counts made fall of 1992 found 0.1 and 0.4 seedlings/m² in ARTRx2 fresh, and stockpiled topsoil. There were no sagebrush seedlings in any of the other plots in spring or fall of 1992.

STRATEGY	COHORT (Year Detected)			Total All Cohorts
	1996	1995	1993	
	(total 1996 sagebrush by count ²)			
Fallow-ARTR ¹	42 c	55 c	297 a	538
ARTRx2	42 d	74 c	286 a	644
ATCA-ARTR	14 b	46 b	64 b	308
Control	0	1	0	1

¹Fallow-ARTR= plots fallowed in 1992 and seeded to sagebrush in 1993; ARTRx2= sagebrush was seeded in 1992 and 1993; ATCA-ARTR= 'Wytana' seeded in 1992 and sagebrush over-seeded in 1993; and Control= not seeded.

²Total for 90 quadrats. Cohort values within rows followed by the same letter are not significantly different at $P \leq 0.05$ as tested by confidence limits for cohort/total proportions using the normal approximation (Steel and Torrie 1980). The Control was not tested due to lack of variance among years; confidence intervals for seeding strategies did not include 1 or 0. This implies that all other strategies were significantly greater than the Control and is the only valid comparison among strategies.

tographs also show that each cohort population—including the cohort resulting from the 1996 germination—was significantly greater than the control for all strategies (Table 2). Only 1 sagebrush was found among all unseeded plots in the study, evidence that; (1) the annual appearance of new seedlings in seeded plots did not result from natural seed dispersion and, (2) fresh-stripped topsoil did not act as a seed source.

Young and Evans (1989) reported basin big sagebrush (*Artemisia tridentata* Nutt. ssp. *tridentata*) did not maintain seed viability for more than a few months. However, seed dormancy in Wyoming big sagebrush may contribute to greater seed longevity (McDonough and Harniss 1974, Booth et al. 1997). This is the first study to measure the effect of Wyoming big sagebrush seed dormancy on seedling emergence from the soil, and to document the appearance of new seedlings during 4 annual post-seeding counts.

The 1994 cohort was the largest (Table 2). This was likely due to favorable 1993 weather (Table 1). Many seedlings likely established during the cool, wet, 1993 spring but remained too small to detect in 1993. Or, there may have been considerable 1993 post-count seedling establishment. In either case, the pulse in seedling establishment is consistent with other

reports of thick stands of sagebrush establishing with favorable weather conditions (Lommasson 1948, Went 1955, Booth et al. 1999).

The Need to Seed

The lack of shrubs on unseeded control plots (Table 2) is evidence of the need to seed shrubs, even on fresh-stripped topsoil. Howard and Samuel (1979) found < 0.1 sagebrush, and < 0.4 total-shrub seedlings/m² 1 year after fresh-stripped topsoil was spread at Kemmerer, Wyoming. Approximately the same result was obtained at Oak Creek, Colo. (Howard and Samuel 1979). These are unacceptably low densities (Federal Register 1996) for mines in shrub-dominated landscapes.

Benefits of High Sagebrush Seeding Rates

The ARTRx2 (sagebrush seeded in 1992, and in 1993) total seeding rate was 4.4 kg/ha or 1,760 seeds/m² and it produced the most sagebrush by the all-cohort count (Table 2). For comparison, Fallow-ARTR (fallow in 1992, sagebrush seeded in 1993) was seeded at 800 seeds/m² (2.0 kg/ha). Booth et al. (1999) reported a linear relationship between shrub densities of old (> 10 years) stands and shrub seeding

Table 3. Means for the sagebrush-only, seed efficiency analysis ($P = 0.15$ for differences among seeding strategies). Seeding-strategy symbols are as described in Table 2.

Seeding Strategy	Number sagebrush (mean/1,000 seeds)	Mean separations among seeding strategies
Fallow-ARTR	7.5	Fallow-ARTR vs. ARTRx2 $P = 0.08$
ATCA-ARTR	4.3	ARTRx2 vs. ATCA-ARTR $P = 0.82$
ARTRx2	3.9	ATCA-ARTR vs. Fallow-ARTR $P = 0.11$

Fig. 1. Seed efficiency as shrubs (1996 count)/1,000 seeds by seeding strategy. Means followed by the same letter are not different at $P < 0.001$ for ATCA-ARTR versus all other values, and at $P = 0.10$ for Fallow-ARTR versus ARTRx2. The seed efficiency of sagebrush within the ATCA-ARTR treatment is given for reference. Shrub seeding strategies and symbols are: ARTRx2 = sagebrush was seeded in 1992 and 1993; Fallow-ARTR = fallowed in 1992 and seeded to sagebrush in 1993; ATCA-ARTR = 'Wytana' saltbush seeded in 1992 and sagebrush over seeded in 1993, ATCA = 'Wytana' fourwing saltbush, ARTR = sagebrush. Data were calculated using 107,930 'Wytana' seeds/kg (J. Sheetz, personal communication) and 4.0 million Wyoming big sagebrush seeds/kg (Meyer, In press).

rates up to 1,000 seeds/m² for shrub-seed mixtures containing Wyoming big sagebrush. They recommended the 1,000 seeds/m² rate (2.5 kg/ha) for mixtures with Wyoming big sagebrush. These data support that recommendation.

Seed Efficiency as affected by Seeding Strategy and Topsoil Management

The ATCA-ARTR (fourwing saltbush seeded in fall 1991, sagebrush seeded in 1993) strategy had the greatest seed efficiency (total shrubs/1,000 seeds) and was the most consistently successful strategy (Fig. 1). The success of mixed-shrub seedings was also reported by Booth et al. (1999). Fallow-ARTR was the second most efficient strategy and ranked first when only sagebrush was considered (Fig. 1 and Table 3).

Lack of a difference in sagebrush seed efficiency between ARTRx2 and ATCA-ARTR (Table 3), suggests "Wytana" had no measurable effect (positive or negative) on sagebrush establishment and survival. Although 1993 precipitation was 165% of average, the remaining years of the study had below average precipitation (Table 1).

Thus, lack of a saltbush effect is not due to lack of competition for moisture in the year following seedling establishment.

Topsoil had no influence on sagebrush, or total shrub seed efficiency ($P = 0.82$ for sagebrush and $P = 0.76$ for total shrubs). The topsoil x seeding strategy interaction was also not significant ($P = 0.23$ for sagebrush and 0.32 for total shrubs).

Shrub Density Not Affected by Seeding Strategy or Topsoil Management

Shrub density (shrubs/m²) was not affected by seeding strategies ($P = 0.62$) or topsoil management ($P = 0.97$). The interaction was $P = 0.12$. This interaction is not

considered important because (1) interactions are more likely to show significance since they combine main effects, and (2) there is no consistent pattern among means (Table 4). Saltbush density averaged 5.0 shrubs/m² in the ATCA-ARTR treatments.

Table 4. Total shrub density (shrubs/m²) by topsoil and seeding strategies (topsoil x seeding strategy $P = 0.12$). Differences among means are not significant. Seeding strategy symbols are as described in Table 2.

Topsoil	Seeding Strategy	Density (Shrubs/m ²)
Stored	ARTRx2	10.2
	F-ARTR	4.9
	ATCA-ARTR	7.7
Fresh	ARTRx2	4.6
	F-ARTR	8.3
	ATCA-ARTR	9.5

Sagebrush Heights Not Affected by Seeding Strategy, Topsoil Management, or Proximity to Saltbush

Heights of sagebrush plants did not vary by seeding strategy ($P = 0.91$), topsoil ($P = 0.57$), the interaction ($P = 0.87$), or proximity to 'Wytana' fourwing saltbush ($P = 0.56$) (Table 5).

Soil Erosion

The annual photographs of 360 quadrants systematically located throughout the study area are a reliable record of soil surface conditions during the study. The photographs show barley straw remained on the plots through 1995, though by that time many perennial grasses and forbs were present. Erosion rills and soil pedestals do not appear in the photographs, nor were they noted when field data were collected.

Summary of Topsoil Results

There were no differences between fresh stripped and stored topsoil for any test variable ($P = 0.57$ for sagebrush height

Table 5. Sagebrush mean height (mm) by seeding strategy, topsoil source, and distance from "Wytana" fourwing saltbush. Means are not different (P values ≥ 0.56). Seeding-strategy symbols are as described in Table 2.

Seeding Strategy	Sagebrush height (mm)	Topsoil	Sagebrush height (mm)	'Wytana' distance	Sagebrush height
ARTRx2	48	Stored	54	≤ 7.6 cm	43
Fallow-ARTR	51	Fresh	48	> 7.6 cm	55
ATCA-ARTR	53				

was the lowest observed significance level of any test of topsoil effects). This was unexpected since the fresh-stripped topsoil contained greater numbers of vesicular mycorrhizae spores (Schuman et al. 1998). Also, Stahl et al. (1998) have shown in greenhouse studies that mycorrhizae-infected sagebrush seedlings survive greater drought stress than non-mycorrhizal seedlings. The reasons topsoil had no effect may be partly due to soil surface variation among the plots and replications. During 1993–1994 (see precipitation data in Table 1) parts of the study area subsided as much as 30 cm. (estimated), resulting in flow-patterns across plots and replications and decreasing site uniformity. Lack of a topsoil effect may also have been due to the management of the stored-topsoil (Schuman et al. 1998).

Whatever the reasons, detecting an effect from topsoil under field conditions was difficult even with uniform plots. In the adjacent study (Schuman et al. 1998), soil surfaces remained uniform but sagebrush densities on fresh-stripped topsoil were significantly greater ($P < 0.10$) than those on stored topsoil only where grass was not seeded (Table 2 and text, page 226, in Schuman et al. 1998).

The high sagebrush seed efficiency and shrub densities $\geq 1/\text{m}^2$ occurred on both types of soils, suggesting that micro-site moisture differences had a greater influence on sagebrush seedling establishment than did topsoil source; and, that stored topsoil, managed as in this study, will support dense stands of sagebrush (Table 4).

Fallowing and Shrub Stand Establishment

The Fallow-ARTR strategy produced significantly ($P = 0.10$) more surviving shrubs/1,000 seeds (1996 count) than were produced by the ARTRx2 strategy. Although the effect of this seeding strategy for the sagebrush-only analysis was marginally significant ($P = 0.15$), there are reasons to believe the strategy was as effective for sagebrush alone as for the 2 shrubs together.

Shrubs have extensive root systems that utilize moisture deep in the soil profile (West and Tueller 1972, Anderson et al. 1972) and fallowing is an effective means of replenishing that soil moisture. This is especially true for topsoiled areas protected by stubble mulch (Schuman et al. 1980, Schuman and Powers 1981). It is logical to conclude that a fallowing strategy would increase the seed efficiency of all shrubs

and I recommend it be tested in other situations for promoting shrub revegetation. Fallowing can also be effective without a stubble mulch. Chet Skilbred, Sr. Environmental Scientist for Glenrock Coal Company, Glenrock, Wyoming, offers the following for successful sagebrush revegetation (Nov. 1998 letter to author).

“Glenrock Coal Company's (GCC) field procedure is to deep rip (about 1 m) the regraded spoils and allow these spoils to accumulate moisture prior to application of the topsoil. Following application of about 76 cm of the topsoil, GCC again deep rips. This field practice seems to accelerate (moisture) recharge and provide a better seedbed.”

Meeting The Shrub Density Standard

The shrub densities that resulted from the seeding treatments are more than adequate to meet wildlife needs and environmental law (Table 4, Federal Register 1996). While I acknowledge the influence of 1993's favorable weather in producing high shrub densities, I also believe revegetation procedures that produced up to 10 times greater-than-required shrub densities (Table 4) with favorable weather, will be useful when weather patterns are less favorable.

There are several findings of this study that have application for meeting the Wyoming shrub density standard. One, there is the probable increase in seed efficiency from fallowing. Two, use of stubble-mulch-protected fallow with high Wyoming big sagebrush seeding rates (2.5 kg/ha) in a mix with other shrubs such as ‘Wytana’ is likely to result in synergistic increases in shrub densities. Three, as demonstrated by this study, high seeding rates for Wyoming big sagebrush are important for seeding-year establishment and to create a soil seed bank that may produce significant populations of new seedlings annually for 4 post-seeding growing seasons (Table 2). Four, as demonstrated by this study, seeding sagebrush with ‘Wytana’, where the ‘Wytana’ density is ≤ 5 seedlings/ m^2 , is unlikely to hinder sagebrush stand development. Where ‘Wytana’ was seeded with sagebrush the mixed-shrub stand was 43% sagebrush and the difference in total-shrub density equaled 10,000 more 1996-shrubs/ha than resulted from the double-seeding strategy, ARTRx2.

Conclusions

The “exclusion” and “pioneer-plant” hypotheses, as applied to fourwing saltbush on coal-mined land, are both rejected for lack of evidence. I also found no evidence that sagebrush stand development was greater on fresh-stripped topsoil than on topsoil stored for 5 years. I conclude that where soils are handled as they were in this study, the variability associated with micro-site moisture differences will have a greater effect on sagebrush establishment and survival than will topsoil source.

The soil-seed bank of Wyoming big sagebrush remained viable and capable of producing seedlings through 4 post-seeding growing seasons and I believe that situation will occur with most Wyoming big sagebrush seedlings of good quality seed. Lastly, I believe fallowing to be an effective tool for shrub revegetation.

Literature Cited

- Anderson, D.J., R.A. Perry, and J.H. Leigh. 1972. Some perspectives on shrub / environment interactions, p. 172–181. *In*: C.M. McKell et al.(eds), Proc. wildland shrubs - their biology and utilization, July 1971, Logan, Ut., Intermount. Forest and Range Exp. Sta., Gen. Tech. Rep. INT-1, Forest Serv., Ogden, Ut.
- Booth, D.T. 1985. The role of fourwing saltbush in mined land reclamation: a viewpoint. *J. Range Manage.* 38:562–565.
- Booth, D.T., Y. Bai, and E.E. Roos. 1997. Preparing sagebrush seed for market: effects of debearder processing. *J. Range Manage.* 50:51–54.
- Booth, D.T., J.K. Gores, G.E. Schuman, and R.A. Olson. 1999. Shrub densities on pre-1985 reclaimed mine lands in Wyoming. *J. Restoration Ecol.* 7:1–9.
- Brock, J.H. 1982. Interseeding and interplanting techniques for southwest reclamation, p.192–195. *In*: E.F. Aldon and W.R. Oaks (eds), Proc. reclamation of mined lands in the Southwest, Oct. 1982, Albuquerque, N.M., New Mexico Chapter Soil Conserv. Soc. Amer., Albuquerque, N.M.
- Federal Register. 1996. Office of Surface Mining and Enforcement. 30 CFR Part 950. Wyoming Regulatory Program - final rule; approval of amendment. 61 (152):40735.
- Howard, G.S. and M.J. Samuel. 1979. The value of fresh-stripped topsoil as a source of useful plants for surface mine revegetation. *J. Range Manage.* 32:76–77.
- Littell, R.C., G.A. Milliken, W.W. Stroup, and R.D. Wolfinger. 1996. SAS system for mixed models. SAS Inst. Inc., Cary, N.C.
- Lommasson, T. 1948. Succession in sagebrush. *J. Range Manage.* 1:19–21 (reprinted in *Rangelands* 15 (1993):109–110).

- McDonough, W.T. and R.O. Harniss. 1974.** Effects of temperature on germination in three subspecies of big sagebrush. *J. Range Manage.* 27:204–205.
- McKell, C.M. and J.R. Goodin. 1973.** United States arid shrublands in perspective, p. 12–18. *In: Proc. 3rd Workshop of U.S. / Australia Rangelands Panel*, Tucson, Arizona. Soc. for Range Manage. Denver, Colo.
- Meyer, S.E. 1990.** Shrubland restoration—an ecologist's perspective. Handout: Workshop on plant species and wildlife habitat establishment successes and failures. Billings, Mont. USDA Forest Service, Intermountain Research Station, Shrub Sci. Lab., Provo, Ut.
- Meyer, S.E.** In press. *Artemisia*. *In: F. Bonner and S. Krugman (eds). Woody plant seed manual*, 3rd edition. USDA-Forest Service. (electronic pre-print available at: <http://www.wpsm.net/Genera.htm#e>)
- Monsen, S.B. and S.E. Meyer. 1990.** Seeding equipment effects on establishment of big sagebrush on mine disturbances, p. 192–199. *In: Proc. 5th Billings symposium on disturbed land rehabilitation*, Mar. 1990, Billings, Mont., (Vol. I), Reclam. Res. Unit. Pub. No. 9003, Montana State Univ., Bozeman, Mont.
- Mueller-Dombois, D. and H. Ellenberg. 1974.** Aims and methods of vegetation ecology. John Wiley and Sons, N.Y.
- SAS. 1988.** SAS/STAT user's guide, release 6.03 Edition. SAS Inst. Inc., Cary, N.C.
- SAS. 1996.** SAS/STAT software: changes and enhancements through release 6.11. SAS Inst. Inc., Cary, N.C.
- Schuman, G.E. and J.F. Power. 1981.** Topsoil management on mined lands. *J. Soil and Water Conserv.* 36:77–78.
- Schuman, G.E., D.T. Booth, and J.R. Cockrell. 1998.** Cultural methods for establishing stands of Wyoming big sagebrush on mined lands. *J. Range Manage.* 51:223–230.
- Schuman, G.E., E.M. Taylor, Jr., F. Rauzi, and G.S. Howard. 1980.** Standing stubble versus crimped straw mulch for establishing grass cover on mined lands. *J. Soil and Water Conserv.* 35:25–27.
- Skilbred, C.L. 1990.** Direct seeding of sagebrush species on regraded mine lands in east central Wyoming. Handout: Workshop on plant species and wildlife habitat establishment successes and failures, Billings, Mont. Glenrock Coal Co., Glenrock, Wyo.
- Soil Conservation Service (SCS). 1988.** Plant materials handbook. Distributed by US Dept. of the Interior, Office of Surface Mining, Reclamation and Enforcement.
- Stahl, P.D., G.E. Schuman, S.M. Frost, and S.E. Williams. 1998.** Arbuscular mycorrhizae and water stress tolerance of Wyoming big sagebrush seedlings. *Soil Sci. Soc. Amer. J.* 62:1309–1313.
- Stevens, R., W.L. Moden, and D.W. McKenzie. 1981.** Interseeding and transplanting shrubs and forbs into grass communities. *Rangelands* 2:55–58.
- Steel, R.G.D. and J.H. Torrie. 1980.** Principles and procedures of statistics. McGraw-Hill Book Company, N.Y.
- Wagner, W.L., W.C. Martin, and E.F. Aldon. 1978.** Natural succession on strip-mined lands in northwestern New Mexico. *Reclamation Rev.* 1:67–73.
- Went, R.W. 1955.** The ecology of desert plants. *Scientific Amer.* 192:68–75.
- West, N.E. and P.T. Tueller. 1972.** Special approaches to studies of competition and succession in shrub communities, p. 165–171. *In: C.M. McKell et al. (eds), Proc. wildland shrubs—their biology and utilization*, July 1971, Logan, Ut., Intermount. Forest and Range Exp. Sta., Gen. Tech. Rep. INT-1, Forest Serv., Ogden, Ut.
- Young, J.A. and R. Evans. 1989.** Dispersal and germination of big sagebrush (*Artemisia tridentata*) seeds. *Weed Sci.* 37:201–206.

Herbicide residues and perennial grass on establishment perennial pepperweed sites

JAMES A. YOUNG, CHARLIE D. CLEMENTS, AND ROBERT R. BLANK

Authors are Range Scientists and Soil Scientist, USDA, Agricultural Research Service, 920 Valley Road, Reno, Nev. 89512.

Abstract

Perennial pepperweed (*Lepidium latifolium* L.) is a creeping rooted exotic weed that has infested native hay meadows, riparian areas and agronomic fields throughout the western United States. This highly invasive species causes major losses in forage quality and creates numerous management problems. On many sites infested with perennial pepperweed, a near mono-culture exist. Sustainable suppression programs require the establishment of a competitive perennial species. You can not establish seedlings of a perennial competitive species without some initial substantial reduction in perennial pepperweed stands through weed control. Because tillage is not feasible with this creeping rooted species, herbicidal weed control is the primary option. Experience has shown, that the massive and extensive root system of perennial pepperweed can not be completely eliminated with one application of a herbicide. This means that repeated applications of a selective herbicide are required after the perennial seedlings of a competitive species are established. Perennial pepperweed is a broadleaf species that is somewhat susceptible to applications of 2,4-D. Therefore, the choice revegetation species is limited to a perennial grass that is resistant to 2,4-D applications at low rates as a seedlings and moderate rates once established. The saline/alkaline nature of the soils where perennial pepperweed is often found limit the adapted perennial grasses to tall wheatgrass (*Elytriga elongata* [Host] Nevski). The herbicide chlorsulfuron has been shown to be more effective in initially controlling perennial pepperweed than 2,4-D. We determined that applications of chlorsulfuron at rates sufficient to control perennial pepperweed resulted in herbicidal residues that severely reduced or eliminated the establishment of tall wheatgrass seedlings. Application of 2,4-D at flower budding for perennial pepperweed (June), followed by seeding tall wheatgrass in the fall (October), and application of low rates of 2,4-D over the wheatgrass seedlings the next spring (May), gave the best grass seedling establishment and suppression of the perennial weed.

Resumen

El "Pepperweed" (*Lepidium latifolium* L.) perenne es una maleza exótica de enraizamiento rastrero que ha infestado las praderas nativas para producción de heno, las áreas ribereñas y los campos de cultivo del oeste de los Estados Unidos. Esta especie altamente invasiva causa pérdidas mayores en la calidad del forraje y crea numerosos problemas de manejo. En muchos sitios infestados el "Pepperweed" perenne casi forma un monocultivo. Los programas de supresión sustentable requieren del establecimiento de especies perennes competitivas, pero usted no puede establecer plántulas de especies perennes competitivas sin una reducción substancial inicial de "Pepperweed" perenne mediante el control de la maleza. Debido a que la labranza no es factible con estas especies de enraizamiento rastrero, el control con herbicidas es la principal opción. Las experiencias han mostrado que el sistema radical masivo y extenso del "Pepperweed" perenne puede no ser completamente eliminado con una aplicación de herbicida, esto significa que se requieren aplicaciones repetidas de un herbicida selectivo después de que las plántulas de especies perennes competitivas son establecidas. El "Pepperweed" perenne es una especie de hoja ancha que es algo susceptible a las aplicaciones de 2,4-D. Por lo tanto la elección de las especies para revegetación esta limitada a los zacates perennes que son resistentes a las aplicaciones de 2,4-D en bajas dosis cuando el zacate esta en etapa de plántula y a las aplicaciones moderadas una vez que esta establecido. La naturaleza salina/alcalina de los suelos donde a menudo se encuentra el "Pepperweed" perenne limita la selección al zacate perenne "Tall wheatgrass" (*Elytriga elongata* [Host] Nevski), adaptado a estas condiciones. El herbicida chlorsulfuron ha mostrado ser mas efectivo en el control inicial del "Pepperweed" perenne que el 2,4-D. Determinamos que aplicaciones de chlorsulfuron en dosis suficientes para controlar el "Pepperweed" perenne resultan en residuos del herbicida que reducen severamente o eliminan el establecimiento de plántulas de "Tall wheatgrass". Las aplicaciones de 2,4-D en la etapa de aparición de las yemas florales del "Pepperweed" perenne (Junio), seguida por la siembra de "Tall wheatgrass" en otoño (Octubre) y la aplicación en la próxima primavera (Mayo) de dosis bajas de 2,4-D sobre las plántulas de "Tall wheatgrass" dan el mejor establecimiento de las plántulas de zacate y la supresión de la maleza perenne.

Key Words: Chlorsulfuron, tall wheatgrass, saline/alkaline soils

Perennial pepperweed (*Lepidium latifolium* L.), a native to eastern Europe and Asia (Robbins 1940), was accidentally introduced into North America early in the 20th century (Young et al. 1995). A member of the mustard family, this weed has spread to portions of all western states and adjacent Canada. In the Intermountain Area, perennial pepperweed first became established in riparian and wetland areas. It spread to native hay mead-

ows and alfalfa (*Medicago sativa* L.) fields. Native hay meadows located on flood plains are particularly susceptible to perennial pepperweed invasion. The weed is highly adapted, but not restricted to growth on salt affected soils and soils with sodium hazards (Blank and Young 1997).

Perennial pepperweed plants can produce large quantities of viable seeds (Miller et al. 1986). The plants have extensive creeping root systems. Very small fragments of these roots will produce new plants (Young et al. 1997). This makes mechanical control by tillage virtually impossible.

The invasion of native hay meadows by perennial pepperweed is a threat to the range livestock industry of the Intermountain Area because these meadows are a critical portion of the forage base for both hay production and grazing of crop aftermath. Perennial pepperweed can be partially suppressed by grazing, but if grazing is deferred for hay production the plants become quite woody and the resulting hay is of very poor quality. If herbicidal weed control is practiced on these meadows with near mono-cultures of perennial pepperweed, spontaneous regeneration of the meadow is very slow and re-invasion of the weed will occur. This makes seeding of a perennial forage species necessary. The choice of revegetation for these seasonally dry meadows with salt affected soils is limited. Tall wheatgrass (*Elytrigia elongata* [Host] Nevski) is the most widely used species.

The standard herbicide for control of perennial pepperweed has traditionally been 2,4-D [(2,4-dichlorophenoxy) acetic acid] (Young et al. 1998). More recently, herbicides of the sulfonyleurea family, especially chlorsulfuron {2-chloro-N-[(4-methoxy-6-methyl-1, 3, 5-triazin-2-yl) -aminocarbonyl] benzenesulfonamide} have been found to be very effective for the control of perennial pepperweed. Both 2,4-D and chlorsulfuron can be applied at appropriate rates and kill perennial pepperweed in established stands of meadow species and not injure the perennial grasses and grass-like species (Young et al. 1998).

To give the perennial grass plants a chance to biologically suppress perennial pepperweed, repeated herbicide applications are necessary over the seedling stands. This obviously requires the use of a selective herbicide.

The longevity of chlorsulfuron residues and their influence upon tall wheatgrass seedling establishment was unknown for the saline/alkaline soil environments of native hay meadows. Our purpose was to compare seedling establishment of tall wheatgrass on sites where perennial pepperweed was controlled with 2,4-D or chlorsulfuron applications.

Methods

Field trials were located at the main Station Farm of the Nevada Agricultural Experiment Station at Reno, Nev. (39.30 N. Lat., 119.42 W. Long.). The site was a previously irrigated field which in 1993 became so dominant with perennial pepperweed that crop production was no longer feasible. All weed control and seeding trials in this study were conducted without irrigation. The site is on the flood plain of the Truckee River at the confluence of Steamboat Creek. The topographic position of the site is very similar to typical native hay meadows in the Intermountain Area. The principal soil is the Voltaire series, a fine-loamy, mixed, mesic Fluvaquertic Haplaquoll. Soils are moderately to highly influenced by accumulations of salts. The electro-conductivity of the surface soil ranged from 7.4 to 9.8 s m⁻¹ during the summer months. The soil profiles have a well developed natric horizon.

Herbicides were applied with 484 liter ha⁻¹ of water with a boom mounted on an all-terrain vehicle. Initial herbicide applications were made in mid June when perennial pepperweed was in the flower bud stage. The following October, the cultivar Largo of tall wheatgrass was seeded with a rangeland drill at the rate of 7.2 kg/ha. The initial treatments were, 2,4-D as an amine at 2.2 kg/ha, chlorsulfuron at 71 g/ha, and control. The plots 30 by 100 m in area were arranged in a randomized block design. Initial herbicide application was in June 1996. On separate plots the treatments were repeated in 1996, 1997, and 1998. In April of 1997, one half of

Table 1. Density per m² perennial pepperweed plants in May and October 1997, 1998, and 1999 for treatments made in 1996, 1997, 1998.¹

Treatment	Year applied	Year sampled	Perennial pepperweed density	
			May	Oct.
			-- plants/m ² --	
Control	1996	1997	14.1b	24.1a
	1997	1998	20.1a	23.6a
	1998	1999	21.4a	24.6a
2,4-D	1996	1997	0.1c	4.0c
	1997	1998	0.1c	4.6c
	1998	1999	0.1c	5.2c
Chlorsulfuron	1996	1997	0.1c	0.1c
	1997	1998	0.1c	0.1c
	1998	1999	0.1c	0.1c

each treatment plot was sprayed with 0.6 kg/ac of 2,4-D over top of the tall wheatgrass seedlings. This was also done for the 1997 and 1998 treatments. The treatments that did not have establishment of tall wheatgrass seedlings were re-seeded each subsequent October. For example the plots originally seeded in 1996 were seeded again in 1997 and again in 1998, if no seedlings established.

The plots were evaluated in May and October annually by randomly locating 4 quadrants 1 m² in each treatment. The density of tall wheatgrass plants per meter of row was determined by randomly locating 10 plots 1 m in length along the drill rows in each treatment and counting the plants. Data were subject to analysis of variance and means separated by Duncan's Multiple Range Test.

Table 2. Density per m² of perennial pepperweed plants in October 1997, 1998 and 1999 for treatments made in 1996, 1997, and 1998 and re-treated with 0.6 kg/ha of 2,4-D in May 1997, 1998, and 1999.¹

Treatment	Year applied	Year sampled	2,4-D re-applied	Perennial pepperweed density
				October (plants/m ²)
Control ²	—	—	—	24.1a
Control	1996	1997	1997	8.4a
	1997	1998	1998	20.1a
	1998	1999	1999	19.9a
2,4-D	1996	1997	1997	0.8b
	1997	1998	1998	0.3b
	1998	1999	1999	0.4b
Chlorsulfuron	1996	1997	1997	0.0b
	1997	1998	1998	0.1b
	1998	1999	1999	0.1b

¹Means followed by the same letter are not significantly different at the 0.01 level of probability as determined by Duncan's Multiple Range Test.

²Average of the control plots that were not re-treated with 2,4-D from 1996 through 1998.

Table 3. Density of tall wheatgrass plants per meter of row in May 1997, 1998, and 1999 (seedling year) and plant density on same plots in 1998, 1999, and 2000 (second season after planting) with and without re-application of 0.6 kg/ha of 2,4-D.¹

Treatment and year seeded		Tall wheatgrass density			
		Without second 2-4-D Application		With second 2-4-D Application	
		Seedlings	2 nd year plants	Seedling	2 nd year plants
------(per m of row)-----					
Control	1996	0	0	0	0
	1997	0	0	0	0
	1998	0	0	0	0
2,4-D	1996	0b	0b	7.1a	6.4a
	1997	0.1b	0b	9.1a	7.8a
	1998	0.3b	0b	8.6a	7.4a
Chlorsulfuron	1996	0	0	0	0
	1997	0	0	0	0
	1998	0	0	0	0

¹Within treatments means followed by the same letters are not significantly different at the 0.01 level of probability as determined by Duncan's Multiple Range Test. No letters no differences. Seedling and second year plants compared separately.

Results and Discussion

In May, 11 months after herbicide application, the control of perennial pepperweed plants with either 2,4-D or chlorsulfuron applications appears excellent (Table 1). By October of the year after application, there had been considerable return of perennial pepperweed in the plots treated with 2,4-D.

Application of a light rate of 2,4-D (0.6 kg/ha) over the top of the tall wheatgrass seedlings the spring after they were planted, did not significantly ($P \geq 0.01$) reduce the density of perennial pepperweed in control treatments (Table 2). It did significantly reduce the density of perennial pepperweed in plants in plots that had in the previous year been treated with 2.2 kg/ha of 2,4-D. The 2,4-D treatment over the seedlings had no influence on the few perennial pepperweed plants that existed on the plots previously treated with chlorsulfuron.

The establishment of tall wheatgrass seedlings was very straight forward. If you did not control perennial pepperweed no tall wheatgrass seedlings established (Table 3). If you initially controlled perennial pepperweed with applications of 2,4-D a few seedlings of tall wheatgrass were initially present, but no plants were present the second year after seeding. If you initially controlled perennial pepperweed with 2,4-D and followed with a lower rate of 2,4-D over the seedlings the spring after the seeds were planted, very good stands of tall wheatgrass were obtained (Table 3). The plots treated with chlorsulfuron remained virtually free of perennial pepperweed, but no seedling establishment of tall wheatgrass occurred.

The plots treated with chlorsulfuron were re-seeded annually with tall wheatgrass. The plots where chlorsulfuron was applied in 1996, were seeded in 1996, 1997, 1998, and 1999. Tall wheatgrass seedlings never established on these areas. Until 1999, the areas initially treated with chlorsulfuron remained weed free except for occasional plants of perennial pepperweed that escaped the initial herbicide application. In 1999 Russian thistle (*Salsola turgus* L.), lamb's quarter (*Chenopodium album* L.), and annual kochia (*Kochia scoparia* [L.] Schrader) plants grew on the treated area, but seedlings of tall wheatgrass were not found in the spring 2000.

These large, replicated experimental treatments were repeated for 3 consecutive years with highly consistent results. Diehard defenders of chlorsulfuron point out that we have done no chemical analysis of the soil to prove that residues of the herbicide are responsible for the failure to establish tall wheatgrass seedlings. The consistency of seedling failure in plots treated with chlorsulfuron while side by side plots treated with 2 applications of 2,4-D have excellent stands of the perennial grass is very compelling evidence for persistent residues. The failure of annual weeds to invade areas treated with chlorsulfuron for 3 years is additional evidence for the existence of residues.

The few perennial pepperweed plants that escape initial applications of chlorsulfuron are a cause of concern. They increased in area by extending creeping roots and putting up additional stems even though perennial grass seedlings could not be established on the plots. The plants are not necessarily resistant to chlorsulfuron.

They may be accidents of faulty herbicide distribution in the initial application and their depth of rooting allows them to spread below soil horizons with herbicide residues. The existence, persistence, and spread of these plants creates an additional hazard with the use of chlorsulfuron to control perennial pepperweed.

The apparent persistence of chlorsulfuron residues that limit perennial grass establishment is probably heightened by the high pH of the salt affected soils on the study site. Most native hay meadows where perennial pepperweed is invading have similar soils.

Literature Cited

- Blank, R. R. and J. A. Young. 1997. *Lepidium latifolium*: Influences on soil properties, rate of spread, and competitive stature. pp. 69-80 In: J. H. Brock, W. Wade, P. Pysek, and D. Green (eds.) Plant Invasion: Studies From North America and Europe. Backhuys Publ., Leiden, The Netherlands.
- Miller, G. K., J. A. Young, and R. A. Evans. 1986. Germination of seeds of perennial pepperweed. Weed Sci. 34:252-255.
- Robbins, W. W. 1940. Alien plants growing without cultivation in California. Bull. 637. Calif. Agr. Exp. Sta., Berkeley, Calif.
- Young, J. A., D. E. Palmquist, and R. R. Blank. 1998. The ecology and control of perennial pepperweed (*Lepidium latifolium* L.) Weed Techn. 12:402-405.
- Young, J. A., D. E. Palmquist, and S. O. Wotring. 1997. The invasive nature of *Lepidium latifolium*: A review. pp. 59-68 In: J. H. Brock, W. Wade, P. Pysek, and D. Green (eds.) Plant Invasion: Studies From North America and Europe. Backhuys Publ., Leiden, The Netherlands.
- Young, J. A., C. E. Turner, and L. F. James. 1995. Perennial pepperweed. Rangelands 17:121-123.

Drought and grazing: IV. Blue grama and western wheatgrass

E.J. ENEBOE, B.F. SOWELL, R.K. HEITSCHMIDT, M.G. KARL, AND M.R. HAFERKAMP

Authors are former graduate student and Associate Professor, Dept. of Animal and Range Sci. Mont. State Univ., Bozeman, Mont. 59715; Supervisory Rangeland Scientist, former Postdoctoral Rangeland Scientist, and Rangeland Scientist USDA-ARS, Fort Keogh Livestock and Range Research Laboratory, 243 Fort Keogh Rd., Miles City, Mont. 59301.

Abstract

An understanding of the impacts of grazing during and following drought on rangeland ecosystems is critical for developing effective drought management strategies. This study was designed to examine the effects of drought and grazing on blue grama [*Bouteloua gracilis* (H.B.K) Lag. ex Griffiths] and western wheatgrass [*Pascopyrum smithii* Rydb. (Love)] tiller growth dynamics. Research was conducted from 1993 to 1996 at the Fort Keogh Livestock and Range Research Laboratory located near Miles City, Mont. An automated rainout shelter was used during 1994 to impose a severe late spring to early fall (May to October) drought on 6 of twelve, 5- x 10-m non-weighing lysimeters. Twice replicated grazing treatments were: 1) grazed both the year of (1994) and the year after (1995) drought; 2) grazed the year of and rested the year after drought; and 3) no grazing either year. Drought had minimal impact on tiller relative growth rates of plants grazed twice, although it reduced ($P \leq 0.01$) rates of axillary tiller emergence for blue grama (79%) and western wheatgrass (91%). Defoliation periodically increased relative growth rates ($P \leq 0.05$) and tiller emergence ($P \leq 0.01$) of both species. Neither drought nor grazing affected tiller densities or tiller replacement rates of either species nor did they affect productivity of blue grama. Drought, however, reduced ($P \leq 0.01$) productivity of western wheatgrass 50% in 1994 whereas grazing reduced productivity ($P \leq 0.01$) by 46% in 1994 and 69% in 1995. Moderate stocking levels (40–50% utilization) during and after drought did not adversely affect the sustainability of these dominant native grasses.

Key Words: *Bouteloua gracilis*, *Pascopyrum smithii*, production, rainout shelter, rest, water potential

The Northern Great Plains support 7 million animal units (AUs) in the U.S. and Canada (USDA 1993, Willms and Jefferson 1993). Campbell (1936) stated that 2 or 3 years out of 10 would be drought years in the Northern Great Plains. Drought and grazing can affect plant productivity and decrease plant longevity (Ludlow 1986). Large portions of plant communities within the Northern Great Plains are dominated by blue grama (*Bouteloua gracilis*,

Resumen

Un entendimiento de los impactos del apacentamiento durante y después de la sequía en los ecosistemas de pastizal es crítico para desarrollar estrategias efectivas de manejo de la sequía. Este estudio se diseñó para examinar los efectos de la sequía y el apacentamiento en la dinámica de crecimiento de los hijuelos de “Blue grama” [*Bouteloua gracilis* (H.B.K) Lag. ex Griffiths] y “Western wheatgrass” [*Pascopyrum smithii* Rydb. (Love)]. La investigación se condujo de 1993 a 1996 en el Laboratorio de Investigación de Ganado y Pastizales Fort Keogh cerca de Miles City, Mont. Durante 1994 se utilizó un protector de lluvia automatizado para aplicar una sequía severa de fines de primavera e inicios de otoño (Mayo a Octubre) en 6 de los 12 lisímetros de 5 x 10 m. Los tratamientos de apacentamiento se repitieron 2 veces y fueron: 1) apacentado en el año de la sequía (1994) y el año siguiente (1995), 2) apacentado el año de la sequía y descansado el año siguiente y 3) sin apacentamiento en ambos años. La sequía tuvo un impacto mínimo en las tasas relativas de crecimiento de los hijuelos de plantas apacentadas doble, aunque redujo ($P \leq 0.01$) las tasas de emergencia de hijuelos auxiliares del “Blue grama” (79%) y “Western wheatgrass” (91%). La defoliación periódica incrementó las tasas relativas de crecimiento ($P \leq 0.05$) y la emergencia de hijuelos ($P < 0.01$) de ambas especies. Ni la sequía ni el apacentamiento afectaron las densidades de hijuelos o las tasas de remplazo de estos en ninguna de las especies, tampoco afectaron la productividad del “Blue grama”. Sin embargo, la sequía redujo la productividad ($P \leq 0.01$) de “Western wheatgrass”, en 50% en 1994, mientras que el apacentamiento redujo la productividad ($P \leq 0.01$) en 46% en 1994 y 69% en 1995. Niveles moderados de carga (40–50% de utilización) durante y después de la sequía no afectan adversamente la sustentabilidad de estos zacates nativos dominantes.

[H.B.K] Lag. ex Griffiths) and western wheatgrass (*Pascopyrum smithii*, Rydb.). It is apparent that these 2 plant species have evolved with the combined effects of drought and herbivory. Therefore, it is important when managing rangelands to know how individual plants persist in the face of these stressors.

Many researchers have examined the role of tillers in plant survival (Richards et al. 1987, Olson and Richards 1988, Bullock et al. 1994, Zhang and Romo 1995), but quantitative studies on the impacts of grazing during and after drought on tiller population dynamics are lacking. It has been hypothesized that grazing during and following drought can suppress recovery rates of individual plants as well as plant communities (Pieper and Heitschmidt

This research was conducted under a cooperative agreement between USDA-ARS and the Montana Agric. Exp. Sta. Mention of a proprietary product does not constitute a guarantee or warranty of the product by USDA, Montana Agric. Exp. Sta., or the authors and does not imply its approval to the exclusion of other products that may also be suitable. USDA-Agricultural Research Service, Northern Plains Area, is an equal opportunity/affirmative action employer and all agency services are available without discrimination.

Manuscript accepted 26 Mar. 01.

1988, Burkhardt 1996). To test this hypothesis, we examined the effects of grazing during and after a growing season drought on xylem water potentials, tiller relative growth rates (RGR), seasonal axillary tiller emergence, annual tiller replacement, tiller densities, and aboveground net primary production (ANPP) of blue grama and western wheatgrass. Heitschmidt et al. (1999) have published effects of drought on soil water, vegetative productivity and plant species composition.

Materials and Methods

Study Area

This study was part of a large rainout shelter project conducted on the USDA, ARS Fort Keogh Livestock and Range Research Laboratory near Miles City, Mont. (46°19'45"N 105°49'45"W). This area is representative of the semi-arid mixed grass prairie of the Northern Great Plains. Native vegetation on the 22,500-ha research station is a grama-needlegrass-wheatgrass (*Bouteloua-Stipa-Agropyron*) mix (Küchler 1964). Long-term annual precipitation averages 34-cm (NOAA 1996) with about 60–70% received during the mid-April through mid-September growing season (Fig 1). Temperatures may exceed 38°C during summer and decrease to –40°C during winter. The average frost-free period is 150 days.

The experiment was conducted from 1993 to 1996 on native rangeland that had not been grazed 2 years prior to the study. Precipitation was 30% (530 mm) above average (NOAA 1996) the year before the study. The study site was located on a gently sloping (4%), clayey range site in high fair range condition. The soils were very deep, well-drained, fine, montmorillonitic, frigid Aridic Ustochrepts. Vegetation at the site was dominated by blue grama (40–45% by weight) and western wheatgrass (30–35% by weight).

Lysimeters and Treatments

Twelve, 5- X 10-m non-weighing lysimeters were arranged perpendicularly to the slope along a 65-m transect in 2 groups of 6 lysimeters with a 5-m area between groups within a grazing enclosure. An automated rainout shelter was constructed to control the amount of precipitation received on 1 of the 2 sets of 6 lysimeters. The 12- X 35-m metal framed "roof" was mounted on 15-cm diameter plastic wheels atop seven, 5-cm wide rails stationed about 75-cm above the soil surface. Rails extended from the top edge

Fig. 1. Monthly precipitation (cm) from January 1993 through December 1996 and long-term (115 yr) average at Miles City, Mont. including the drought treatment in 1994 (NOAA 1996; Heitschmidt et al. 1999).

(i.e., upslope) to 15-m below the bottom edge of the lysimeters. Rails were located directly over lysimeter borders. The shelter was equipped with a moisture sensitive conductance plate that when wetted, activated a small electric motor and its associated drive system, which moved the shelter across the lysimeters.

Following the 1993 pre-treatment baseline year, twice replicated treatments were: 1) grazed during the year of drought and rested the year after, hereafter referred to as G94; 2) grazed both the year of the simulated drought and the year after, hereafter referred to as the G94-95; and 3) rested in all years, hereafter referred to as the ungrazed treatment (UG). The same 3 treatments were repeated in the non-drought set of lysimeters. Lysimeters were grazed intensively with 6 ewes and their twin lambs for a few hours in early June and early July of both 1994 and 1995 to achieve 40–50% utilization. The simulated drought was imposed (1 growing season) from mid-May to early October 1994.

Precipitation, Soil Water, and Xylem Water Potentials

Precipitation was monitored on site using standard rain gauges (Heitschmidt et al. 1999). Soil water was estimated a minimum of once a month from April through October at depths of 15-, 30-, 60-, 90- and 120-cm using a dielectric soil water probe (Heitschmidt et al. 1999).

Xylem water potentials of blue grama and western wheatgrass plants growing in the ungrazed drought and non-drought treatments were estimated on 7 dates between 18 May and 28 July, 1994 and 6 dates between 15 May and 2 August,

1995. Measurements were made at 0430 and 1230 hours on the youngest fully expanded leaves of individual plants using standard pressure chamber techniques (Scholander et al. 1965). Sample plants were randomly selected along a transect within each lysimeter. Sample size per species/sample date/sample time/lysimeter was 1 in 1994 and 2 in 1995.

Tiller and Production Measurements

Six permanent 14- X 18-cm quadrats per lysimeter were randomly established within mixed blue grama and western wheatgrass communities. Quadrat locations were restricted to areas not previously sampled, and at least 50-cm inside the plot edge. Colored wire rings were used to permanently identify 10 study tillers per quadrat, 5 each of blue grama and western wheatgrass. The same quadrats were used for the duration of the research. If a marked tiller produced axillary tillers at anytime during the growing season, the axillary tillers were marked with a different color to distinguish them from primary tillers. Different tillers were marked in the same manner in 1995.

From an initial population of 360 tillers per species, repeated, season-long measurements ($n = 17$ in 1994; $n = 14$ in 1995) were taken on 270 blue grama and 329 western wheatgrass tillers in 1994 and 320 blue grama and 341 western wheatgrass tillers in 1995. Differences between marked and measured tillers were due to lost markers or excluding data from tillers which were not grazed twice. Tiller measurements began in mid-May and continued weekly through August with additional measurements for quantification of any autumn

growth. Information gathered on an individual tiller during each visit included: plant height, phenology, number of leaves, axillary tillering and tiller senescence.

Measuring tillers nondestructively prevented direct estimates of cumulative biomass through time. Height measurements were converted to biomass by developing height-weight relationships of tillers located on the same clayey range site in the near vicinity of the lysimeters. For each species, tillers were measured, clipped at the soil surface and bundled together with other tillers of the same height (± 1 cm). Five bundles per species representing the range of heights for those tillers found in the lysimeters were collected before each grazing event. Individual bundles containing 5 western wheatgrass and 10 blue grama tillers were placed in plastic bags, transported to the laboratory and immediately cut into segments. Tiller bundles were cut from the base upward in segments of 1-cm for blue grama and 3-cm for western wheatgrass in a manner similar to Tusler (1993), so all height ranges of plants found in the lysimeters were represented. All segments were oven dried at 60°C for 48 hours before weighing.

Tiller relative growth rates ($\text{g g}^{-1} \text{ day}^{-1}$) were calculated according to Radford (1967) as:

$$\text{Tiller relative growth rates} = (\log_e W_{t+1} - \log_e W_t) * I^{-1} \quad (1)$$

where W was tiller weight (g), t was initial time, and I was time increment in days.

Density of western wheatgrass was determined by counting total number of live tillers within each quadrat. Because of the "mat-like" growth form of blue grama, density was determined by counting the number of tillers within a 5.75-cm² circular plot, or 2% of the quadrat area, randomly located within each permanent quadrat. Densities were measured on 24 May 1994, 1995, and 1996.

Standing crop inside 20 randomly located 250-cm² quadrats per lysimeter was harvested monthly by species from 1993 to 1996 (Heitschmidt et al. 1999). Samples were oven dried at 60°C, separated into live and dead components and then weighed. Aboveground net primary production was calculated for blue grama and western wheatgrass by summing all positive increases in standing crop from April to November.

Data Summarization and Analyses

Soil water measurements were analyzed using repeated measures analysis of variance (AOV) with year, depth, treatments

and dates in the model. Years and/or dates and all associated 2- and 3-way interactions were analyzed as within plot repeated measures and tested using full model residuals (Heitschmidt et al. 1999).

Pre-dawn and mid-day water potential data were analyzed separately using repeated measures AOV with drought treatment, plant species, and date as main effects. The error terms for testing the main effects of drought treatments were the replication by treatment interaction. The error terms for testing the main effects of species and the interaction effects of species and drought treatments were replication by treatment by species. The full model residuals were used to test the repeated measures effects of dates and all associated 2- and 3-way interaction effects.

Growth records were summarized using average tiller relative growth rate within 3 time periods. Time periods were: 1) the last 2 weeks of May before the first grazing event; 2) the entire month of June between the first and second grazing event; and 3) July to October of 1994 and July to early September 1995. The number of 1994 post-grazing sampling dates was 8, but this was reduced to 4 in 1995, as both species were essentially dormant throughout both summer periods.

A univariate, repeated measures analysis of variance model was used to analyze tiller relative growth rate data. A 2-way AOV was used to determine the effects of drought and grazing on percent tiller recruitment. Tiller relative growth rates and tiller recruitment are reported for tillers that were grazed twice, since the majority ($\geq 85\%$) of the tillers in the lysimeters were grazed during both grazing events. This was done to reduce confounding effects of combining once grazed and twice grazed tillers.

Tiller densities from May 1994 (i.e., pre-treatment) were included as a covariate in the 2 following years' data. Means were considered to be significantly different when $P \leq 0.05$, unless noted otherwise. Individual lysimeters were considered experimental units for all analyses.

Heitschmidt et al. (1999) reported plant functional group and species compositional differences among treatment plots in 1993. We initially used the pre-treatment year (1993) blue grama and western wheatgrass productivity estimates as covariates in subsequent year analyses. Since the covariates were never significant ($P \geq 0.22$), they were subsequently excluded from the final analyses.

Drought treatments might be considered pseudo-replicated, according to Hurlbert

(1984), since the rainout shelter size and cost precluded classical treatment replication. The use of a single rainout shelter to test the effects of drought is common in the literature (Busso 1988, Busso et al. 1989, 1990, Frank and Ries 1990, NeSmith and Ritchie 1992, Busso and Richards 1993, 1995). Statistical tests used in our study were conservative, since the experimental units were not quadrats, individual plants or individual tillers. In addition, analyses were conducted in a manner similar to the first paper in this series (Heitschmidt et al. 1999).

Results

Precipitation, Soil Water, and Water Stress

In 1993, the pre-treatment year, total annual precipitation was 38% above the long-term average of 34-cm (Fig. 1). Annual precipitation in 1994 was 24.7-cm, 24% below average. Precipitation from 1 May to 31 October 1994 was 16.3 cm compared to the 27.1-cm average. Total annual precipitation for 1995 and 1996 was similar to the long-term average (Heitschmidt et al. 1999).

Heitschmidt et al. (1999) previously reported no differences in soil water dynamics between imposed 1994 drought and natural precipitation and grazing treatment lysimeters. The only significant main effects were year and date.

The drought treatment did not affect either pre-dawn or mid-day leaf water potential of either blue grama ($P = 0.93$) or western wheatgrass ($P = 0.40$; Table 1). Water potentials were affected by plant species (midday; $P \leq 0.01$), date ($P \leq 0.01$) and their interaction ($P \leq 0.01$). Date was the most important factor accounting for 85% of the total sum of squares for predawn and 58% for midday water potentials. Species accounted for less than 5% of the total sum of squares. The date effect followed anticipated seasonal trends of increasing water potentials with decreasing soil water content. The absence of significant drought treatment-by-date ($P \geq 0.18$) and drought treatment-by-date-by-species ($P \geq 0.86$) interactions showed that the magnitude of water stress was similar in both the drought and non-drought treatment plots during 1994 (i.e., the year of the imposed drought) as well as 1995.

Utilization

Ninety-eight percent of marked blue grama tillers (265 of 270) in 1994, and 97% (309 of 320) in 1995 remained in a

Table 1. Predawn and midday leaf water potentials (MPa) for western wheatgrass (Pasm) and blue grama (Bogr) plants growing in drought and nondrought¹ lysimeters at Fort Keogh in 1994 and 1995.

Year	Date	Pre-dawn ²		Mid-day ²	
		Pasm	Bogr	Pasm	Bogr
----- (MPa) -----					
1994	18 May	−0.32d	−0.42d	−2.36cde	−0.62e
	31 May ³	−0.24d	−0.31d	−2.81bcd	−2.12cd
	14 Jun ³	−0.44cd	−0.20d	−3.62ab	−2.69bc
	23 Jun ³	−0.75cd	−1.39c	−3.16abc	−2.11e
	30 Jun	−4.18a	−4.04b	−2.90bcd	−2.29cd
	13 Jul ⁴	−1.04bc	−4.92a	−4.00a	−4.28a
	28 Jul ³	−4.46a	−5.00a	−3.15abc	−4.48a
1995	15 May	−0.43cd	−0.26d	−1.58e	−0.71e
	2 Jun	−0.99bc	−0.59d	−2.22de	−2.08cd
	16 Jun	−0.51cd	−0.31d	−2.48cd	−1.75d
	30 Jun ³	−0.46cd	−0.50d	−2.02de	−0.70e
	17 Jul	−1.42b	−1.42c	−2.84bcd	−2.62bcd
	2 Aug	−3.88a	−4.25b	−3.18abc	−3.30b

¹There were no significant ($P \geq 0.10$) differences in drought versus nondrought treatments.

²Means within columns with different letters are significantly different at $P \leq 0.05$.

³Significant ($P \leq 0.05$) mid-day species effects.

⁴Significant ($P \leq 0.05$) predawn species effects.

vegetative phenological stage. On average, utilization was 39% and 47% on blue grama tillers for the first and second grazing events in 1994, and 23% and 45% for the first and second grazing events in 1995. Over 85% of the marked blue grama tillers in the grazed lysimeters were grazed twice in both years.

Ninety-eight percent (323 of 329) in 1994 and 94% (322 of 341) in 1995 of marked western wheatgrass tillers remained in a vegetative phenological stage during the growing seasons. On average, utilization was 49% and 51% for the first and second grazing events in 1994 and 53% and 46% for the first and second grazing events in 1995. Over 90% of marked western wheatgrass tillers were grazed twice in 1994 and 1995.

Tiller Relative Growth Rates

Analyses of relative growth rates of twice-grazed blue grama tillers revealed significant ($P \leq 0.01$) treatment-by-time interactions (Fig. 2). Relative growth rates were reduced ($P = 0.01$) 29% by drought before grazing treatments were imposed (i.e., May) but not different ($P \geq 0.30$) from June through October in 1994 (Fig. 2). Growth rates of defoliated tillers were 107% greater ($P \leq 0.01$) than undefoliated tillers after the first grazing event (i.e., June), but similar ($P = 0.08$) thereafter and not different ($P \geq 0.10$) from zero from July through October (Fig. 2).

The year following the imposed drought (i.e., 1995), the blue grama time-by-drought ($P = 0.02$) and time-by-grazing treatment interactions were significant ($P \leq 0.01$). In May, relative regrowth rates

were 18% greater ($P = 0.01$) for plants exposed to the imposed 1994 drought than for non-drought plants, but rates were similar ($P \geq 0.30$) thereafter (Fig. 2). Relative growth rates in the ungrazed treatment during May 1995 were 19% greater ($P = 0.02$) than in either grazing treatment. However, following the first grazing event of 1995 (i.e., June), relative growth rates were greater ($P = 0.02$) in the G94-95 treatment than the ungrazed control and greater ($P = 0.003$) than the G94 treatment. Relative growth rates from July through August were not different ($P \geq 0.10$) from zero (Fig. 2).

Relative growth rates of marked western wheatgrass tillers grazed twice, were unaffected by drought in 1994 ($P = 0.61$). Relative growth rates were greater ($P \leq 0.01$) in the 2 grazed treatments (G94 and G94-95) compared to the ungrazed treatment (0.007 vs. 0.002 $\text{g}^{-1} \text{day}^{-1}$) in June, and declined from July to October (Fig. 3).

Tiller relative growth rates were not different ($P \geq 0.15$) from zero from July through October (Fig. 3).

Results were similar for western wheatgrass in 1995 in that relative growth rates were unaffected by drought treatment ($P = 0.69$), were greater ($P \leq 0.01$) in the grazed (G94-95) than the 2 ungrazed (G94 and ungrazed) treatments in June, and declined through the season (Fig. 3).

Tiller Recruitment

The percent of primary blue grama tillers which produced an axillary tiller, varied during the 1994 growing season in response to drought and grazing (Table 2). Drought reduced ($P \leq 0.01$) total recruitment 80%, whereas grazing increased ($P \leq 0.01$) recruitment 315% compared to ungrazed treatments. Sixty percent of daughter tillers were produced after the first grazing event. Of those producing axillary tillers, none in the drought treatment produced more than 1 axillary tiller. Eighteen percent in the non-drought treatment produced 2 secondary tillers.

In 1995, the magnitude of recruitment by blue grama was similar ($P = 0.16$) between drought and non-drought treatments (Table 2). Tiller recruitment for combined grazing treatments was 78% greater ($P \leq 0.01$) than without grazing. Ninety-eight percent of the tiller recruitment occurred after the first grazing event. On average, 30% of the blue grama tillers producing axillary tillers produced 2 secondary tillers. It appeared that the seasonal pattern of axillary tillering by blue grama was similar in 1994 and 1995.

Recruitment by western wheatgrass tillers grazed twice also varied in magnitude between the 1994 drought and grazing treatments (Table 2). Drought reduced ($P \leq 0.01$) recruitment 91% (Table 2). Grazed tillers exhibited greater ($P = 0.04$)

Table 2. Least square means (%), SE and P-values proportions of marked primary tillers that produced at least 1 axillary tiller during the growing season for blue grama and western wheatgrass subjected to drought and grazing treatments.

Year	Drought Treatments ¹			P	Grazing Treatments ²			SE	P	D*G ³
	D	ND	SE		G94	G94-95	UG			
Blue Grama ⁴	----- (%) -----				----- (%) -----					
1994	8a	40b	3	≤ 0.01	31a	32a	10b	3	≤ 0.01	0.08
1995	39	49	4	0.16	47a	60a	30b	5	0.01	0.50
Western Wheatgrass ⁴										
1994	7a	79b	3	≤ 0.01	47a	46a	35b	3	0.04	0.07
1995	6	11	3	0.18	5	15	6	3	0.12	0.84

¹D = Drought, ND = Non Drought.

²G94 = Grazed in 1994, G94-95 = Grazed in 1994 and 1995, UG = Ungrazed.

³D*G = Drought by grazing interaction P-value.

⁴Drought or grazing treatment means in the same year (row), with different letters are significantly different at $P \leq 0.05$.

Fig. 2. Mean tiller relative growth rates ($\text{g g}^{-1} \text{day}^{-1}$) for blue grama in response to drought and grazing. Grazing treatments were grazed during and after drought (G94-95), grazed during drought and ungrazed after drought (G94), and ungrazed during and after drought (UG). Different capital letters (A and B) denote significant ($P \leq 0.05$) differences between drought and nondrought within the same monthly period. Small letters (a, b and c) denote significant ($P \leq 0.05$) differences between grazing treatments within the same monthly period.

recruitment compared to ungrazed tillers (Table 2). More than 95% of the recruitment occurred in the fall (September and October) of 1994. No tillers in drought plots recruited more than 1 tiller. In contrast, of the primary western wheatgrass tillers producing axillary tillers in non-drought plants, 11% produced 2 daughter tillers. Eighty percent of the axillary tillers were produced in September through October in 1994.

Tiller recruitment by western wheatgrass during the growing season was similar between drought ($P = 0.18$) and among grazing ($P = 0.12$) treatments in 1995 (Table 2). Only 26% of the western wheatgrass tillers were recruited in the fall (September–October) of 1995. No western wheatgrass tillers produced more than 1 daughter tiller in 1995.

Tiller Density

Estimated pre-treatment tiller densities of blue grama were greater ($P = 0.06$) in

1994 in drought compared to non-drought lysimeters (8,646 vs. 9,854 tillers/ m^2) but not ($P \geq 0.60$) among grazing treatment lysimeters in 1994. Initial tiller densities were included as covariates for the 1995 and 1996 analyses. Tiller densities of blue grama were not ($P = 0.10$) affected by drought in 1995 (8,068 vs. 9,420 tillers m^{-2}), but in 1996, 2 years after the drought was imposed, tiller densities of blue grama stands subjected to drought were 59% greater ($P = 0.02$) than not subject to drought (9,967 vs. 6,263 tillers m^{-2}). Grazing did not ($P = 0.49$) affect densities in 1995 or 1996. No significant ($P \geq 0.20$) drought-by-tiller interactions occurred either year.

Initial (1994) tiller densities of western wheatgrass were different ($P \leq 0.01$) and their covariates were significant ($P \leq 0.04$) in 1995 but not ($P \geq 0.12$) in 1996. Tiller densities were not ($P = 0.71$) affected by drought in 1995 but were reduced 42% ($P = 0.007$) in 1996 (476 vs. 814 tillers m^{-2})

Fig. 3. Mean tiller relative growth rates ($\text{g g}^{-1} \text{day}^{-1}$) for western wheatgrass in response to drought and grazing. Grazing treatments were grazed during and after drought (G94-95), grazed during drought and ungrazed after drought (G94), and ungrazed during and after drought (UG). Different capital letters (A and B) denote significant ($P \leq 0.05$) differences between drought and nondrought within the same monthly period. Small letters (a, b and c) denote significant ($P \leq 0.05$) differences between grazing treatments within the same monthly period.

when compared to non-drought treatments. Tiller densities were not affected ($P = 0.49$) by grazing treatment or drought by grazing treatment ($P \geq 0.52$) interactions in 1995 or 1996.

Aboveground Net Primary Production (ANPP)

Blue grama production averaged 551 kg ha^{-1} across years and grazing treatments (Table 3). Pre-treatment ANPP for blue grama (i.e., 1993) did not differ ($P = 0.11$) between drought treatments, but it was greater ($P = 0.03$) in the 2 grazed treatment plots than the ungrazed (Table 3). Analyses for years 1994 through 1996 showed all drought and grazing treatment effects were non-significant ($P \geq 0.10$). Drought-by-grazing treatment interactions were not significant ($P \geq 0.10$) in any year.

Estimated 1993 ANPP for western wheatgrass did not differ ($P = 0.10$) between drought treatment plots, but was greater ($P = 0.05$) in the G94-95 and

Table 3. Least square means (kg ha⁻¹), SE, and P-values for aboveground net primary production estimates for blue grama and western wheatgrass subjected to drought and grazing treatments.

Year	Drought Treatments ¹		SE	P	Grazing Treatments ²			SE	P	D*G ³
	D	ND			G94	G94-95	UG			
Blue Grama ⁴	----- (kg ha ⁻¹) -----				----- (kg ha ⁻¹) -----					
1993	1,473	1,276	78	0.11	1,421a	1,588a	1,101b	96	0.03	0.14
1994	712	639	90	0.58	680	566	781	110	0.43	0.10
1995	564	476	81	0.47	562	334	663	99	0.13	0.48
1996	516	398	64	0.24	395	357	619	78	0.10	0.90
Western Wheatgrass ⁴										
1993	1,117	1,687	211	0.10	1,138a	1,595b	1,472b	259	0.05	0.49
1994	649a	1,277b	90	≤ 0.01	757a	756a	1,378b	110	0.01	0.98
1995	978	1,376	129	0.07	1,608a	481b	1,442a	158	≤0.01	0.17
1996	961	1,347	166	0.15	1,275	1,029	1,157	204	0.70	0.40

¹D = Drought, ND = Non Drought.

²G94 = Grazed in 1994, G94-95 = Grazed in 1994 and 1995, UG = Ungrazed.

³D*G = Drought by grazing interaction P-value.

⁴Drought or grazing treatment means in the same year (rows), with different letters are significantly different at $P \leq 0.05$.

ungrazed treatment plots than the G94 treatment plots (Table 3). Pre-treatment ANPP were not significant ($P \geq 0.22$) covariates in any initial analyses, therefore, they were not included in the final analysis. Aboveground net primary production was less ($P = 0.01$) in the drought than non-drought treatment in 1994 and greater ($P = 0.01$) in the ungrazed than grazed treatments (G94-95) in 1994. The only difference found thereafter, was that ANPP in G94-95 (which was grazed in 1995) was less ($P \leq 0.01$) in 1995 than in the 2 non-grazed treatments in 1995 (NG and G94). There were no drought by grazing treatment interactions ($P \geq 0.17$) in any year.

Discussion

Based on the results of this study, we conclude that: 1) relative growth rates of tillers which were grazed twice, were largely unaffected by drought and seasonally enhanced by grazing (Fig. 2 and 3); 2) axillary tillering was impeded by drought during the growing season and enhanced by grazing (Table 2); 3) tiller densities were unaffected by drought or grazing; and 4) neither drought nor grazing affected blue grama ANPP whereas drought reduced western wheatgrass ANPP with mixed grazing treatment effects (Table 3).

The major effects of drought were expressed by a slight (19%) reduction in tiller relative growth rates of blue grama in May 1994, a large reduction in tillering for western wheatgrass (91%) and blue grama (80%) during the growing season in 1994, and a large reduction of ANPP for western wheatgrass. Growth and tillering are often reduced by water stress (Brown 1995). Zhang and Romo (1995) reported the number of emerging northern wheatgrass

(*Agropyron dasystachyum* (Hook.) Scribn.) tillers was positively correlated with soil water. Haferkamp et al. (1997 and 1998), Haferkamp and Heitschmidt (1999) and Rummell (1946) reported western wheatgrass tiller density increased with the removal of competition of Japanese brome (*Bromus japonicus* Thunb.).

The responses to the initiation of the drought began to appear early in 1994 as shown by the change in blue grama tiller relative growth rates and the lack of a significant date-by-treatment interaction for western wheatgrass tiller relative growth rates. However, the response to the imposed drought and control lysimeters were similar due to the natural drought-like conditions which existed during 1994. Precipitation was 24% below average, and this drought caused plants to be equally water stressed by May 1994 regardless of drought treatment (Table 1). This conclusion is also supported by the precipitation (Fig. 1), xylem water potentials, and soil water data reported previously by Heitschmidt et al. (1999).

Our results also suggest the effects of a 1-year drought on growth rates did not carry over to the next year. Carry over effects may have been limited by the initial drought as well as above average precipitation that fell in March, April, and May 1995. Busso and Richards (1995) and Busso et al. (1989) did not find the effects of a 1-year drought on numbers of active axillary buds carried over to the next year. Only after 3 consecutive years of drought did Busso et al. (1989) find reduced numbers of metabolically active axillary buds.

Fewer axillary tillers were produced by western wheatgrass in 1995 than in 1994. Increased western wheatgrass tillering is associated with increased fall precipitation the previous year (Haferkamp et al. 1997). However, in this instance, the fall of 1994

was wetter than fall of 1993 (Fig. 1). Thus, the reduction of tillering in 1995 was more likely due to the dry summer of 1994.

Grazing had little long-term effect on blue grama or western wheatgrass. The increase in tiller recruitment with grazing during the growing season agrees with findings of Sims et al. (1973). They reported mowing blue grama plants in late June and early July stimulated additional tillering, mostly from reproductive shoots that had elevated above the mowed height. Mowing earlier in the growing season depressed tillering, whereas mowing in late July and early August stimulated tillering, but insufficient growing season remained for complete development of these late tillers. They also reported increased tillering with mowing for sand bluestem (*Andropogon hallii* Hack.) a rhizomatous warm-season grass.

Our findings that grazing did not reduce ANPP of blue grama, but did decrease ANPP of western wheatgrass can best be explained by the different morphologies of the 2 species. Grass species like blue grama are characterized by short growing shoots and when grazed, these species can maintain much higher proportions of photosynthetic tissue than can species with long shoots like western wheatgrass (Dahl and Hyder 1977). Klipple and Costello (1960) noted that herbage production of western wheatgrass remained the same when utilization of that species increased from about 10% to about 20% but declined sharply when utilization increased to 40%. Launchbaugh (1967) found that forage production of western wheatgrass declined as utilization increased from 44 to 80%. Reed and Peterson (1961), Everson (1966), and Branson (1953) concluded that forage production of western wheatgrass declined with increased utilization.

Many studies have shown the importance of environmental factors on production of mixed-grass rangelands (Coupland 1958, Reed and Peterson 1961, Hyder et al. 1975). Extended drought usually shifts species composition toward short grasses (Smoliak et al. 1972), but species composition shifts toward mid grasses when precipitation is above average (White et al. 1978). Shifts in plant species composition in this study were not observed (Heitschmidt et al. 1999). This lack of change in species composition may have been due to the timing and severity of the imposed drought. We failed to detect an increase in warm-season herbage production as reported by Heitschmidt et al. (1999), but our findings were probably due to slightly different methodologies.

Management Implications

Our results demonstrate a 1-year growing season drought combined with grazing (both during and after drought) did not appear to adversely affect tiller processes. Elimination of livestock grazing during or after a 1-year growing season drought may not be necessary to maintain plant populations on the tiller level for blue grama and western wheatgrass. Moderate stocking levels (40–50% utilization) during and after drought did not adversely affect sustainability of dominant native grasses on these Northern Great Plains rangelands within the conditions of this study.

Literature Cited

- Branson, R.A. 1953.** Two new factors affecting resistance of grasses to grazing. *J. Range Manage.* 6:165–171.
- Brown, R.W. 1995.** The water relations of range plants, p. 291–413. *In:* D.J. Bedunah and R.E. Sosebee (eds.) *Wildland plants: Physiological ecology and developmental morphology*. Soc. Range Manage. Denver, Colo.
- Bullock, J.M., B. Clear Hill and J. Silvertown. 1994.** Tiller dynamics of two grasses—responses to grazing, density and weather. *J. Ecol.* 82:331–340.
- Burkhardt, J.W. 1966.** Herbivory in the Intermountain West. Idaho Forest, Wildl. Range Exp. Sta. Bull. 58, Moscow, Ida.
- Busso, C.A. 1988.** Factors affecting recovery from defoliation during drought in two arid-land tussock grasses. Ph.D. Thesis, Utah State Univ. Logan, Ut.
- Busso, C.A. and J.H. Richards. 1993.** Leaf extension rate in two tussock grasses: Effects of water stress and clipping. *Oecologia* 14:3–15.
- Busso, C.A. and J.H. Richards. 1995.** Drought and clipping effects of tiller demography and growth of two tussock grasses in Utah. *J. Arid. Environ.* 29:239–251.
- Busso, C.A., R.J. Mueller and J.H. Richards. 1989.** Effects of drought and defoliation on bud viability in two caespitose grasses. *Ann. of Bot.* 63:477–485.
- Busso, C.A., J.H. Richards and N.J. Chatterton. 1990.** Nonstructural carbohydrates and spring regrowth of two cool-season grasses: interaction of drought and clipping. *J. Range Manage.* 43:336–343.
- Campbell, R.S. 1936.** Climatic fluctuations, p.135–150. *In:* The Western Range. US Govt. Printing Office. Washington D.C.
- Coupland, R.T. 1958.** The effects of fluctuations in weather upon the grassland of the great plains. *Bot. Rev.* 24:274–312.
- Dahl, B.E. and D.N. Hyder. 1977.** Developmental morphology and management implications, p. 257–290. *In:* R.E. Sosebee (ed.) *Rangeland plant physiology*. Range Science Series No. 4. Soc. Range Manage. Denver, Colo.
- Everson, A.C. 1966.** Effects of frequent clipping at different stubble heights on western wheatgrass (*Agropyron smithii*, Rydb). *Agron. J.* 58:33–35.
- Frank, A.B. and R.E. Ries. 1990.** Effects of soil water, nitrogen, and growing degree-days on morphological development of crested and western wheatgrass. *J. Range Manage.* 43:257–260.
- Haferkamp, M.R. and R.K. Heitschmidt. 1999.** Japanese brome impacts on western wheatgrass in Northern Great Plains rangelands: An update. *Great Plains Research* 9:315–327.
- Haferkamp, M.R., R.K. Heitschmidt, and M.G. Karl. 1997.** Influence of Japanese brome on western wheatgrass yield. *J. Range Manage.* 50:44–50.
- Haferkamp, M.R., R.K. Heitschmidt, and M.G. Karl. 1998.** Clipping and Japanese brome reduce western wheatgrass standing crop. *J. Range Manage.* 51:692–698.
- Heitschmidt, R.K., M.R. Haferkamp, M.G. Karl, and A.L. Hild. 1999.** Drought and grazing: I. Effects on quantity of forage produced. *J. Range Manage.* 52:440–446.
- Hulbert, S.H. 1984.** Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54:187–211.
- Hyder, D.N., R.E. Bement, E.E. Remmenga, and D.F. Hervey. 1975.** Ecological responses of native plants and guidelines for management of shortgrass range. ARS-USDA. Washington, D.C.
- Klipple, G.E. and D.F. Costello. 1960.** Vegetation and cattle responses to different intensities of grazing on shortgrass ranges on the Central Great Plains. U.S. Dep. Agr. Tech. Bull. 1216.
- Küchler, A.W. 1964.** Potential natural vegetation of the conterminous United States. Amer. Geog. Soc. Spec. Pub. 36. Amer. Geog. Soc. N.Y.
- Launchbaugh, J.L. 1967.** Vegetation relationships associated with intensity of summer grazing on a clay upland range site in the Kansas 20- to 24-inch precipitation zone. Kansas Agr. Exp. Sta. Tech. Bull. 154. Manhattan, Kans.
- Ludlow, M.M. 1986.** Simultaneous pressure of water stress and defoliation in rangeland plants, p. 433–436. *In:* P.J. Joss, P.W. Lynch and O.B. Williams (ed.), *Proc. Symp. Rangelands: A resource under siege*, 2nd Int. Rangeland Congress. Cambridge, England.
- National Oceanic and Atmospheric Administration. 1996.** Climatological data, Montana annual summary. Nat. Climatol. Data Center, Asheville, N.C.
- NeSmith, D.S. and J.T. Ritchie. 1992.** Short- and long-term responses of corn to a pre-anthesis soil water deficit. *Agron. J.* 84:107–113.
- Olson, B.E. and J.H. Richards. 1988.** Annual replacement of the tillers of *Agropyron desertorum* following grazing. *Oecologia* 76:1–6.
- Pieper, R.D. and R.K. Heitschmidt. 1988.** Is short-duration grazing the answer? *J. Soil Water Conserv.* 43(2):133–137.
- Radford, P.J. 1967.** Growth analysis formulae - their use and abuse. *Crop Sci.* 7:171–175.
- Reed, M.J. and R.A. Peterson. 1961.** Vegetation, soils, and cattle responses to grazing on northern Great Plains range. USDA For. Serv. Tech. Bull. #1252.
- Richards, J.H., M.M. Caldwell, and B.E. Olson. 1987.** Plant production following grazing: carbohydrates, meristems and tiller survival over winter. *Soc. Range Manage. Symposium*. Boise, Ida.
- Rummel, R.S. 1946.** Some effects of competition from cheatgrass brome on crested wheatgrass and bluestem wheatgrass. *Ecol.* 27:159–167.
- Scholander, P.F., H.T. Hammel, E.D. Bradstreet, and E.A. Hemmingsen. 1965.** Sap pressure in vascular plants. *Sci.* 148:339–346.
- Sims, P.L., R.K. Lang'at, and D.N. Hyder. 1973.** Developmental morphology of blue grama and sand bluestem. *J. Range Manage.* 26:340–344.
- Smoliak, S., J.F. Dormaar, and A. Johnston. 1972.** Long-term grazing effects on Stipa-Bouteloua prairie soils. *J. Range Manage.* 25:246–250.
- Tusler, C.A. 1993.** Livestock defoliation patterns on native range under season-long and spring deferred grazing. M.S. Thesis. South Dakota State University, Brookings, S.D.
- USDA Agricultural Statistics. 1993.** Agricultural statistics. Nat. Agr. Stat. Ser. Washington, D.C.
- White, L.M., J.J. Newbauer III, and J.R. Wight. 1978.** Vegetational differences in native range during 38 years in eastern Montana, p. 260–262. *In:* D.N. Hyder (ed.) *Proc. First Internat. Range Congr. Soc for Range Manage.* Denver, Colo.
- Willms, W.D. and P.G. Jefferson. 1993.** Production characteristics of the mixed prairie: constraints and potential. *Can. J. Anim Sci.* 73:765–778.
- Zhang, J. and J.T. Romo. 1995.** Impacts of defoliation on tiller production and survival in northern wheatgrass. *J. Range Manage.* 48:115–120.

Book Reviews

Toxic Plants of North America. By George E. Burrows and Ronald J. Tyrl. Iowa State University Press, Ames, Iowa. 1342 p. US\$174.95 hardbound. ISBN 0-8138-2266-1.

As a young scientist working in and around the subject of grazing management, I was sceptical about research on poisonous plants. It seemed an area of research which received disproportionately generous funding, sometimes at the expense of systems research on underlying grazing management variables which were often the causes or solutions to problems with poisonous plants. In my early years as a range management scientist at Washington State University, the Washington Cattlemen's Association offered small, competitive research grants to address such livestock problems. In those days, as today, grazing management proposals, in fact any management proposals which did not involve immediate financial return or a *magic bullet*, were shunned like poison. Some of the money went into marketing studies. But if a grazing management problem, such as ingestion of poisonous plants, conspicuously manifested itself as a cattle problem, the Washington State University Veterinary School was apparently, in the view of the Cattlemen's Research Committee, the best bet to solve the problem. The Vet School cared; the Cattlemen's Research Committee knew they cared; and more to the point, they had the technicians, laboratories, computers, vehicles and operating funds to *show* that they cared.

In more recent years working in eastern Washington, the most notable poisonous plant problem I have encountered has involved a regional lupine (*Lupinus sericeus* Pursh). Some varieties of this species have been an occasional problem in causing crooked calves when ingested in sufficient quantities by cows early in gestation. Interest in the poisonous lupine problem mushroomed several years ago when a long-time rancher, who had recently adopted well-publicized intensive grazing practices, suddenly, if not surprisingly, suffered catastrophic calf losses to his spring calving cow herd grazing summer range which his cows had grazed extensively, and more or less safely, for many years. The Veterinary School here at Washington State University, I read in the *Capital Press*, was again coming to the rescue with tactical, technical research to find a cause, and preferably, a solution to

the problem. It seemed to me the kind of heroic response I would have expected from the only unit on campus whose faculty members other professors routinely address as "*Doctor*."

Whatever the cause, few events are more acutely demoralizing to a rancher than losing livestock to poisonous plants, so past and current interest in poisonous plants is understandable. In response to the current interest, the year 2001 has been a big one for publications on poisonous plants, because of the advent of 2 new books. The more conspicuous of the 2, at least in mass, is *Toxic Plants of North America*, an enormous new reference on the subject authored by a veterinarian and a botanist, respectively. (For a review of the second book, *A Guide to Plant Poisoning in North America*, see the review by Pfister, *Rangelands*, 23(6):56-57.) Arranged alphabetically by family in an encyclopedic format, *Toxic Plants of North America* provides comprehensive coverage of all of the poisonous plants of the continent.

A 4-page introductory chapter explains the authors' objectives for the book, and outlines the book's scope, organization, format, and historical perspective. Chapter 2 begins the with the *Aceraceae* (maples), beginning a one-family-to-a-chapter format that ends 76 chapters (1,200 pages) later with the *Zygophyllaceae* (creosote bush) family. The chapters are, of course, of greatly varying lengths depending on the number of poisonous species in each family. The taxonomy in the book is appropriately meticulous. The chapters tend to begin with generalized ecological and morphological descriptions of each family. Sections which follow usually include disease problems, *disease genesis, clinical signs, pathology, and treatment*, but additional sections may be present for different families. Often these sections are technically detailed, especially *disease genesis*, which often contains detailed chemical descriptions and diagrammatic models of the organic toxins involved. After the familial discussions, the taxonomy, morphology, distribution and habitat of each toxic genus are described, once again alphabetically. The descriptions provided are remarkable in their detail, and the range and depth of literature cited in developing the descriptions are equally impressive.

Following the family descriptions, Chapter 77 reviews 36 plant families of questionable risk, including such notables as the *Juncaceae* and the *Cyperaceae*. Chapter 78 is a brief, informal key to the

identification of families. Two brief unofficial appendices follow, one of plant taxa listed by their adverse effects, and the other of plants of special concern for dogs, cats, and other pets. A technical glossary provides brief definitions of terms used in the book. The general index which follows is admirably detailed.

The format of *Toxic Plants of North America* improves the readability of what is already a reasonably readable text. The single column of text covers the inside 2/3 of each page, leaving a wide outside margin open to provide a variety of notes and graphics to support the text, including distributional maps, morphological drawings, taxonomic details, chemical formulae and models, technical notes, and trivial matters of interest. This arrangement, handier than appendices and less formal than footnotes, promotes the continuity of the text without limiting the diversity of the information.

Two months ago in November, on a field trip with my range management principles class, I revisited the ranch that had suffered the lupine problems. Largely in response to the lupine threat, the rancher had shifted his production cycle entirely to fall calving, an historically risky proposition considering the unpredictability of eastern Washington winters. It seemed a radical decision, a decision made by juggling matters of rangeland use, livestock marketing, winter feeding, and relative risks. It was a decision that seemed to have little to do with any solutions that could have come from Vet School research, most of which would have been expected to include marketable clinical treatments and financible clinical trials. It was a courageous decision that would ideally be arrived at through strategic, decision-aided management science of the kind the Vet School doesn't research. Regrettably, in the absence of research support from either the Washington State Experiment Station or the livestock industry, we in range management science rarely research such integrative management science either. And you won't find significant systems orientation or sophisticated protocols of management science in *Toxic Plants of North America*, either. In fact, even simple grazing management solutions are rarely the kind of solutions or "*treatments*" you will find in the book. That the huge book lacks even a few pages of management science perspective beyond the poisonous plants themselves is not surprising; books on poisonous plants rarely transcend clinical management, or at most, tactical managerial prescriptions.

Still, most of the technical pieces of the

poisonous plant problems you are likely to encounter are in this valuable reference. Like the rancher in eastern Washington, you can use the technical information as clues to formulate an analysis and make a decision on your own. But don't count on the Vet School at your land-grant university to conduct this kind of management science research to aid in your decisions, because not only do most of those *doctors* have limited, *clinical* perspectives, they are way too smart to conduct research nobody wants to pay for.

For those involved in research or teaching or management involving poisonous plants, including professional botanists and veterinarians, *Toxic Plants of North America* would seem an indispensable reference. Its many pages of cited literature, combined with its detailed text provide extraordinary continental coverage of our poisonous plants. Even systems-oriented managers, holistic types, and poisonous plant sceptics will find in it food for thought beyond its considerable technical content, because even though they won't find any stocking variables, grazing management, or mind-bending management science in the book, the bend it will produce in their bookshelves will be a weighty reminder of the poisonous plant problem, in all of its gravity.—*David L. Scarnecchia*, Washington State University, Pullman, Washington.

Africa's Elephant: A Biography. By Martin Meredith. 2001. Hodder and Stoughton, London, UK. 244p. £14.99 hardbound. ISBN 0-340-77081-3.

Elephants are rather special animals. Like humans, they enjoy close family ties, they often form life-long friendships, they act out of compassion and loyalty, and they feel strongly about their dead. As a result of these and other laudable features, elephants have been revered by humans since ancient times. This reverence notwithstanding, the story of the African elephant is a sad one. In this splendid book, Martin Meredith provides the reader with an eminently readable account of the fate of the African elephant, from ancient to contemporary times.

In ancient times, the fighting abilities of elephants were well known and admired. Chapters 3 and 4 provide useful accounts of this fact. In 327 BC, when Alexander the Great and his Macedonian army was in the process of invading India, he once had to battle an Indian army consisting of 200 heavily armored elephants. These elephants wrought terrible havoc on the battlefield, seizing and slamming soldiers to

the ground. Even though Alexander won a notable victory, he was "sufficiently impressed by the fighting abilities of Indian elephants to incorporate them into his own army" (p. 13).

In the long struggle for supremacy in the western Mediterranean between Rome and Carthage, the distinguished Carthaginian general Hannibal was a prominent supporter of elephant warfare. We are told that in Trebia in 218 BC, Hannibal's elephants terrified the Roman cavalry and news of the subsequent defeat of the Roman army "at Trebia brought panic to the city of Rome" (p. 20). Even so, after the Roman annexation of Carthaginian territory, the Romans increasingly utilized the fighting capabilities of elephants for pleasure at games. Elephants were routinely pitted against gladiators armed with weapons such as lances and glowing firebrands. The result of the seemingly incessant demand for elephants in Rome was the progressive devastation of North African elephant herds. As Meredith notes somberly, the "Roman Empire in North Africa survived until the fifth century. But by then the North African herds were on their way to extinction" (p. 27).

Moving forward in time, Chapter 8 brings the reader to approximately 1400 AD. In many ways, this time period belonged to adventurous Portuguese seafarers and traders. The Portuguese were soon followed into Africa by a whole host of Europeans—the Dutch, the English, the French, and the Danes. These rapacious Europeans were all after gold, slaves, and of course, ivory. In contrast, the native "Africans hunted elephants mainly for meat" (p. 57). Over time, the growing demand for ivory from the above mentioned European traders turned elephant hunting into a serious business endeavor, with contumelious implications for the African elephant. As noted in Chapter 9, between the 1780s and the 1830s, the price of ivory increased tenfold and this had a terrible impact on the elephant popu-

lation all over Africa. For instance, by 1870, in the Transvaal (in South Africa) elephants were extinct for all practical purposes. The same was true elsewhere in South Africa. "By the 1880s the era of elephant hunting there was virtually over. The great herds had vanished" (p. 72).

Chapter 15 tells us that the rapid disappearance of the once vast elephant herds of Southern Africa gave rise to calls for the creation of elephant safe havens in the 1890s. Specifically, says Meredith, because Paul Kruger—the one-time president of the Transvaal—sensed that the elephant population might truly become extinct, he persuaded the Transvaal parliament to create the Sabi Game Reserve in 1898. A little later, Meredith explains that because some elephants were destroying citrus crops on farms, extermination "was seen as the *only* solution to the growing conflict between elephants and farmers..." (p. 124). Were attempts made to transport the "offending" elephants to the Sabi Game Reserve or to some other safe haven? In particular, given that a major elephant safe haven had just been created because of the threat of extinction, why was extermination seen as the only solution? The author provides no answers to these questions and this is an atypical instance in which Meredith's account is, at the very least, incomplete.

The mating practices of elephants are the subject of the intriguing chapter 19. In this chapter, we learn, *inter alia*, that young bulls frequently engage in trials of strength and mock fights "that serve to establish a hierarchy long remembered..." (p. 157), that bull elephants displaying heightened sexual aggression are said to be "musth," and that although females generally aim to mate with the best available male, "they clearly prefer musth bulls" (p. 160). In this connection, I suspect most readers will be surprised to learn that as early as 1859, Charles Darwin had warned that no animal on earth is as dangerous as an elephant in musth!

Serious elephant management questions are taken up in Chapters 23 and 24. Meredith points out that in the early 1970s, insatiable demand for ivory from the newly prosperous Asian countries such as Hong Kong and Japan resulted in skyrocketing ivory prices. African elephants were suddenly worth small fortunes and this state of affairs resulted in the systematic—and increasingly illegal—slaughter of elephants for their tusks. To combat this problem, the Convention on International Trade in Endangered Species of Flora and Fauna (CITES) was signed but this con-

vention, at least initially, was able to do very little to stop the wanton massacre of elephants. It was only in 1989 that ivory imports were banned and the African elephant was officially designated an endangered species. With the ban on imports, ivory prices tumbled and as "ivory prices continued to fall, the poaching epidemic subsided" (p. 222). Finally, the world community achieved some measure of success in its fight to stop the avaricious killing of African elephants. This notwithstanding, a heavy price was paid. As Meredith points out, during the 1980s at "least half a million [elephants] had perished" (p. 222). These 2 chapters are disturbing but engrossing. They would have been even more engrossing had the author paid more attention to the *economic* aspects of alternate elephant management policies.

In sum, this book contains a marvelous historical account of the African elephant. Even though the book is overtly about elephants, the author is actually asking a deeper question and that question is this: If humans are unable to save the elephant, then, in the final analysis, what chance do they have of saving themselves? I unreservedly recommend this book to all readers. In this context, my only lament is that this book is not yet for sale in the United States.—Amitrajeet A. Batabyal, Rochester Institute of Technology, Rochester, New York.

Millions of Monarchs, Bunches of Beetles: How Bugs Find Strength in Numbers. By Gilbert Waldbauer. 2000. Harvard University Press, Cambridge, MA, and London, England. 264 p. US\$26.50 hardbound. ISBN 0-674-00090-0.

How do termites keep warm and humidified? Why are honey bees referred to as "warm-blooded" (p.94)? Why are colonies of worker ants all females and all related to each other? These are questions one may never have thought to ask but that are answered by *Millions of Monarchs, Bunches of Beetles*, each answer being related to the benefits of group living and group activity, the major theme throughout the book. According to the author, "many plant-feeding and other nonpredatory insects are gregarious during at least some part of their life history" because it is advantageous for them to do so (p.117). On the other hand, most predaceous insects do not tolerate much group interaction, except for mating. Even then, mating can be a hazardous undertaking for males, as the females tend to eat them. Thus, the

focus of this book is mainly on those insect species that do not have cannibalistic tendencies and can work together for food or other needs. *Millions of Monarchs, Bunches of Beetles* encompasses not only aspects of behavior of monarchs and beetles but touches upon many other insects' behaviors as well. The book also includes examples of behaviors of vertebrate animals such as birds, reptiles, humans and other mammals for illustrative comparisons.

The book consists of 14 chapters. The first chapter is a general introduction to the "strength in numbers" concept, followed by a section on evolution and natural selection. The author mentions three types of natural selection, individual, kin and group selection. However, I hold a different view from the author, also shared by university professors and ecologists. I believe there is just one type of natural selection, that of genetic fitness. Ultimately an animal's behavior is to maximize its own genetic fitness, performing a behavior if it believes or receives some sort of benefit/survival for its genes. In any case, the ideas of natural selection brought up by the author gives reason for the forming of insect groups observed in the book and in real life. The insect is part of an aggregation because it receives "individual benefit" from doing so, such as help in feeding, detecting predators, attracting mates, etc. (p.11). Each of the subsequent chapters reiterates the idea of group formation and benefit with examples of specific insects in specific situations.

The second chapter, entitled *Bunches of Beetles*, starts the process of examining an individual species in each chapter in terms

of group activities and benefits. In this case, Chapter 2 focuses on ladybugs, or "ladybirds" as the author refers to them. This beetle is important as a biological control of introduced pests and provides an example of how group dynamics of an animal must be understood in order to utilize it as an effective management tool (e.g. ladybugs for aphid control on crops/gardens).

Subsequent chapters follow the same style as Chapter 2, and include a chapter on monarch butterflies, eastern tent caterpillars, locusts, mayflies and cicadas. Each chapter looks at the species in question in detail, explaining behaviors and adaptations to the environment by aggregations of individuals of the species. Group unity does not benefit all individuals at all times, but it does help a majority of individuals. Another important point is that some species' individuals join together only at certain times of the year or under specific circumstances, otherwise living a relatively solitary life. Monarch butterflies, for example, come together before the winter in great masses to overwinter at specific sites. Locusts, on the other hand, undergo different phases in their lives, one being solitary and the other being gregarious, depending on the conditions around them. Thus, years can pass without a locust swarm being seen due to the influence of the "social environment" (p.145).

Rather than focusing on a particular insect, the remaining chapters of the book cover topics such as climate control or predator defense that are then related to various insect species as well as other invertebrate and vertebrate species. The chapter on climate control, for example,

talks about tent caterpillars, termites, harvestmen and other insects that regulate temperature and humidity in their living environment, despite the weather. Since insects are small, weather can be difficult for them. The author goes into detail about surface area to volume ratio to explain how the smaller an animal is the more heat and moisture it loses. Examples of hummingbirds and shrews are given since they are the smallest animals of their respective groups (birds and mammals) and have to eat enormous amounts of food to keep up with the heat they lose. However, insects behave more like reptiles and amphibians in heat loss since they too are cold-blooded and thus have the same behaviors to regulate their body temperature, basking in the sun to warm themselves and resting in the shade to cool themselves. Yet to deal with water loss, insects have more in common with birds, producing uric acid

for their urine and feces and reducing the amount of water expelled from the body.

Millions of Monarchs, Bunches of Beetles is well organized, having logical and smooth transitions from topic to topic. It is non-technical and entertaining. One of the techniques the author employs to keep the reader entertained is alliteration. In the titles of five out of the six chapters on specific insects he uses alliteration as well as a word that alludes to "many" or "group", such as the chapter titles *Myriads of Mayflies*, *Teams of Tent Caterpillars* and *Legions of Locusts*. The author also includes personal stories and observations as well as stories and accounts of others to give a different perspective and to amuse the reader. Besides that, the book offers views to interest people from many different disciplines, touching on mammals, birds, spiders, crops, trees, behavior, physiology, societies (human and animal), his

tory, etc. It includes many interesting facts, and clarifies information about insects that many readers may not have been aware of beforehand. I now know what a locust is, what fireflies really are (beetles), why a monarch butterfly is poisonous and so on. However, entomology is a field that still needs research. The ecology of many insects is lacking and numerous behaviors have not been scientifically explained. This book has aroused a curiosity in me and has given me the urge to help research the answers. Perhaps a side effect of reading this book will be that more entomologists will be created. But the least that can come from it will be readers that have a greater appreciation for the field of entomology and a better understanding of the insects around them, especially groups of insects such as "myriads of mayflies" and "bunches of beetles."—*Kristen Coles*, Washington State University, Pullman, Washington.

WE CATER TO SOME PRETTY TOUGH CUSTOMERS

... with the West's
largest selection of pas-
ture, range and reclama-
tion seed.

Over 600 native and
adapted varieties for
custom seed blends, plus
a full line of erosion
control and hydroseeding
products.

Environmental consulting
services and training
available.

granite
SEED

Call or fax for our catalog. (801) 768-4422, fax (801) 768-3967
Granite Seed Co., 1697 W. 2100 North, Lehi, UT 84043
www.graniteseed.com

Erratum

Do to technical problems in printing in the November issue of the *Journal of Range Management* Figure 3 in the article titled "Adoption of Brush Busters: Results of Texas county extension survey" by Urs P. Kreuter, Heidi E. Amestoy, Darrell N. Ueckert, and W. Allan McGinty was incorrect. The figure on the left is the correct graph.

Fig. 3. Perceived comparative efficacy, cost effectiveness, and availability of information about specific brush control techniques for mesquite, juniper, and pricklypear. (Data dispersion bars represent 95% confidence limits.)

INSTRUCTIONS FOR AUTHORS (from revised *Handbook and Style Manual*)

Eligibility

The *Journal of Range Management* is a publication for reporting and documenting results of original research and selected invitational papers. Previously published papers are unacceptable and will not be considered for publication. Exceptions to this criterion are research results that were originally published as department research summaries, field station reports, abstracts of presentations, and other obscure and nontechnical handout publications. Manuscripts submitted to the *JRM* are the property of the *Journal* until published or released back to the author(s). Manuscripts may not be submitted elsewhere while they are being considered for this journal. Papers not accepted for publication are automatically released to the authors.

Kinds of Manuscripts

Journal Articles report original findings in Plant Physiology, Animal Nutrition, Ecology, Economics, Hydrology, Wildlife Habitat, Methodology, Taxonomy, Grazing Management, Soils, Land Reclamation (reseeding), and Range Improvement (fire, mechanical chemical). *Technical Notes* are short articles (usually less than 2 printed pages) reporting unique apparatus and experimental techniques. By invitation of the Editorial Board, a *Review* or *Synthesis Paper* may be printed in the journal. *Viewpoint* articles or *Research Observations* discussing opinion or philosophical concepts regarding topical material or observational data are acceptable. Such articles are identified by the word *viewpoint* or *observations* in the title.

Manuscript Submission

Contributions are addressed to the Editor, Gary Frasier, *Journal of Range Management*, 7820 Stag Hollow Road, Loveland, Colorado 80538. Manuscripts are to be prepared according to the instructions in the *Journal's Handbook and Style Manual*. If the manuscript is to be one of a series, the Editor must be notified. Four copies of the complete manuscript, typed on paper with numbered line spaces are required. Authors may retain original tables and figures until the paper is accepted, and send good quality photocopies for the review process. Receipt of all manuscripts is acknowledged at once, and authors are informed about subsequent steps of review, approval or release, and publication.

Manuscripts that do not follow the directives and style in *Journal* handbook will be returned to the authors before being reviewed. A manuscript number and submission date will be assigned when the paper is received in the appropriate format.

Manuscript Review

Manuscripts are forwarded to an Associate Editor, who usually obtains 2 or more additional reviews. Reviewers remain anonymous. These reviewers have the major responsibility for critical evaluation to determine whether or not a manuscript meets scientific and literary standards. Where reviewers disagree, the Associate Editor, at his discretion, may obtain additional reviews before accepting or rejecting a manuscript. The Associate Editor may also elect to return to the author those manuscripts that require revision to meet format criteria before the *Journal* review.

The Associate Editor sends approved manuscripts, with recommendations for publication, to the Editor, who notifies the author of a projected publication date. Manuscripts found inappropriate for the *JRM* are released to the author by the Associate Editor. Manuscripts returned to an author for revision are *returned to the Associate Editor for final acceptability of the revision*. Revisions not returned within 6 months, are considered terminated. Authors who consider that their manuscript has

received an unsatisfactory review may file an appeal with the Editor. The Editor then may select another Associate Editor to review the appeal. The Associate Editor reviewing the appeal will be provided with copies of an correspondence relating to the original review of the manuscript. If the appeal is sustained, a new review of the manuscript may be implemented at the discretion of the Editor.

Authors should feel free to contact the Associate Editor assigned to their manuscript at any stage of the review process: to find out where the paper is in the process; to ask questions about reviewer comments; to ask for clarification or options if a paper has been rejected.

Page Proofs

Page proofs are provided to give the author a final opportunity to make corrections of errors caused by editing and production. Authors will be charged when extensive revision is required because of author changes, even if page charges are not assessed for the article. One author per paper will receive page proofs. These are to be returned to the **Production Editor, 445 Union Blvd., Suite 230, Lakewood, Colorado 80228**, within 48 hours after being received. If a problem arises that makes this impossible, authors or their designates are asked to contact the Production Editor immediately, or production and publication may proceed without the author's approval of his edited manuscript.

Page Charges and Reprint Orders

Authors are expected to pay current page charges. Since most research is funded for publication, it will be assumed that the authors are able to pay page charges unless they indicate otherwise in writing, when submitting a manuscript. When funds are unavailable to an author, no page charges will be assessed. Only the Editor will have knowledge of fund status of page charges; the Associate Editors and reviewers will accept or reject a manuscript on content only.

An order form for reprints is sent to one author with the page proofs. Information as to price and procedure are provided at that time. The minimum order is 100; no reprints are provided free of charge.

Basic Writing Style

Every paper should be written accurately, clearly, and concisely. It should lead the reader from a clear statement of purpose through materials and methods, results, and to discussion. The data should be reported in coherent sequence, with a sufficient number of tables, drawings, and photographs to clarify the text and to reduce the amount of discussion. Tables, graphs, and narrative should not duplicate each other.

Authors should have manuscripts thoroughly reviewed by colleagues in their own institution and elsewhere before submitting them. Peer review before submission insures that publications will present significant new information or interpretation of previous data and will speed *JRM* review process.

Particular attention should be given to literature cited: names of authors, date of publication, abbreviations or names of journals, titles, volumes, and page numbers.

It is not the task of Associate Editors or *Journal* reviewers to edit poorly prepared papers or to correct readily detectable errors. Papers not properly prepared will be returned to the author.