

Journal of Range Management

TABLE OF CONTENTS: VOL. 54, NO. 1, January 2001

FEATURE ARTICLE

- 2 Viewpoint: The response of central North American prairies to seasonal fire** by David M. Engle and Terrence G. Bidwell

Animal Ecology

- 11 Prairie dog effects on harvester ant species diversity and density** by Justin E. Kretzer and Jack F. Cully, Jr.
- 15 Coyote responses to changing jackrabbit abundance affect sheep predation** by L. Charles Stoddart, Richard E. Griffiths, and Frederick F. Knowlton
- 21 Assessing independence of animal locations with association matrices** by Keith T. Weber, Milo Burcham, and C. Les Marcum

Grazing Management

- 25 Sheep grazing spotted knapweed and Idaho fescue** by Bret E. Olson and Roseann T. Wallander
- 31 Range condition, tenure, management, and bio-physical relationships in Sonora, Mexico** by Jose A. Coronado-Quintana and Mitchel P. McClaran
- 39 Rotationally stocked beef cattle responses to daily and weekly residence** by N.S. Boyd, T. Astatkie, A.H. Fredeen, and R.C. Martin

Hydrology

- 44 Variations in soil moisture content in a rangeland catchment** by Rohit Salve and Barbara Allen-Diaz

Improvement

- 52 Spotted knapweed response to season and frequency of mowing** by Matthew J. Rinella, James S. Jacobs, Roger L. Sheley, and John J. Borkowski

Measurement/Sampling

- 57 Estimating herbage standing crop with visual obstruction in tallgrass prairie** by Lance T. Vermeire and Robert L. Gillen
- 61 Detecting fragmentation of cover in desert grasslands using line intercept** by Robert O. Kuehl, Mitchel P. McClaran, and Justin Van Zee



The Trail Boss

SF
85
.J67
Sci
Current
Journal

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

Copyright 2001 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. SECOND CLASS 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

Managing Editor

J. CRAIG WHITTEKIEND
445 Union Blvd., Ste 230
Lakewood, Colorado 80228
(303) 986-3309
Fax: (303) 986-3892
e-mail address:
srmden@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@ix.netcom.com

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

VIVIEN G. ALLEN
Texas Tech University
Dept. of Plant & Soil Science
Box 42122
Lubbock, Texas 79409-2122

YUGUANG BAI

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

DAVID BELESKY

USDA-ARS
1224 Airport Road
Beaver, West Virginia 25813

ROBERT R. BLANK

USDA-ARS
920 Valley Road
Reno, Nevada 89512

JOE E. BRUMMER

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

DAVID GANSKOPP

USDA-ARS
HC-71 4.51 HWY 205
Burns, Oregon 97720

67 Estimation of horizontal cover by William B. Collins and Earl F. Becker

Plant/Animal

71 Dry-weight-rank method assessment in heterogenous communities by Steven L. Dowhower, W. Richard Teague, R. James Ansley, and William E. Pinchak

77 Animal age and sex effects on diets of grazing cattle by E.E. Grings, R.E. Short, M.R. Haferkamp, and R.K. Heitschmidt

82 Nutritive value and aversion of honey mesquite leaves to sheep by R. Baptista and K.L. Launchbaugh

Plant Ecology

89 Effects of biosolids on tobosagrass growth in the Chihuahuan desert by Pedro Jurado and David B. Wester

Book Review

96 Riding the Higher Range: The Story of Colorado's Coleman Ranch and Coleman Natural Beef by Stephen M. Voynick

ROBERT GILLEN

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

ELAINE E. GRINGS

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

MARK JOHNSON

Louisiana State University
Forestry and Wildlife Management
Baton Rouge, Louisiana 70803

PAUL OHLENBUSCH

Kansas State University
Department of Agronomy
Throckmorton Hall
Manhattan, Kansas 66506

ROBERT PEARCE

Resources Concept
340 N. Minnesota St.
Carson City, Nevada 89703

MICHAEL H. RALPHS

USDA-ARS
Poisonous Plant Lab
1150 E 1400 N
Logan, Utah 84341-2881

FAISAL K. TAHA

Director of Technical Programs
Biosaline Agriculture Center
P.O. Box 14660
Dubai, U.A.E.

ALLEN TORELL

New Mexico State University
Agricultural Economics
Box 3169
Las Cruces, New Mexico 88003

MIMI WILLIAMS

USDA-ARS
22271 Chinsegut Hill Rd
Brooksville, Florida 34601-4672



President

JOHN L. McLAIN
340 N. Minnesota St.
Carson City, Nevada 89703-4152

1st Vice-President

JAMES T. O'ROURKE
61 Country Club Road
Chadron, Nebraska 69337

2nd Vice-President

RODNEY K. HEITSCHMIDT
USDA-ARS
Ft. Keogh LARRL
Rt 1, Box 2021
Miles City, Montana 59301-9801

Executive Vice-President

J. CRAIG WHITTEKIEND
445 Union Blvd. Suite 230
Lakewood, Colorado 80228-1259
(303) 986-3309
Fax: (303) 986-3892
e-mail address:
srmden@ix.netcom.com

Directors

1998-2000

PATRICK L. SHAVER
2510 Meadow Lane
Woodburn, Oregon 97071-3727

CAROLYN HULL SIEG
Rocky Mountain Research Station
2500 Pine Knoll Dr.
Flagstaff, Arizona 86001-6381

1999-2001

JAMES LINEBAUGH
3 Yhvana Dr.
Carson City, NV 89706-7717

GLEN SECRIST
Idaho Dept. of Agriculture
3818 S. Varian Ave.
Boise, Idaho 83709-4703

2000-2002

RICHARD H. Hart
USDA-ARS
High Plains Grasslands Station
8408 Hildreth Rd.
Cheyenne, Wyoming 82009-8809

DON KIRBY
North Dakota State University
Animal & Range Science
 Fargo, North Dakota 58105

The term of office of all elected officers and directors begins in February of each year during the Society's annual meeting.

THE SOCIETY FOR RANGE MANAGEMENT, founded in 1948 as the *American Society of Range Management*, is a nonprofit association incorporated under the laws of the State of Wyoming. It is recognized exempt from Federal income tax, as a scientific and educational organization, under the provisions of Section 501(c)(3) of the Internal Revenue Code, and also is classed as a public foundation as described in Section 509(a)(2) of the Code. The name of the Society was changed in 1971 by amendment of the Articles of Incorporation.

The objectives for which the corporation is established are:

- to properly take care of the basic rangeland resources of soil, plants, and water;
- to develop an understanding of range ecosystems and of the principles applicable to the management of range resources;
- to assist all who work with range resources to keep abreast of new findings and techniques in the science and art of range management;
- to improve the effectiveness of range management to obtain from range resources the products and values necessary for man's welfare;
- to create a public appreciation of the economic and social benefits to be obtained from the range environment;
- to promote professional development of its members.

Membership in the Society for Range Management is open to anyone engaged in or interested in any aspect of the study, management, or use of rangelands. Please contact the Executive Vice-President for details.

The Journal of Range Management is a publication of the Society for Range Management. It serves as a forum for the presentation and discussion of facts, ideas, and philosophies pertaining to the study, management, and use of rangelands and their several resources. Accordingly, all material published herein is signed and reflects the individual views of the authors and is not necessarily an official position of the Society. Manuscripts from anyone—nonmembers as well as members—are welcome and will be given every consideration by the editors. Editorial comments by an individual are also welcome and, subject to acceptance by the editor, will be published as a "Viewpoint."

In Cooperation With: Some of the articles appearing in *The Journal of Range Management (JRM)* are presented in cooperation with The American Forage and Grassland Council (AFGC). This cooperation consists of *JRM* acceptance of professional papers in forage grazing management and related subject areas from AFGC members and the appointment of 2 AFGC affiliated associate editors to *JRM*'s Editorial Staff. The American Forage and Grassland Council Offices: P.O. Box 94, Georgetown, Texas 78627; Larry Jeffries, President; Dana Tucker, Executive Secretary.

Contribution Policy: The Society for Range Management may accept donations of real and/or personal property subject to limitations set forth by State and Federal law. All donations shall be subject to management by the Executive Vice President as directed by the Board of Directors and their discretion in establishing and maintaining trusts, memorials, scholarships, or other types of funds. Individual endowments for designated purposes can be established according to Society policies. Gifts, bequests, legacies, devises, or donations not intended for establishing designated endowments will be deposited into the SRM Endowment Fund. Donations or requests for further information on Society policies can be directed to the Society for Range Management, Executive Vice-President, 445 Union Blvd., Suite 230, Lakewood, Colo. 80228-1259. We recommend that donors consult Tax Advisors in regard to any tax consideration that may result from any donation.

Viewpoint: The response of central North American prairies to seasonal fire

DAVID M. ENGLE AND TERRENCE G. BIDWELL

Authors are professors, Department of Plant and Soil Sciences, Oklahoma State University, Stillwater, Okla. 74078.

Abstract

Natural fires on the native grasslands of Oklahoma and Kansas were important for maintaining ecosystem structure and function. Today, land managers largely conduct prescribed fires in the late dormant season or they do not burn at all. When wild-fires occur in other seasons, conventional wisdom assumes that desirable forage species for cattle are compromised. This assumption is based on a few fire studies limited in breadth and scope. To address this, we revisited numerous data sets to quantify the influence of season of fire on plant production and species composition. Research demonstrates that tallgrass prairie burned in the late spring starts growth earlier, grows more rapidly early in the growing season, and produces more tall grasses than unburned prairie. We contrast this response with the literature reporting the results of fire occurring in other seasons. Fire effects vary with fire frequency, fire-return interval, grazing history, herbicide use, successional stage, weather pattern, edaphic features, and topography. Our review of research suggests that a variety of responses to fire season are possible and rules-of-thumb that generalize responses are misleading. Most of the research on fire also does not report the interaction of fire and herbivory. Thus it is difficult to judge the influence of fire within the context of herbivory. Results from ongoing research suggest that the prairie is far more resilient under the interaction of fire and herbivory than earlier believed.

Resumen

En los pastizales nativos de Oklahoma y Kansas los incendios naturales han sido importantes para mantener la estructura y función de los ecosistemas naturales. En la actualidad, los administradores de pastizales realizan quemadas controladas al final de la época de latencia, pero sin quemar la totalidad del pastizal. Cuando ocurren incendios sin control en otras épocas del año, las especies deseables para el ganado se ven seriamente afectadas. Sin embargo, esto ha sido sustentado en pocos estudios con limitada profundidad y durabilidad. Para comprobar esto, se revisaron numerosos grupos de datos para cuantificar la influencia de la época de incendio en la producción y composición de las especies forrajeras. Las investigaciones en esta área han demostrado que los pastos altos quemados al final de la primavera, inician el crecimiento más temprano, más rápido y con mayor producción al inicio de la época de crecimiento, que aquellos pastos altos que no son quemados. Comparamos esta respuesta con la informada en la literatura, sobre incendios ocurridos en otras épocas del año. Los efectos del incendio pueden variar con la frecuencia de incendio, intervalo de retorno del incendio, historia de pastoreo, uso de herbicidas, estado de sucesión, comportamiento climático, características edáficas, y topografía. Nuestra revisión sugiere que son posibles una variedad de respuestas a la época de incendio y reglas básicas que generalicen la respuesta han sido olvidadas. La mayoría de las investigaciones realizadas sobre incendios no mencionan la interacción de incendio y herbívoros. Por lo que es difícil juzgar, la influencia del fuego dentro del contexto del herbívoro. Resultados de la presente investigación sugieren que la pradera se recupera más rápidamente a la interacción de fuego y herbívoro de lo que se creía inicialmente.

Key Words: native grasslands, prescribed fire, fire frequency, fire interactions, fire return interval, wildfire

Fire on the native grasslands of Oklahoma and Kansas, as in other portions of the Great Plains, provided a portion of the energy required for the development and maintenance of these grasslands (Bragg 1995). Natural fire was possible from late in the growing season before the first killing freeze in autumn, through the dormant season (i.e., after the first freeze in autumn and before the last freeze in spring), and up to several weeks after the last freeze in spring (Bragg 1982, Higgins 1986). The timing of fires with respect to season or within a season potentially influences plant species composition and productivity, and therefore influences rangeland management in the modern landscape. In this paper we demonstrate that a variety of plant species composition and production responses to season of fire are possible, and

that prairie is far more resilient to burning in any season than is accepted commonly by conventional wisdom.

Prescribed fire for livestock management in the grasslands of Oklahoma and Kansas is usually intended to enhance forage quality for cattle. Fires conducted early in the freeze-free period of the spring, traditionally referred to as late spring, coincide with resumption of active growth of warm-season grasses following winter dormancy. Late spring burning has been recommended for optimum cattle production (Launchbaugh and Owensby 1978). Fires conducted in winter or early spring are intended to enhance wildlife habitat (Riggs et al. 1996) and avoid disrupting nesting of ground-nesting birds (Zimmerman 1997). Burning earlier than late spring may also ensure adequate time to fulfill all burning plans (Roberts et al. 1999).

Published with the approval of the Director, Oklahoma Agricultural Experiment Station through project S-1822.
Manuscript accepted 8 May 2000.

Wildfire may occur any time of the year provided dry, fine fuel is sufficient to carry the fire. Wildfire often disrupts management by consuming standing forage and damaging wood structures. But wildfire and even prescribed fire in seasons other than late spring also present the potential of reducing post-fire forage production and changing species composition. To this point, managers adjusting stocking rate or making other management decisions in the wake of wildfire or prescribed fire outside the traditional late spring burning period have but a few published recommendations on which to base their decisions (Launchbaugh and Owensby 1978, Ohlenbusch 1992). A comprehensive examination of the available literature and perhaps additional research are needed to support management decisions on timing prescribed burns and responding to wildfire. We reviewed the literature and revisited some original data sets to quantify the influence of season of burning on plant production and species composition in Oklahoma and Kansas native grasslands.

Voluminous research demonstrates that tallgrass prairie burned in the late spring starts growth earlier, grows more rapidly early in the growing season, and produces more tallgrasses than unburned prairie. However, we intend to contrast the effects of burning at seasons other than in late spring, even as early as late in the previous growing season, with burning late spring and with not burning.

We use published data to construct a perspective of how native grasslands in Oklahoma and Kansas respond to season of fire, and we focus our review of fire effects on herbage production and composition. By far, the majority of fire literature comes from the tallgrass prairie, but we present the available data on mixed prairie as well. To be consistent with most of the published literature, we divide our treatment into 2 broad seasons of fire based on the ratio of dead to live of warm-season grasses, which comprise the bulk of the fine fuel in these grasslands. First, the dormant season follows the first killing freeze of autumn when the first 0°C temperature dramatically increases the ratio of dead to live of fine fuels. The dormant season continues for several weeks into the freeze-free period (i.e., late spring), which is after the final 0°C temperature of the winter when fine fuels still have a high ratio of dead to live but after warm-season grasses have commenced growth. Second, the growing season refers to the freeze-free period of the year when fine fuels have substantial amounts of live tissue above

ground and therefore a low ratio of dead to live. However, fine fuels in the late growing season have greater ratios of dead to live than fine fuels in the early growing season. The greater ratio of dead to live combined with the warmer and drier weather conditions of late growing season favor fire spread and higher fire intensity (Bragg 1982). Except perhaps in severe drought, the dead-to-live ratio is less in the late growing season than in the dormant season.

Tallgrass Prairie

Dormant-Season Fire

Data from 2 studies in the northern Flint Hills near Manhattan, Kansas (Anderson et al. 1970, Towne and Owensby 1984) are often cited to support management decisions with regard to timing prescribed fire within the dormant season on tallgrass prairie. However, a considerable body of literature from other tallgrass prairie study sites in Kansas and Oklahoma expands the basis for judging the effects of dormant-season fire on herbage production and species composition (Tables 1 and 2).

Some of the first scientific reports of fire in tallgrass prairie were unreplicated observations following wildfire, included little if any information about the fire environment, and the comparison unburned area was subjectively selected (see Kelting 1957, Adams and Anderson 1978, Adams et al. 1982). An early study that impeded the acceptance of prescribed fire in Oklahoma reported that fire reduced plant production and resulted in soil erosion (Elwell et al. 1941), but the effects of fire were confounded by grazing and site differences. Other studies (Kelting 1957, Adams et al. 1982) did not include herbage production as a response measurement, complicating the application to rangeland management where herbivory by livestock or wildlife is important.

Few studies outside of those in the northern Flint Hills of Kansas examined the effect of burn date within the dormant season. In a study that included considerable variation in burning dates, burn date either had no influence, or later burn dates reduced herbage production and decreased production of forage grasses. In this study, Bidwell et al. (1990) investigated the influence of fire type (headfire vs. backfire) and burning (burn vs. no burn) on herbage production and composition at 2 clipping dates (June and August) in the first growing season after burning in each of 2 years (1986 and 1987). The study was

conducted in a moderately grazed tallgrass prairie in northcentral Oklahoma. We subjected the original data to simple linear regression using date of burning (March 6 to April 23) as the independent variable and total herbage production and species groups as dependent variables. Total herbage production in June and August 1986 declined with later burning dates in the dormant season, but no significant linear relationship was detected for either harvest date in 1987 (Fig. 1). The effect of burn date on total herbage production was greatest in June 1986 when plots burned in early March produced nearly double that of plots burned in late April (Fig. 1, Table 1). Production of perennial grasses was greater in plots burned in early March than in plots burned in late April of 1986, but burning date had no influence on perennial grass production in 1987 (Tables 1 and 2). Similarly, production of tallgrasses, forbs, and legumes in 1986 declined generally with later burning dates.

In a synthesis of research from the northern Flint Hills of Kansas, Launchbaugh and Owensby (1978) stated that early dormant-season burning (i.e., at dates in the dormant season earlier than late spring) reduces plant production and increases forbs at the expense of desirable forages, especially the warm-season tallgrasses. This body of research indicates convincingly that burning earlier than late spring (about 1 May at this latitude) in grazed prairie reduces overall herbage production and favors forbs over perennial grasses compared to unburned prairie (McMurphy and Anderson 1963, 1965, Owensby and Anderson 1967, Anderson et al. 1970, Towne and Owensby 1984, Gibson 1989). Combined with a long-term study on ungrazed plots (Towne and Owensby 1984) (Tables 1 and 2), these data demonstrate that a late-spring burning date in the northern Flint Hills of Kansas optimizes production of desirable forage grasses relative to burning earlier in the dormant season. But, we argue that burning at dates earlier in the dormant season did not increase forbs or consistently decrease perennial forage grasses compared to the no-burn treatment. Conventional wisdom in the region holds that burning in the dormant-season other than in the late dormant-season (late spring) always reduces herbage production and increases weedy forbs relative to desirable forage grasses.

Vegetation response to fire in tallgrass prairie varies with factors other than burning date. The response varies with fire history (fire frequency and fire-return interval) (Gibson and Hulbert 1987, Blair

Table 1. Response of herbage production to fire in different times of the dormant season in tallgrass prairies. Measurements were the growing season after fire unless otherwise indicated. Comparison is with unburned check unless otherwise indicated.

Timing of fire	Location	Serai stage	Change as a percent (and change in biomass, kg/ha) as a result of fire			Comments	Reference
			Perennial grass	Forb + legume	Total production		
Fall	Central Oklahoma	Mid to late	Not reported	Not reported	-53 to -59% (-1,520 to -720)	Ungrazed abandoned cropland and grazed prairie burned annually for 8 years. Exact burn dates not reported. Sampled at end of 8 years of burning.	Elwell et al. (1941)
November	Central Oklahoma	Mid to late	Not reported	+58% (140)	+64% (840)	Wildfire on area not grazed or mowed in previous years. Dominated by little bluestem. Dry year following the fire. Peak green biomass reported for total production.	Adams and Anderson (1978)
Early March to late April. Measured in June	Northcentral Oklahoma	Late	1986 burns +74% (+25/day) 1987 burns nc ¹	1986 burns +146% (+6/day) 1987 burns nc ¹	1986 burns +94% (+36/day) 1987 burns nc ¹	Fires (in 1986 and 1987) followed moderate grazing. Responses averaged over fire type. Comparison with late April burn.	Bidwell et al. (1990)
Early March to late April. Measured in August	Northcentral Oklahoma	Late	1986 burns +17% (+16/day) 1987 burns nc ¹	1986 burns nc ¹ 1987 burns nc ¹	1986 burns +21% (+21/day) 1987 burns nc ¹	Fires (in 1986 and 1987) followed moderate grazing. Responses averaged over fire type. Comparison with late April burn.	Bidwell et al. (1990)
November, February and April	Northcentral Oklahoma	Mid	nc	Nov. burn nc to +126% (nc to +290) in year 2 of one study Feb. burn nc Apr. burn nc	Year 1 Nov. burn nc to -33% (nc to -870) Feb. burn nc to -25% (nc to -670) Apr. burn nc to -42% (nc to +2050)	Decrease in total production concomitant with threeawn reduction.	Engle et al. (1990)
Winter to late spring	Northern Kansas Flint Hills	Late	Dec. burn +14% (500) Mar. burn +11% (400) Apr. burn +22% (800) May burn +36% (1300)	Dec. burn -38% (300) Mar. burn -38% (300) Apr. burn -38% (300) May burn -75% (600)	Dec. burn nc Mar. burn nc Apr. burn +14% (600) May burn +16% (700)	Ungrazed plots annually burned 1928-1982. Production data average of 1973-1982. Perennial grasses column includes all grasses.	Towne and Owensby (1984)
Early spring to late spring	Northern Kansas Flint Hills	Late	Mar. burn -33% (1310) Apr. burn -18% (690) May burn nc ²	Mar. burn nc Apr. burn nc May burn -47% (140)	Not reported	Grazed pastures burned annually 1950-1966. Data from uplands. Forage (non weedy) reported for perennial grasses and weeds for forbs+legumes.	Anderson et al. (1970)
Mid November to late April	Northern Kansas Flint Hills	Late	Not reported	Not reported	After 1 year Mid Nov. +26% (620) Late Apr. +29% (680) After 2 years Mid Nov. +68% (3270) Mid Apr. +76% (3660)	Burned two consecutive years. Data averaged over irrigated and rain-fed because irrigation had no effect. Plots not grazed.	James (1985)

¹nc = no change (P > 0.05) was detected, i.e., by analysis of the slope coefficient in regression analysis, from early March to late April burning.

²nc = no difference (P > 0.05) as compared to unburned checks or late spring burning.

Table 2. Change in composition of herbage in tallgrass prairie in response to fire in different times of the dormant season other than late spring in tallgrass prairies of the central Great Plains. Measurements were the growing season after fire unless otherwise indicated.

Timing of fire	Location	Serai stage	Change ¹ in relative composition following burning as compared to late spring burn or check						Comments	Reference
			Tallgrass	Perennial grass	Little bluestem	Forb+ legume	Forb	Legume		
November	Central Oklahoma	Mid to late	Not reported	Not reported	Not reported	Not reported	+	+	Wildfire on area not grazed or mowed in previous years. Dominated by little bluestem Dry year following the fire. Peak green biomass reported for total production.	Adams and Anderson (1978)
February	Central Oklahoma	Late	+	+	+	-	nr	nr	Area not grazed for 2 years before fire. Big bluestem-reduced by fire, but other tallgrasses increased.	Ketling (1957)
March	South-central Oklahoma	Mid to late	-	-	-	+	nc	+	Abandoned cropland naturally revegetated with tallgrasses and woody species. Comparison is pre- and post-burn.	Adams et al. (1982)
Early March. Measured in June	North-central Oklahoma	Late	+(1986) nc (1987)	+(1986) nc (1987)	+(1986) nc (1987)	+(1986) nc (1987)	+(1986) nc (1987)	nc (1986) nc (1987)	Burned (in 1986 and 1987) following moderate grazing. Responses averaged over fire type. Comparison with late April burn.	Bidwell et al. (1990)
Early March. Measured in August	North-central Oklahoma	Late	nc (1986) nc (1987)	+(1986) nc (1987)	nc (1986) nc (1987)	nc (1986) nc (1987)	nc (1986) nc (1987)	nc (1986) -(1987)	Burned in 1986 and 1987 following moderate grazing. Responses averaged over fire type. Comparison with late April burn.	Bidwell et al. (1990)
November, February, and April	North-central Oklahoma	Mid	nc	nc	nc	nc to + in year 2 of Nov.	Not reported	Not reported	Production of desirable hay species, mostly perennial grasses, increased by burns that reduced prairie threawn. Compared to no burn.	Engle et al. (1990)
November to March	Central and Eastern Kansas	Mid	Not reported	+	Not reported	Not reported	+	Not reported	December burn controlled prairie threawn and released forbs and perennial grasses. Compared to no burn.	Owensby and Launchbaugh (1977)
Winter to late spring compared to no burn	Northern Kansas Flint Hills	Late	+	+	-Dec. and May +Mar. and Apr.	nc Dec. +Mar. -Apr. -May	Not reported	Not reported	Big bluestem basal cover reported for tallgrasses and perennial forbs basal cover reported for forbs+legumes. Little bluestem basal cover.	Towne and Owensby (1984)
Early spring to late spring compared to no burn	Northern Kansas Flint Hills	Late	+all burn dates	Not reported	-Mar. nc Apr. and May	+Mar. -Apr. -May	Not reported	Not reported	Grazed pastures burned annually 1950-1966. Big bluestem reported for tallgrasses. Perennial forbs reported for forbs + legumes. Data are canopy cover.	Anderson et al. (1970)
November, March, and late April compared to no burn	Northern Kansas Flint Hills	Late	+all burn dates	-to+	+all burn dates	+Nov. +Mar. -Apr.	Not reported	Not reported	Areas burned annually but not grazed. Data are canopy cover	Gibson (1989)

¹ + = increase, - = decrease, nc = no difference (P > 0.05) as compared to unburned checks or late spring burning.

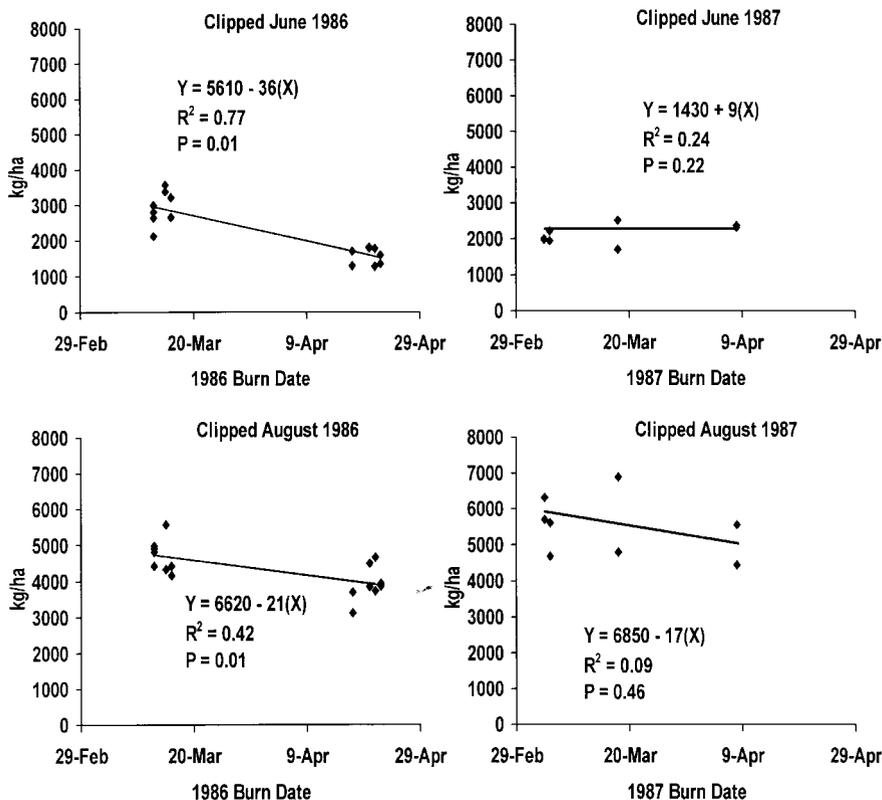


Fig. 1. Total herbage produced following dormant-season fires in moderately grazed tallgrass prairie in northcentral Oklahoma as measured on 2 dates in the first growing season. The independent variable is Julian date. Calendar dates are presented on the x-axes to aid interpretation. The slope coefficients of the equations for 1987 were not significant ($P > 0.05$).

1997, Engle et al. 1998), grazing history (Ewing and Engle 1988, Collins et al. 1998), and possibly with differences in herbicide use. Soil texture and topographic position also have a pronounced influence on response (Anderson et al. 1970, Abrams et al. 1986, Briggs and Knapp 1995) and may explain some of the apparent discrepancies among studies. For example, soil-water properties in the Flint Hills with soils derived from chert differ from soils derived from shale in northcentral Oklahoma. The greater water-holding capacity of Oklahoma soils coupled with an increase in soil temperature after burning that effectively prolongs the length of the early growing season (Hulbert 1969, 1988, Rice and Parenti 1978) could explain enhanced production with earlier burning in the study by Bidwell et al. (1990) compared to the Flint Hills studies. Herbage production often is higher on burned areas than areas not burned in the more humid prairie peninsula where excessive mulch accumulations depress production (Old 1969, Kucera and Ehrenreich 1962). Herbage production may also increase following late spring burning in Oklahoma and Kansas tallgrass

prairies in which excessive mulch accumulates in the absence of burning or heavy grazing or where the fire-altered microclimate does not negatively influence growing conditions (Graves and McMurphy 1969, Anderson et al. 1970, Powell et al. 1979, Towne and Owensby 1984, James 1985, Bidwell et al. 1990).

Successional stage may also override the influence of season of fire on vegetation. For example, early dormant-season fire (November-February) reduces prairie threeawn (*Aristida oligantha* Michx.) on areas heavily infested with this unpalatable annual grass by reducing mulch levels and combusting the seed (Owensby and Launchbaugh 1977, Engle et al. 1990). Late-spring burning (April), especially when repeated annually for several years, also may reduce prairie threeawn (Graves and McMurphy 1969, Engle et al. 1990) and truncate the decades of dominance by prairie threeawn possible in the absence of fire (Rice 1971, Engle et al. 1990). The resulting increase in desirable forage species for cattle is generally less than the loss of prairie threeawn, so total herbage production decreases the year after burning (Tables 1 and 2) (Owensby and

Launchbaugh 1977, Engle et al. 1990).

Burning early in the dormant season may have livestock management benefits. Burning increases the length of the growing season by warming the soil in spring (Hulbert 1988) and increasing photosynthetically active radiation (Knapp 1984), which can speed the production of herbage early in the growing season (Smith and Owensby 1972, Adams and Anderson 1978, Knapp 1984, Mitchell et al. 1996). Although burning earlier than late spring may kill some cool-season annuals and biennial forbs (Keltling 1957, Towne and Knapp 1996), it can also stimulate production of some cool-species species, including sedges (Mitchell et al. 1996), that can provide a high-quality forage important to wildlife and livestock (Coppedge et al. 1998b). Moreover, even though early burning may sometimes increase forbs, the increase is relatively small and does not appear to come at the expense of perennial grasses when compared to areas not burned (Tables 1 and 2).

Late Growing-Season Fire

The comparatively meager research on late growing-season fire in tallgrass prairie is ironic considering the frequency of growing-season fire in both prehistoric and contemporary times. Because of the often hot dry conditions under which fire in this season occurs, one might assume a fire in the late growing season would lead to long-term changes in species composition and reduced herbage production. The limited research literature suggests the opposite.

Ewing and Engle (1988) investigated the influence of late-summer fire in 2 northcentral Oklahoma tallgrass prairies, one with a history of no grazing and the other a history of moderate grazing by cattle (Tables 3 and 4). As is common in tallgrass prairie (Hulbert 1969, Hulbert 1988), the ungrazed prairie had a substantial accumulation of mulch and litter, which supported an intense fire relative to the grazed prairie. Carry-over effects of fires to a second year after the burns were reported by Engle et al. (1992). This study emphasizes the role of grazing history in how vegetation responds to fire, and it supports the results of Bidwell et al. (1990) that timing of measurement of fire effects also influences how the effects of fire might be interpreted. It also indicates that late growing-season fire leads to neither large nor long-term changes in production and species composition.

Adams et al. (1982) compared pre-fire and post-fire responses to a mid-July fire

Table 3. Response of herbage production to fire in different times in the growing season on tallgrass prairies. Measurements were the growing season after fire.

Timing of fire	Location	Seral stage	Change as a percent (and change in biomass kg/ha) as a result of fire			Comments	Reference
			Perennial grass	Forb + legume	Total production		
Late summer (September 5) Measured in June	Northcentral Oklahoma	Mid	Year 1 -41% (-960) Year 2 nc ¹	Year 1 -112% (-260) Year 2 +171% (+294)	Year 1 nc Year 2 nc	Burned in 1985. Moderately grazed. 4,400 kg/ha fuel.	Ewing and Engle (1988), Engle et al. (1992)
Late summer (September 5) Measured in June	Northcentral Oklahoma	Late	Year 1 -27% -540 kg/ha Year 2 nc	Year 1 +173% +1,610 kg/ha Year 2 nc	Year 1 nc Year 2 nc	Burned in 1985. Ungrazed. 10,300 kg/ha fuel.	Ewing and Engle (1988), Engle et al. (1992)
Late summer (September 5) Measured in August	Northcentral Oklahoma	Mid	Year 1 nc		Year 1 nc	Burned in 1985. Moderately grazed. 4,400 kg/ha fuel.	Ewing and Engle (1988), Engle et al. (1992)
Late Summer (September 5) Measured in August	Northcentral Oklahoma	Late	Year 1 nc	Year 1 nc	Year 1 nc	Burned in 1985. Ungrazed. 10,300 kg/ha fuel.	Ewing and Engle (1988), Engle et al. (1992)
Late summer (September)	Northcentral Oklahoma	Late	Year 1 -39% (-1,200) Year 2 nc	nc	Year 1 -16% (-580) Year 2 nc	Burned in 1988 and 1989. Plots burned in moderately grazed pasture. 8,200 kg/ha fuel Forb production was highly variable among treatment plots.	Engle et al. (1993)
Late summer to early fall (Early August to early October)	Southcentral Oklahoma	Mid	Loamy -54% (-1,280) Shallow nc	+53% (+690)	nc	Burned 2 sites (shallow and loamy) up to 3 times in 5 years. Not grazed the year of the first burn and after for the duration of the study. Prairie threeawn abundant at the time of the first burn. Response reported for first burn only.	Engle et al. (1998)

¹nc = no change ($P > 0.05$) was detected as compared to unburned checks.

in an abandoned cropland naturally revegetated to tallgrass prairie (Table 4). Canopy cover of all grasses except switchgrass (*Panicum virgatum* L.) decreased the year after the fire in the burned area. Legumes increased and forbs decreased. Herbaceous vegetation was green, humidity was high, and wind speed low during this fire, suggesting a low intensity fire.

Engle et al. (1993) conducted the first replicated study on growing-season fires in grazed tallgrass prairie. Fire in this northcentral Oklahoma tallgrass prairie reduced herbage production for 1 year after the fire, but forb production was highly variable among plots and no statistically significant change in forbs was detected. Tallgrasses tolerated these September fires, but little bluestem (*Schizachyrium scoparium* (Michx.) Nash) was reduced for at least 2 years after fire. Little bluestem, a bunch grass, also

decreased after burning on the ungrazed burn area in the study reported by Ewing and Engle (1988).

A study in mid-seral tallgrass prairie in southcentral Oklahoma suggests that tallgrass prairie is resilient to fire in the late growing season (Engle et al. 1998). Tallgrasses and little bluestem, which were minor components of the vegetation, were reduced by 1 fire as were perennial grasses as a group on the more productive loamy site (Tables 3 and 4). The less productive, shallower site responded with fewer shifts in vegetation and no reduction in total production. The response after as many as 3 burns over 5 years indicates that late growing-season fire is an ephemeral, short-lived influence on plant production and species composition (Engle et al. 1998, 2000).

Mixed Prairie

The mixed prairie by definition is more arid than tallgrass prairie and fire in any season should dry the site further and reduce production. Although the research literature is not as rich as for the tallgrass prairies where fire is used more routinely in range management, sufficient research exists to indicate a variable response to fire in mixed prairie.

Early to mid dormant-season wildfires reduced grass production in western Kansas (Launchbaugh 1964, 1969, 1978 as cited in Owensby, unpublished). In contrast, a prescribed fire in late spring, timed to coincide with growth of dominant grasses, increased grass and total herbage yield (Launchbaugh 1978 as cited in Owensby, unpublished). Late spring burning 3 consecutive years resulted in variable changes in species composition and production (Launchbaugh 1978 as cited in

Table 4. Change in composition of herbage in tallgrass prairie in response to fire in different times of the growing season in tallgrass prairies. Comparison is with unburned check unless indicated otherwise. Measurements were the growing season after fire.

Timing of fire	Location	Serai stage	Change ¹ in relative composition following burning						Comments	Reference
			Tallgrass	Perennial grass—	Little bluestem	Forbs+ legume	Forb	Legume		
July 14	South-central Oklahoma	Mid to late	+	Not reported	—	—	—	+	Abandoned cropland naturally revegetated with tallgrasses and woody species. Comparison is pre- and post-burn.	Adams et al.
Late summer (September 5) Measured in June	North-central Oklahoma	Mid	nc (year 1) nc (year 2)	— (year 1) nc (year 2)	nc (year 1) nc (year 2)	— (year 1) nc (year 2)	— (year 1) + (year 2)	nc (year 1) nc (year 2)	Burned in 1985. Moderately grazed 4,400 kg/ha fuel.	Ewing and Engle (1988). Engle et al. (1992)
Late summer (September 5) Measured in June	North-central Oklahoma	Late	nc (year 1) nc (year 2)	— (year 1) nc (year 2)	— (year 1) nc (year 2)	+ (year 1) + (year 2)	+ (year 1) nc (year 2)	nc (year 1) nc (year 2)	Burned in 1985. Ungrazed. 10,300 kg/ha fuel.	Ewing and Engle (1988). Engle et al. (1992)
Late summer (September 5) Measured in August, Year 1	North-central Oklahoma	Mid	nc	nc	nc	nc	nc	nc	Burned in 1985. Moderately grazed 4400 kg/ha fuel.	Ewing and Engle (1988). Engle et al. (1992)
Late summer (September 5) Measured August	North-central Oklahoma	Late	nc	nc	—	nc	nc	nc	Burned in 1985. Ungrazed 10,300 kg/ha fuel	Ewing and Engle (1988), Engle et al. (1992).
Late summer (September)	North-central Oklahoma	Late	nc	— (year 1) nc (year 2)	— (year 1) — (year 2)	Not reported	Not reported	Not reported	Burned in 1988 and 1989. Plots burned in moderately grazed pasture. 8,200 kg/ha fuel. Forb production was highly variable among treatment plots.	Engle et al. (1993)
Late summer to early fall (Early August to early October)	South-central Oklahoma	Mid	Loamy — Shallow nc	nc	Loamy — Shallow nc	+	Not reported	Not reported	Burned 2 sites (shallow and loamy) up to 3 times in 5 years. Not grazed the year of the first burn and after for the duration of the study. Prairie three-awn abundant at the time of the first burn. Response reported for only first burn.	Engle et al. (1998)

¹+ = increase, — = decrease, nc = no difference (P > 0.05) as compared to unburned checks or pre-burn.

Owensby, unpublished) suggesting that weather conditions can have an overriding influence on response to fire.

Burns in the early dormant season may concomitantly increase forbs, including western ragweed (*Ambrosia psilostachya* DC.) (Hopkins et al. 1948), but western ragweed does not compete with grasses and appears to fluctuate independent of grass production (Launchbaugh 1969, Vermiere 1997). Moreover, an increase in forbs does not appear universal following early dormant-season burns. Burning mixed prairie in late January with the

objective of increasing forb production, primarily western ragweed, did not increase forb production nor reduce grass production in northwestern Oklahoma on sandy soils (Peoples et al. 1994).

Appropriate Management after Fire

This review of research on post-burn vegetation response in Oklahoma and Kansas native grasslands suggests a wide

variety of responses are possible, and rules-of-thumb that generalize responses to wildfire may be misleading. Launchbaugh and Owensby (1978) recommended reducing stocking rate on areas burned by wildfire in Kansas by 25 to 75% the first year and 25 to 50% the second year after the fire. A more recent recommendation is to reduce stocking rate by 15 to 25% in the tallgrass prairie and by 50% in mixed prairie (Ohlenbusch 1992). These recommendations have been applied throughout Oklahoma and Kansas to native grasslands

burned by wildfire. Furthermore, as an extension to the common practice of applying herbicides at regular intervals to reduce forbs and favor grasses (New 1997), managers often apply herbicide the growing season following wildfire in expectation of an increase in forbs. The results from the published studies we present here suggest grassland environments in Oklahoma and Kansas are too diverse for these recommendations to apply uniformly.

A number of factors can alter the effects of early dormant-season and growing-season fires on species composition and herbage production in native grasslands and should be considered when adjusting stocking rate or deciding on whether to apply a broadleaf herbicide. Successional stage at the time of a fire is perhaps the most important factor influencing post-fire species composition. However, most studies on the effects of fire in Oklahoma and Kansas grasslands have been conducted in late seral vegetation in which forbs were a minor component of the vegetation. It is logical to assume that if abundant before fire, forbs should increase after fire if the fire reduces the competitiveness of other species and if the timing is not coincident with a susceptible stage of development of the forbs in question (Howe 1994). Conversely, if forbs are scarce because of moderate-continuous stocking, a history of late dormant-season fire, or previous use of broadleaf herbicides, then forbs probably will not increase with early dormant-season fire.

Post-fire observations of native grasslands in early and mid successional stages as well as confounding factors such as post-fire grazing practices may be the source of some of the conventional wisdom that early season fire increases forb abundance. We think preferential livestock grazing of a burned area in a partially burned pasture has caused many managers to misinterpret the effects of wildfire. When making decisions on stocking rate or herbicide applications after wildfire, rangeland managers should also consider the pre- and post-fire growing conditions and the exact timing of the fire relative to growth stage of key species. Species composition and standing crop (which influences fire behavior) at the time of the fire, soil texture and site potential, pre- and post-fire management (grazing management, herbicide use, fertilization, prescribed burning, and others), and land use history (grazing, cultivation, and others) also confound the influence of fire on species composition and should be taken into account in post-fire management.

Conclusions

It was once held firmly by Oklahoma scientists that fire in any season and in any climate decreased plant production and increased weedy species unpalatable to livestock (for example, see Bunch et al. 1958). This kind of response to fire follows preferential grazing of the burned areas that offer more palatable forage to livestock and is in reality the result of overstocking (Launchbaugh and Owensby 1978). In one of the first controlled studies involving livestock grazing on areas with a mixture of burned and unburned areas, Penfound and Kelting (1950) noted that virtually no grass leaves were grazed in the unburned areas. Studies now in place at several locations in the central Great Plains are investigating the influence of fire at varied seasons and spatial contexts on ecosystem responses to include large herbivores allowed to preferentially graze burned patches within a matrix of unburned native grassland (e.g., Coppedge et al. 1998a, 1998b). The early indications suggest that these grasslands are far more productive and resilient under fire and preferential spot grazing than earlier believed.

How, then, should a manager respond to a fire timed at a season or date with which the manager is unaccustomed? Many rangeland managers, especially in Oklahoma, are unaccustomed to fire in any season and have never burned their rangelands, so that the consequences of any fire are unknown to the manager. An adjustment in stocking rate of domestic livestock is likely the prudent course of action, but understocking for more than 1 or 2 years is likely unwarranted especially in the more mesic regions of Oklahoma and Kansas. Of course, appropriate post-fire management also depends on current weather conditions, intrinsic managerial options (e.g., herd composition and flexibility), and management objectives. Managerial attentiveness must therefore be at its highest to respond to the range of possible responses of native grasslands to fire.

We conclude that a variety of composition and production responses to season of fire are possible, and that the native grasslands of Kansas and Oklahoma are more resilient to burning in any season than is commonly held by conventional wisdom. Moreover, the body of literature suggests that broadly applied rules-of-thumb cannot be constructed for post-fire management regardless of the season. Thus, the only objective, accurate method to assess the relatively minor effects of fire (wildfire or prescribed fire) in any season is to measure

the vegetation after fire. Although rules-of-thumb appear valid for dormant-season fires in the late-seral tallgrass prairies of the northern Flint Hills, the body of literature indicates we cannot at this time accurately predict vegetation response in other seasons and other locations.

Literature Cited

- Abrams, M.D., A.K. Knapp, and L.C. Hulbert. 1986. A ten-year record of above-ground biomass in a Kansas tallgrass prairie: Effects of fire and topographic position. *Amer. J. Bot.* 73:1509-1515.
- Adams, D.E. and R.C. Anderson. 1978. The response of a central Oklahoma grassland to burning. *Southwest. Natur.* 23:623-632.
- Adams, D.E., R.C. Anderson, and S.L. Collins. 1982. Differential response of woody and herbaceous species to summer and winter burning in an Oklahoma grassland. *Southwest. Natur.* 27:55-61.
- Anderson, K.L., C.E. Owensby, and E.F. Smith. 1970. Burning bluestem range. *J. Range Manage.* 23:81-92.
- Bidwell, T.G., D.M. Engle, and P.L. Claypool. 1990. Effects of spring headfires and backfires on tallgrass prairie. *J. Range Manage.* 43:209-212.
- Blair, J.M. 1997. Fire, N availability, and plant response in grasslands: a test of the transient maxima hypothesis. *Ecol.* 78:2359-2368.
- Bragg, T.B. 1982. Seasonal variations in fuel and fuel consumption by fires in a bluestem prairie. *Ecol.* 63:7-11.
- Bragg, T.B. 1995. The physical environment of the Great Plains grasslands. pp. 49-81. *In:* A. Joern and K.H. Keeler (eds.). *The changing prairie-North American grasslands.* Oxford Univ. Press. New York.
- Briggs, J.M. and A.K. Knapp. 1995. Interannual variability in primary production in tallgrass prairie: Climate, soil moisture, topographic position, and fire as determinants of aboveground biomass. *Amer. J. Bot.* 82:1024-1030.
- Bunch, C., E. Roberts, and R.E. Chiles. 1958. Stop grass fires. Oklahoma State Univ. Ext. Serv. Leaflet L-32.
- Collins, S.L., A.K. Knapp, J.M. Briggs, J.M. Blair, and E.M. Steinauer. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. *Sci.* 280:745-747.
- Coppedge, B.R., D.M. Engle, C.S. Toepfer, and J.H. Shaw. 1998a. Effects of seasonal fire, bison grazing and climatic variation on tallgrass prairie vegetation. *Plant Ecol.* 139:235-246.
- Coppedge, B.R., D.M. Leslie, Jr., and J.H. Shaw. 1998b. Botanical composition of bison diets on tallgrass prairie in Oklahoma. *J. Range Manage.* 379-382.
- Elwell, H.M., H.A. Daniel, and F.A. Fenton. 1941. The effects of burning pasture and woodland vegetation. *Oklahoma Agr. Exp. Sta. B-247.*

- Engle, D.M., T.G. Bidwell, J.F. Stritzke, and D. Rollins. 1990. Atrazine and burning in tallgrass prairie infested with prairie threeawn. *J. Range Manage.* 43:424-427.
- Engle, D.M., T.G. Bidwell, and A.L. Ewing. 1992. Effects of late summer fire in tallgrass prairie. p. 9 *In*: T.G. Bidwell (ed.). Range research highlights. Coop. Ext. Serv. Oklahoma State Univ. Circ. E-905, Stillwater.
- Engle, D.M., M.W. Palmer, J.S. Crockett, R.L. Mitchell, and R. Stevens. 2000. Influence of late season fire on an early successional Oklahoma prairie. *J. Veg. Sci.* 11:135-144.
- Engle, D.M., J.F. Stritzke, T.G. Bidwell, and P.L. Claypool. 1993. Late-summer fire and follow-up herbicide treatments in tallgrass prairie. *J. Range Manage.* 542-547.
- Engle, D.M., R.L. Mitchell, and R.L. Stevens. 1998. Growing-season fire effects on forage production in mid-successional tallgrass prairie. *J. Range Manage.* 51:115-121.
- Ewing, A.L. and D.M. Engle. 1988. Effects of late summer fire on tallgrass prairie microclimate and community composition. *Amer. Midl. Natur.* 120:212-223.
- Gibson, D.J. 1989. Hulbert's study of factors effecting botanical composition of tallgrass prairie. Proc. 11th North Amer. Prairie Conf. pp. 115-133.
- Gibson, D.J. and L.C. Hulbert. 1987. Effects of fire, topography and year-to-year climatic variation on species composition in tallgrass prairie. *Vegetatio* 72:175-185.
- Graves, J.E. and W.E. McMurphy. 1969. Burning and fertilization for range improvement in central Oklahoma. *J. Range Manage.* 22:165-168.
- Higgins, K.F. 1986. Interpretation and compendium of historical fire accounts in the Northern Great Plains. U.S. Fish and Wildl. Serv. Res. Publ. 161.
- Hopkins, H.F., F.W. Albertson, and A. Riegel. 1948. Some effects of burning upon a prairie in west-central Kansas. *Trans. Kan. Acad. Sci.* 51:131-141.
- Howe, H.F. 1994. Response of early- and late-flowering plants to fire season in experimental prairies. *Ecol. Appl.* 4:121-133.
- Hulbert, L.C. 1969. Fire and litter effects in undisturbed bluestem prairie in Kansas. *Ecol.* 50:874-877.
- Hulbert, L.C. 1988. The causes of fire effects in tallgrass prairie. *Ecol.* 69:46-58.
- James, S.W. 1985. An unexpected effect of autumn burning in tallgrass prairie. *Amer. Midl. Natur.* 114:400-403.
- Kelting, R.W. 1957. Winter burning in central Oklahoma grassland. *Ecol.* 38:520-523.
- Knapp, A.K. 1984. Post-burn differences in solar radiation, leaf temperature and water stress influencing production in a lowland tallgrass prairie. *Amer. J. Bot.* 71:220-227.
- Kucera, C.L. and J.H. Ehrenreich. 1962. Some effects of annual burning on central Missouri prairie. *Ecol.* 43:334-336.
- Launchbaugh, J.L. 1964. Effects of early spring burning on yields of native vegetation. *J. Range Manage.* 17:5-6.
- Launchbaugh, J.L. 1969. Range condition classification based on regressions of herbage yields on summer stocking rates. *J. Range Manage.* 22:97-101.
- Launchbaugh, J.L. 1978. Effects of fire on shortgrass vegetation. Proc. Prairie Prescribed burning Symp. and Workshop. 25 Apr. 1978. Northern Prairie Wildl. Res. Center, Jamestown, N. D.
- 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. Manhattan, Kans.
- McMurphy, W.E. and K.L. Anderson. 1963. Burning bluestem range-forage yields. *Kans. Acad. Sci. Trans.* 66:49-51.
- McMurphy, W.E. and K.L. Anderson. 1965. Burning Flint Hills range. *J. Range Manage.* 18:265-269.
- Mitchell, R.B., R.A. Masters, S.S. Waller, K.J. Moore, and L.J. Young. 1996. Tallgrass prairie vegetation response to spring burning dates, fertilizer, and atrazine. *J. Range Manage.* 49:131-136.
- New, M.G. 1997. Survey of weed management practices in pastures and rangelands in Oklahoma and selectivity of various herbicide treatments on cultivars of forage bermudagrass (*Cynodon dactylon*). M.S. Thesis. Oklahoma State Univ. Stillwater, Okla.
- Ohlenbusch, P.D. 1992. Management following wildfire. Kansas Coop. Ext. Serv. L-514 (revised). Manhattan, Kans.
- Old, S.M. 1969. Microclimate, fire and plant production in an Illinois prairie. *Ecol.* 39:355-384.
- Owensby, C.E. and K.L. Anderson. 1967. Yield responses to time of burning in the Kansas Flint Hills. *J. Range Manage.* 20:12-16.
- Owensby, C.E. and J.L. Launchbaugh. 1977. Controlling prairie threeawn (*Aristida oligantha* Michx.) in central and eastern Kansas with fall burning. *J. Range Manage.* 30:337-339.
- Penfound, W.T. and R.W. Kelting. 1950. Some effects of winter burning on a moderately grazed pasture. *Ecol.* 31:554-560.
- Peoples, A.D., R.L. Lochmiller, D.M. Leslie, Jr., and D.M. Engle. 1994. Producing northern bobwhite food on sandy soil in semiarid mixed prairies. *Wildl. Soc. Bull.* 22:204-211.
- Powell, J., H.T. Zawi, J.J. Crockett, L.I. Croy, and R.D. Morrison. 1979. Central Oklahoma rangeland response to fire, fertilization, and grazing by sheep. Oklahoma Agr. Exp. Sta. Bull. B-744.
- Rice, E.L. 1971. Inhibition of nodulation on inoculated legumes by leachates from pioneer plant species from abandoned fields. *Amer. J. Bot.* 58:368-371.
- Rice, E.L. and R.L. Parenti. 1978. Causes of decreases in productivity in undisturbed tall grass prairie. *Amer. J. Bot.* 65:1091-1097.
- Riggs, R.A., S.C. Bunting, and S.E. Daniels. 1996. Prescribed fire, pp. 295-319 *In*: P.R. Krausman (ed.). Rangeland Wildlife. Soc. Range Manage. Denver, Colo.
- Roberts, K.W., D.M. Engle, and J.R. Weir. 1999. Weather constraints to scheduling prescribed burns. *Rangelands* 21:6-7.
- Smith, E.F. and C.E. Owensby. 1972. Effects of fire on true prairie grasslands. Proc. Tall Timbers Fire Ecology Conf. 12:9-22.
- Towne, E.G. and A.K. Knapp. 1996. Biomass and density responses in tallgrass prairie legumes to annual fire and topographic position. *Amer. J. Bot.* 83:175-179.
- Towne, G. and C. Owensby. 1984. Long-term effects of annual burning at different dates in ungrazed Kansas tallgrass prairie. *J. Range Manage.* 37:392-397.
- Vermiere, L. 1997. Western ragweed growth and competitiveness on mixed and tallgrass prairie. M.S. Thesis. Oklahoma State Univ.
- Zimmerman, J.L. 1997. Avian responses to fire, grazing, and drought. pp. 167-180, *In*: F.L. Knopf and F.B. Samson (eds.). Ecology and conservation of Great Plains vertebrates. Ecological Studies, Vol. 125. Springer. New York.

Prairie dog effects on harvester ant species diversity and density

JUSTIN E. KRETZER AND JACK F. CULLY, JR.

Authors are a graduate student in the Division of Biology and Assistant Unit leader, Kansas Cooperative Fish & Wildlife Research Unit, USGS-BRD, Division of Biology, Kansas State University, Manhattan, Kan. 66506.

Abstract

The purpose of this study was to determine if black-tailed prairie dogs (*Cynomys ludovicianus* Ord) influence harvester ant nest density and species composition within the shortgrass prairie biome of southwestern Kansas. Two treatments were established: areas colonized by prairie dogs and areas not colonized by prairie dogs. We recorded 183 harvester ant nests of 3 species. Harvester ant nest density did not differ significantly between prairie dog colonies (3.08 nests ha⁻¹) and non-colonized shortgrass prairie sites (4.54 nests ha⁻¹), but species composition did. *Pogonomyrmex rugosus* Emery was the most frequent species on prairie dog colonies where it accounted for 87% of ant nests present, as opposed to 33% on sites where prairie dogs were absent. *Pogonomyrmex barbatus* Smith was the most abundant species on non-colonized areas, making up 49% of the ant nests sampled. *Pogonomyrmex occidentalis* Cresson comprised 11% of ant nests sampled, and was nearly absent from prairie dog colonies (20 nests on non-colonized sites vs. 1 nest on prairie dog colonies). The average number of harvester ant species found per site was consistently greater on sites where prairie dogs were absent.

Key Words: *Cynomys ludovicianus*, *Pogonomyrmex*, diversity, shortgrass prairie, Kansas

Harvester ants (*Pogonomyrmex* spp.) are widespread in the arid and semi-arid regions of western North America. Harvester ants are locally abundant and are considered pests in rangelands where densities are high. These ants may alter plant community structure by denuding vegetation and harvesting seeds and litter surrounding colonies (Rogers and Lavigne 1974). Hewitt et al. (1974) state that harvester ants have the most consistent impact on rangeland of any insect other than grasshoppers. Ants also are considered important contributors to soil formation (Rogers and Lavigne 1974). Because earthworms are not abundant in semi-arid rangelands, the ant is the most important invertebrate that moves soil vertically (Jacot 1936).

Black-tailed prairie dogs (*Cynomys ludovicianus* Ord) are native herbivores that are capable of dramatically altering grassland habitats (King 1955, Koford 1958, Hoogland 1995, Winter 1999) and are considered by some to be keystone species (Miller et al. 1994, Wuerthner 1997, Kotliar et al. 1999). Because of serious declines in the past, and ongoing declines over large portions

We were assisted in the field by Dwayne Winslow. Bobby Brown confirmed ant species identification, and Jeffrey Pontius provided valuable statistical advice. Research was funded by the U.S.D.I. Fish and Wildlife Service, U.S.D.A. Forest Service, and Kansas State University.

Manuscript accepted 18 Apr. 2000.

Resumen

El propósito de este estudio fue determinar si los perros de la pradera (*Cynomys ludovicianus* Ord.) influyen en la densidad y diversidad de especies de hormigas cosechadoras de la bioma de praderas de zacates cortos del sudoeste de Kansas. Se establecieron dos tratamientos: áreas colonizadas por perros de la pradera y áreas no colonizadas. Registramos 183 hormigueros de 3 especies de hormigas cosechadoras. La densidad de hormigas cosechadoras no difirió significativamente entre las áreas colonizadas por perros de la pradera (3.08 hormigueros ha⁻¹) y las no colonizadas (4.54 hormigueros ha⁻¹), pero la composición de especies sí difirió. La especie de hormiga *Pogonomyrmex rugosus* Emery fue la más frecuente en las áreas colonizadas por perros de la pradera en la que el 87% de los hormigueros registrados fueron de esta especie, en contraste con el 33% de los hormigueros de los sitios donde los perros de la pradera estuvieron ausentes. La especie de hormiga *Pogonomyrmex barbatus* Smith fue la más abundante en las áreas no colonizadas con el 49% de los hormigueros muestreados. La especie *Pogonomyrmex occidentalis* Cresson comprendió el 11% de los hormigueros y estuvo casi ausente en las colonias de perros de la pradera (20 hormigueros en las áreas no colonizadas vs. 1 en las áreas colonizadas). El promedio del número de especies de hormigas cosechadoras encontradas por sitio fue consistentemente mayor en los sitios donde los perros de la pradera estuvieron ausentes.

of their range, the Fish and Wildlife Service conducted a status review of black-tailed prairie dogs that found the species warrantable but precluded for listing under the Endangered Species Act (USDI 2000).

In addition to alterations in vegetative communities, black-tailed prairie dog activities can cause significant changes in the species composition and densities of a variety of vertebrate groups occupying mixed-grass prairie habitats (O'Meilia et al. 1982, Agnew et al. 1986); however, there currently are only a few detailed studies describing the influence of prairie dogs on invertebrate communities. In mixed-grass prairies of South Dakota, total density of soil nematodes was higher in prairie dog colonies than in uncolonized sites (Ingham and Detling 1984). Conversely, in northern Oklahoma, arthropod biomass was lower on prairie dog colonies than on uncolonized areas (O'Meilia et al. 1982).

The purpose of this research was to determine if black-tailed prairie dogs influence harvester ant (*Pogonomyrmex* spp.) species composition and nest density. We documented the density and species composition of harvester ant nests at study sites on and off black-tailed prairie dog colonies at the Cimarron National Grassland, Kans.

Methods

This study was conducted on the Cimarron National Grasslands in Morton County, Kans. (Latitude 37° 07'N–Longitude 102° 00'W), during July 1997. Two treatments were established with 5 sample sites each scattered across the northern half of the grassland: areas colonized by prairie dogs and areas of similar habitat not colonized by prairie dogs. We selected 5 prairie dog colonies, which varied in size from 30 to 54 ha. These sites were selected because they were among the largest prairie dog colonies on the grasslands. Five non-colonized study sites, which varied in size from 32 to 65 hectares were selected in pastures with slope and vegetation similar to the prairie dog sites, but without prairie dogs. All study sites were shortgrass community type dominated by buffalograss (*Buchloe dactyloides* (Nutt.) Engelm.) and blue grama (*Bouteloua gracilis* (H.B.K.) Lag. Ex Griffiths), with low topographic relief. Soil types at all sites were characterized by loamy and silty-loam soils in the Richfield (fine, smectite, mesic Aridic, Arguistolls)—Ulysses (fine-silty, mixed, superactive, mesic Aridic, Haplustolls) association with slopes between 0–6% (Dickey et al. 1963).

Livestock was managed on the Cimarron National Grasslands under rotational grazing, with intensity adjusted to the available forage; therefore, not all study sites were grazed at the same time each year. One prairie dog colony, and 2 non-colonized sites were not grazed by livestock during 1996 or 1997. The combination of prairie dogs and livestock creates a situation where grazing intensity and soil disturbance may be very high.

Prairie dog burrow density was calculated at each colony using a plotless density estimator modified from Cook and Stubbendieck (1986). Because nearest neighbor estimates of density are appropriate only for randomly distributed objects, and we have evidence that prairie dog burrows are regularly dispersed (Cully, unpublished data), we adapted a point to burrow estimator as follows. One hundred meter long tapes were laid at random at 8 locations in each colony. Random points were selected in each 10 m section of the tape for 75 points at each colony. The distance from the random point to the nearest burrow opening was measured to the nearest 0.1 m. Density was calculated as $D = 10,000/\pi d^2$ where D = density ha^{-1} , and d = mean point to burrow distance, which forms the radius of a circular area.

Harvester ant nest density and species composition was quantified along 8 strip transects, 300 m long x 20 m wide at each study site. Two people walked parallel along the transects, 20 m apart, for a total of 4.8 ha sampled per study site. Within this area, all harvester ant nests were counted and identified to species according to Cole (1968). Voucher ant worker collections were made and species identifications were verified by Mr. Bobby Brown, Museum of Entomological and Prairie Arthropod Research at Kansas State University where specimens are preserved. Differentiation of species in the field was simple and accurate due to differences in size and color of workers, as well as different clearing and mound shapes among species (Table 1).

Table 1. Characteristics of the 3 species of harvester ants found at the Cimarron National Grassland in Morton Co., Kans., USA.

Species	Color	Size	Mound shape
<i>Pogonomyrmex rugosus</i>	black with red abdomen	large	flat
<i>P. barbatus</i>	red	large	flat
<i>P. occidentalis</i>	red	small	dome

At prairie dog sites, sampling transects began at the boundary of the prairie dog colony. In areas where prairie dogs were absent, sampling began at the edge of the study site. If the study site was 45 ha or smaller, the second transect was offset 75 m at the opposite side of the study site. At non-colonized sites, and at prairie dog colonies where the study site was larger than 45 ha, the second transect was similarly offset and started at the approximate mid-point of the site and ran in the same direction as the first. The third transect was again offset, then started at the opposite edge and ran back towards the center of the study site. This ensured that all parts of the site were thoroughly sampled as opposed to just sampling the edges or middle portions. These data were used to estimate the density of ant nests at each study site, which was the sample unit.

Total harvester ant nest density (nests ha^{-1}) and species composition were compared between prairie dog colonies and non-colonized shortgrass prairie sites. T-tests were used to statistically test for differences in total harvester ant nest density, nest density of each species sampled, and harvester ant species richness between the 2 treatments ($\alpha = 0.05$). A nonparametric Wilcoxon exact test was used when deviations from normality occurred. When normality was met but variances in data were

not equal among treatments a Satterthwaite t-test was used instead of Cochran t-test (SAS Inst. Inc. 1993).

Results

Black-tailed prairie dog burrow density at the 5 colonies was moderate ($\bar{x} = 81$, $SD = 56$ burrows ha^{-1}). A total of 183 harvester ant nests of 3 species was recorded. The total density of harvester ant nests did not differ significantly between prairie dog colonies and non-colonized shortgrass prairie sites (Table 2). *Pogonomyrmex rugosus* Emery was encountered most often and accounted for 55% of the ant nests sampled, followed by *P. barbatus* Smith (34%), and *P. occidentalis* Cresson

(11%). Although total harvester ant nest density was not significantly different on black-tailed prairie dog colonies, species composition was influenced by prairie dogs. Mean nest densities of *P. rugosus* and *P. occidentalis* did not differ significantly between treatments. However, mean species richness and nest densities of *P. barbatus* were significantly different between treatments. The nest density of *P. barbatus* was greater on study sites where prairie dogs were absent. While all 3 species of harvester ants were sampled both on and off prairie dog colonies, mean species richness was significantly greater on non-colonized shortgrass prairie sites ($\bar{x} = 2.6$, $SE = 0.25$, $df = 4$) than at prairie dog colonies ($\bar{x} = 1.4$, $SE = 0.25$, $df = 4$; $P = 0.0476$).

Discussion

Total harvester ant nest densities, as well as the density of each individual species, were lower than those reported in other studies with a variety of land-use types (Whitford et al. 1976, Soulé and Knapp 1996). On the Cimarron National Grassland, total harvester ant densities were similar to densities of *P. occidentalis* in heavily grazed pastures of northeastern Colorado (Rogers and Lavigne 1974). However, *P. occidentalis* densities on the

Table 2. Total number of harvester ant nests sampled, and mean (+/-SE) nest density on prairie dog colonies (PDOG) and shortgrass prairie sites where prairie dogs are absent (NODOG) at the Cimarron National Grassland, Kansas.

Species	Number of Nests		Mean Density		P-value and test
	PDOG	NODOG	PDOG	NODOG	
			----- (nests/ha) -----		
<i>Pogonomyrmex rugosus</i> Emery	64	36	2.67 (1.46)	1.50 (0.54)	0.4760 Cochran
<i>Pogonomyrmex barbatus</i> Smith	9	53	0.38 (0.19)	2.21 (0.65)	0.0470* Satterthwaite
<i>Pogonomyrmex occidentalis</i> Cresson	1	20	0.04 (0.04)	0.83 (0.54)	0.1270 Wilcoxon
Total <i>Pogonomyrmex</i> spp.	74	109	3.08 (1.29)	4.54 (0.43)	0.3152 Cochran

*Significant at the 0.05 level.

Cimarron National Grasslands were lower than in Colorado (Rogers and Lavigne 1974) and Oklahoma (O'Meilia et al. 1982) where *P. occidentalis* has been reported previously. Nagel (1969) reported lower densities of *P. occidentalis* in Morton County, Kansas, compared to other western Kansas counties.

Livestock grazing may or may not influence ant abundance and density. Nagel (1969) suggested that mated queen *P. occidentalis* select areas of rangeland with sparse vegetation and soils with high light reflectance, typical of over-grazed areas. In the Chihuahuan Desert in southeastern Arizona, ant abundance was not affected by livestock grazing (Heske and Campbell 1991). Likewise, Kirkham (1967) did not find any differences in *Pogonomyrmex owyheei* Cole densities in Wyoming due to different grazing intensities over a 10-year period. Likewise, in northern Colorado, light and moderate grazing resulted in 22% and 33% increases in harvester ant colony densities, but heavy grazing reduced colony density by 87% (statistical analyses were not presented) compared to the ungrazed sites (Rogers and Lavigne 1974). In northern Colorado *P. occidentalis* densities are negatively associated with vegetative succession on abandoned fields, with the greatest concentrations found in areas with abundant forbs and perennial grasses, and lower densities in late succession shortgrass stages (Costello 1944).

In northern Oklahoma, O'Meilia et al. (1982) did not detect any differences in *P. occidentalis* densities between prairie dog towns and non-colonized pastures. Because of the extreme rarity of *P. occidentalis* on prairie dog colonies and variance in numbers found on non-colonized sites, we did not detect a statistical difference between treatments in this study, however, there was a trend towards greater abundance of *P. occidentalis* nests on non-colonized shortgrass prairie sites compared to prairie dog colonies (20 vs. 1 nest encountered respectively).

Pogonomyrmex rugosus and *P. barbatus* are closely related species with a wide niche overlap. These 2 species have simi-

lar habitat and forage requirements. Both species prefer seeds from grasses and forbs but will also collect a variety of other materials (Whitford et al. 1976, Hölldobler and Lumsden 1980, Gordon 1993). In New Mexico grasslands, nest densities of *P. rugosus* and *P. barbatus* were approximately 20 nests per ha in areas supporting one or both species (Whitford et al. 1976), which is higher than we found. Despite the close relationship between the 2 species, they responded to prairie dog activities in different ways. *Pogonomyrmex rugosus* nest density was similar between the 2 treatments; whereas, *P. barbatus* nest densities were significantly higher in areas without prairie dogs.

Harvester ant species richness was significantly lower on prairie dog colonies. Although all 3 species of ants were encountered both on and off prairie dog colonies, non-colonized shortgrass sites consistently had 2 or 3 species present, whereas only 1 or 2 species were usually found on prairie dog colonies. *Pogonomyrmex rugosus* was the most frequent species on prairie dog colonies where it accounted for 87% of ant colonies encountered, as opposed to 33% where prairie dogs were absent. *Pogonomyrmex barbatus* was the most abundant species on non-colonized areas, making up 49% of the ant nests sampled there. *Pogonomyrmex barbatus* and *P. occidentalis* were nearly absent from prairie dog colonies. *Pogonomyrmex barbatus* was 5 times as frequent and *P. occidentalis* was 20 times more frequent on non-colonized prairie sites.

Crist and Wiens (1994) reported reduced seed harvesting of *P. occidentalis* in shortgrass pastures occupied by prairie dogs. They attributed this pattern of lower seed removal to the presence of short-horned lizards (*Phrynosoma douglassi* Bell) on prairie dog colonies, rather than to the vegetative structure of those sites. Whitford and Bryant (1979) and Munger (1984a, 1984b) demonstrated that horned lizard (*Phrynosoma cornutum* Harlan) predation decreases the foraging activity of harvester ants. However, we do not believe that a reduction in foraging activi-

ty of these ants, due to predation by horned lizards, is responsible for the observed decrease in species richness or in *P. barbatus* and *P. occidentalis* densities found on prairie dog colonies during this study. In a concurrent study in 1997, there was no difference in relative abundance of horned lizards between prairie dog colonies and non-colonized shortgrass prairie sites (Kretzer and Cully in press).

Our results are that prairie dog colony habitats are marginal, or unattractive to *P. barbatus* and *P. occidentalis*, but are attractive to *P. rugosus*. We do not know what factors are responsible for these species differences. Long-term disturbance by black-tailed prairie dogs alters plant community structure (Bonham and Lerwick 1976, O'Meilia et al. 1982, Coppock et al. 1983, Agnew et al. 1986, Archer et al. 1987, Winter 1999). Harvester ants exploit patchy but relatively stable food supplies (Hölldobler and Lumsden 1980). It is possible that changes in vegetative composition and cover, that result from prairie dog activities affect soil characteristics, food availability, and suitable nest sites in ways that have a negative influence on densities of *P. barbatus* and *P. occidentalis* with concomitant reductions in harvester ant species richness.

Black-tailed prairie dogs are known to alter the distribution, abundance, and species composition of a wide variety of plant and animal groups (Agnew et al. 1986, Archer et al. 1987, Koford 1958, Bonham and Lerwick 1976, Coppack et al. 1983, Ingham and Detling 1984, O'Meilia et al. 1982, Miller et al. 1990, Miller et al. 1994). Prairie dogs create patches of habitat that differ from the surrounding grasslands and add heterogeneity to shortgrass prairie landscapes (Whicker and Detling 1988, 1993). Our results show that prairie dogs influence closely related ant species in dramatically different ways. They also demonstrate that it is inappropriate to make broad generalizations about the positive or negative influences that prairie dogs have on other grassland organisms.

Literature Cited

- Agnew, W., D. W. Uresk, and R. M. Hansen. 1986.** Flora and fauna associated with prairie dog colonies and adjacent ungrazed mixed-grass prairie in western South Dakota. *J. Range Manage.* 39:135–139.
- Archer, S., M. G. Garret, and J. K. Detling. 1987.** Rates of vegetation change associated with prairie dog (*Cynomys ludovicianus*) grazing in North American mixed-grass prairie. *Vegetatio* 72:159–166.
- Bonham, C. D. and A. Lerwick. 1976.** Vegetation changes induced by prairie dogs on shortgrass range. *J. Range Manage.* 29:221–225.
- Cole, A. C. 1968.** *Pogonomyrmex* harvester ants; a study of the genus in North America. Univ. Tennessee Press, Knoxville, Tenn.
- Cook, C. W. and J. Stubbendieck. 1986.** Range research: basic problems and techniques. Soc. for Range Manage., Denver, Colo.
- Coppack, D. L., J. E. Ellis, J. K. Detling, and M. I. Dyer. 1983.** Plant herbivore interactions in a North American mixed-grass prairie. II. Responses of bison to modification of vegetation by prairie dogs. *Oecologia* 56:10–15.
- Costello, D. F. 1944.** Natural revegetation of abandoned plowed land in the mixed prairie association of northeastern Colorado. *Ecol.* 25(3):312–326.
- Crist, T. O. and J. A. Wiens. 1994.** Scale effects of vegetation on forager movement and seed harvesting by ants. *Oikos* 69:37–46.
- Dickey, H. P., W. R. Swafford, and O. L. Markley. 1963.** Soil survey of Morton County, Kansas. USDA. Soil Survey Series 1960, No. 8.
- Gordon, D. M. 1993.** The spatial scale of seed collection by harvester ants. *Oecologia* 95:479–487.
- Heske, E. J. and M. Campbell. 1991.** Effects of an 11-year livestock enclosure on rodent and ant numbers in the Chihuahuan Desert, southeastern Arizona. *Southw. Natur.* 36(1):89–93.
- Hewitt, G. B., E. W. Huddleston, R. J. Lavigne, D. N. Ueckert, and J. G. Watts. 1974.** Rangeland Entomology. Range Science Series No. 2. Soc. for Range Manage., Denver, Colo.
- Hölldobler, B. and C. J. Lumsden. 1980.** Territorial strategies in ants. *Sci.* 210:732–739.
- Hoogland, J. L. 1995.** The black-tailed prairie dog: social life of a burrowing mammal. University of Chicago Press, Chicago and London.
- Ingham, R. E. and J. K. Detling. 1984.** Plant-herbivore interactions in a North American mixed-grass prairie. *Oecologia* 63:307–313.
- Jacot, A. P. 1936.** Soil structure and biology. *Ecol.* 17:359–79.
- King, J. 1955.** Social behavior, social organization, and population dynamics in a black-tailed prairie dog town in the Black Hills of South Dakota. *Contrib. Lab. Vert. Biol.* 67. Univ. Michigan, Ann Arbor, Mich.
- Kirkham, D. R. 1967.** Harvester ant (*Pogonomyrmex owyheeii* Cole) abundance in relation to grazing, vegetation and soil in north-central Wyoming. Unpubl. M.S. Thesis, Univ. Wyoming, Laramie, Wyo.
- Koford, C. B. 1958.** Prairie dogs, whitefaces, and blue grama. *Wildl. Monogr.* 3.
- Kotliar, N. B., B. W. Baker, A. D. Whicker, and G. Plumb. 1999.** A critical review of assumptions about the prairie dog as a keystone species. *Environ. Manage.* 24:177–192.
- Kretzer, J. E. and J.F. Cully, Jr. (In Press)** Black-tailed prairie dog effects on reptiles and amphibians in Kansas shortgrass prairie. *Southw. Natur.*
- Miller, B., G. Ceballos, and R. Reading. 1994.** The prairie dog and biotic diversity. *Conserv. Biol.* 8:677–681.
- Miller, B., C. Wemmer, D. Biggens, and R. Reading. 1990.** A proposal to conserve black-footed ferrets and the prairie dog ecosystem. *Environ. Manage.* 14:763–769.
- Munger, J. C. 1984a.** Optimal foraging? Patch use by horned lizards (Iguanidae: *Phrynosoma*). *Am. Nat.* 123:654–680.
- Munger, J. C. 1984b.** Long-term yield from harvester ant colonies: implications for horned lizard foraging strategy. *Ecol.* 65:1077–1086.
- Nagel, H. 1969.** Western harvester ants in Kansas: colony founding, nest structure and function, factors affecting density, and effect on soil formation. M.S. Thesis, Kansas State Univ., Manhattan, Kans.
- O’Meilia, M. E., F. L. Knopf, and J. C. Lewis. 1982.** Some consequences of competition between prairie dogs and beef cattle. *J. Range Manage.* 35:580–585.
- Rogers, L. E. and R. J. Lavigne. 1974.** Environmental effects of western harvester ants on the shortgrass plains ecosystem. *Environ. Entomol.* 3:994–997.
- SAS Institute Inc. 1993.** SAS/STAT* User’s Guide, Release 6.03 edition, Cary, N.C.
- Soulé, P. T. and P. A. Knapp. 1996.** *Pogonomyrmex owyheeii* nest site density and size on a minimally impacted site in central Oregon. *Great Basin Nat.* 56(2):162–166.
- U. S. D. I., Fish and Wildlife Service. 2000.** Endangered and threatened wildlife and plants; 12 month finding for a petition to list the black-tailed prairie dog as threatened. *Federal Register* 64:14424–14428.
- Whicker, A. D. and J. K. Detling. 1988.** Ecological consequences of prairie dog disturbances. *BioSci.* 38(11):778–785.
- Whicker, A. D. and J. K. Detling. 1993.** Control of grassland ecosystem processes by prairie dogs, p. 18–27. *In* Oldemeyer, J. L., D. E. Biggins, B. J. Miller, and R. Crete (ed.), Management of prairie dogs complexes for the reintroduction of the black-footed ferret. U.S. Fish and Wildl. Serv., Biol. Rep. 13.
- Whitford, W. G. and M. Bryant. 1979.** Behavior of a predator and its prey: the horned lizard (*Phrynosoma cornutum*) and harvester ants (*Pogonomyrmex* spp.). *Ecol.* 60:686–694.
- Whitford, W. G., P. Johnson, and J. Ramirez. 1976.** Comparative ecology of the harvester ants *Pogonomyrmex barbatus* (F. Smith) and *Pogonomyrmex rugosus* (Emery). *Insectes Sociaux* 23(2):117–132.
- Winter, S. 1999.** Plant and breeding bird communities of black-tailed prairie dog colonies and non-colonized areas in southwest Kansas and southeast Colorado. M.S. Thesis, Kansas State Univ., Manhattan, Kans.
- Wuerthner, G. 1997.** Viewpoint: The black-tailed prairie dog—headed for extinction. *J. Range Manage.* 50:459–466.

Coyote responses to changing jackrabbit abundance affect sheep predation

L. CHARLES STODDART, RICHARD E. GRIFFITHS, AND FREDERICK F. KNOWLTON

Authors were wildlife biologists, USDI, U. S. Fish and Wildlife Service, Denver Wildlife Research Center, Utah State University, Logan, Ut 84322-5295 during the time data were collected and the initial manuscript drafted.

Abstract

Domestic sheep ranchers generally perceive abundances of natural prey and coyotes (*Canis latrans*) as important factors affecting coyote predation rates on sheep. To determine the effect of a changing natural prey base on coyote predation rates, we estimated coyote density and predation rates on ewes and lambs during part of 1 cycle of black-tailed jackrabbit (*Lepus californicus*) abundance on a 2,300 km² area of the Idaho National Engineering Laboratory in southcentral Idaho from 1979–1985. We used 100, 1.6-km scat collection lines and 80, 1.6-km flushing transects to assess coyote and jackrabbit densities, respectively. Ewe and lamb loss rates were determined from questionnaires sent to all 13 producers grazing sheep on the area. Spring coyote density varied from 0.10 to 1.39 coyotes km⁻² in response to a systematic fluctuation in jackrabbit density from 0 to 243 jackrabbits km⁻². Reported total loss rates of ewes and lambs varied from 2.2 to 42.1 ewes/10⁵ ewe-days and 33.0 to 163 lambs/10⁵ lamb-days and were linearly and directly related to coyote density ($P < 0.005$). Ewe and lamb loss rates were independent of jackrabbit density ($P > 0.18$) except for 1 year when jackrabbits were virtually absent from the study area and the loss of lambs escalated dramatically. Our data suggest the increased losses of lambs resulted from reduced buffering by natural prey.

Key Words: *Canis latrans*, *Lepus californicus*, sheep loss rate, coyote numerical response, buffering

Coyote (*Canis latrans*) predation on domestic sheep is a problem for many western sheep ranchers. Ranchers perceive coyote density and abundance of natural prey as important factors affecting predation rates on sheep (Gee et al. 1977, Nielsen 1977, Nass et al. 1984). Objective information concerning the relationships of these variables to coyote predation on sheep is limited largely because measuring and manipulating coyote and prey numbers is difficult. The effect of natural prey abundance on sheep predation is enigmatic because, while prey abundance can be an important

Portions of this study were conducted under the guidance and support of the U.S. Fish and Wildlife Service through Interagency Agreement No. DE-AI07-81ID12315 with the Department of Energy. The Denver Wildlife Research Center transferred to the Animal and Plant Health Inspection Service (APHIS) of USDA on 3 March 1986 and later was transferred to Fort Collins, Colo, and renamed the National Wildlife Research Center.

Authors wish to thank M. R. Conover, F. H. Wagner, and L. A. Windberg for reviewing drafts of this manuscript.

Manuscript accepted 2 Apr. 2000.

Resumen

Los criadores de borregos domésticos generalmente perciben a la abundancia de presas naturales y coyotes (*Canis latrans*) como factores importantes que afectan las tasas de depredación de borregos por coyotes. Para determinar el efecto de una población cambiante de presas naturales en las tasas de depredación del coyote estimamos la densidad de coyotes y las tasas de depredación de ovejas y corderos durante parte de un ciclo de abundancia de liebres cola negra (*Lepus californicus*), el estudio se condujo de 1979 a 1985 en un área de 2,300 km² del Laboratorio Nacional de Ingeniería de Idaho, situado en la parte sur-central de Idaho. Utilizamos 100 líneas "scat" de colección de 1.6 km y 80 transectos de abundancia de 1.6 km para evaluar las densidades de coyotes y liebres respectivamente. Las tasas de pérdida de ovejas y corderos se determinaron mediante cuestionarios enviados a todos (13) los productores de borregos en apacantamiento del área. En primavera la densidad de coyotes vario de 0.10 a 1.39 km⁻² en respuesta a una fluctuación sistemática de la densidad de liebres de 0 a 243 liebres km⁻². Las tasas de pérdida total de ovejas y corderos reportadas por los productores vario de 2.2 a 42.1 ovejas/10⁵ días-borrega y de 33 a 163 corderos/10⁵ cordero-días y estuvieron lineal y directamente relacionados a la densidad de coyotes ($P < 0.005$). Las tasas de pérdida de ovejas y corderos fueron independientes de la densidad de liebres ($P > 0.18$), excepto en un año cuando las liebres estuvieron virtualmente ausentes del área de estudio y la pérdida de corderos aumento dramáticamente. Nuestros datos sugieren que el aumento de pérdidas de corderos resulta de la reducción en la acción de amortiguamiento que ofrecen las presas naturales.

determinant of coyote density (Clark 1972, Knowlton and Stoddart 1983, Knowlton and Gese 1995, Knowlton et al. 1999), natural prey can also buffer sheep against predation by coyotes (McAdoo 1975, Guthery 1977, Kaufeld 1977, Gober 1979).

We examined coyote predation rates on ewes and lambs during an irruption and decline in black-tailed jackrabbit (*Lepus californicus*) abundance in the northern Great Basin. Historically, jackrabbit numbers in this area have cycled dramatically (Wagner and Stoddart 1972, Gross et al. 1974). Jackrabbits also comprise a large fraction of coyotes' diet in this region and coyote numbers fluctuate in response to changing jackrabbit numbers (Clark 1972, Hoffman 1979, Johnson and Hansen 1979, and Knowlton and Stoddart 1992).

Materials and Methods

Study Area

We conducted this study on the Idaho National Engineering Laboratory (INEL), a 2,300 km² National Environmental Research Park (43°40' N 112°30' W) in southcentral Idaho. The INEL is representative of the Northern Cold Desert Biome with big sagebrush (*Artemisia tridentata* Nuttall)-wheatgrass (*Agropyron dasystachum* Hooker) communities as the dominant association (Atwood 1970, Harniss and West 1973). Approximately 1,400 km² of the periphery of the INEL was grazed by sheep and subjected to limited coyote removal by the U.S. Fish and Wildlife Service to control depredations. The interior portion was closed to domestic livestock grazing and to coyote removal. The entire INEL was closed to public trespass.

Procedures

In 1975, Denver Wildlife Research Center personnel initiated a study of coyote and jackrabbit population dynamics on the INEL. Indices of coyote and jackrabbit abundance were measured each spring and fall on a 1,200 km² area, including grazed and ungrazed portions of the INEL (Davison 1980, L.C. Stoddart unpublished report). We converted the indices to estimates of density and used them as seasonal estimates for the grazed portion of the INEL.

Coyote indices were obtained using 100, 1.6-km scat collection lines randomly located along unimproved roads. Each spring and fall the lines were first cleared of scats and then newly deposited scats were counted and removed after 14 and 28 days. The index was the deposition rate of fresh scats (scats/km/day). We converted the indices to estimates of coyote density (no./km²) using the regression equation, density = (index - 2.66) x 0.054, developed in a mark-recapture study of coyote density on the INEL (Knowlton 1984). The coyote scat collection lines were not operated in spring 1979. This, and the following 4 years, were years of coyote population increase (L.C. Stoddart unpublished report). We estimated spring 1979 coyote density by averaging the ratios of spring to fall coyote density estimates for 1980 through 1983 (0.56) and multiplying the fall 1979 density estimate by this ratio.

Indices of black-tailed jackrabbit abundance were obtained using 80, geographically fixed, 1.6-km line transects randomly located in the study area. Each spring and fall, each transect was walked between 0900 and 1600 hours when jackrabbits were generally sedentary. The perpendicular

distance from the transect line to the point from which each observed jackrabbit flushed was recorded and the data analyzed using program TRANSECT (Burnham et al. 1980). Because line transects walked in sagebrush habitat generally underestimate jackrabbit density by 41.5% (Wywiałowski and Stoddart 1988), we multiplied the jackrabbit indices by 1.71 for our estimates of jackrabbit density. For estimates of coyote and jackrabbit density in winter, we used the mean of the preceding fall and succeeding spring density estimates.

Winter and spring sheep grazing and loss information were obtained from questionnaires sent to each rancher grazing sheep on the INEL from 1979 to 1985. Sheep monitored in this study generally lambed in February and grazed on the INEL for about 25 to 45 days from mid-April to mid-June. Ewes returned to the INEL for about 50 days in December and January. We asked ranchers to provide numbers of lambs and ewes grazed, number of lambs and ewes lost each spring and winter while on the INEL each year. We also asked them to estimate the numbers of lambs and ewes lost to coyote predation.

Loss rates of ewes and lambs for each ranch were calculated each year and season by dividing the reported number of ewes and lambs lost by the number of

ewe- and lamb-days grazed respectively on the INEL. Loss rates were tested for outlying estimates by first normalizing the distributions of pooled age and seasonal loss rates with the square root transformation and then using a sum-of-squares outlier test (Li 1964 p. 548). Weighted mean total loss rates were calculated similarly each year and season after pooling the data. We calculated weighted mean predation rates on lambs and ewes in like fashion using reported numbers of lambs and ewes killed by coyotes instead of total numbers lost. Linear regression analysis was used to evaluate the relationships between weighted mean coyote predation rates on ewes and lambs and coyote and jackrabbit densities.

Results and Discussion

Jackrabbit Densities

Between 1975 and 1978, prior to this study, jackrabbit abundance on the INEL steadily increased from near zero to about 12 jackrabbits km⁻² (L. C. Stoddart unpublished report). The population continued to increase during the first 2 years of this study, peaked at about 225–250 jackrabbits km⁻² in the winter to spring period 1980–81, and then declined steadily to near zero by spring 1984 (Fig. 1).

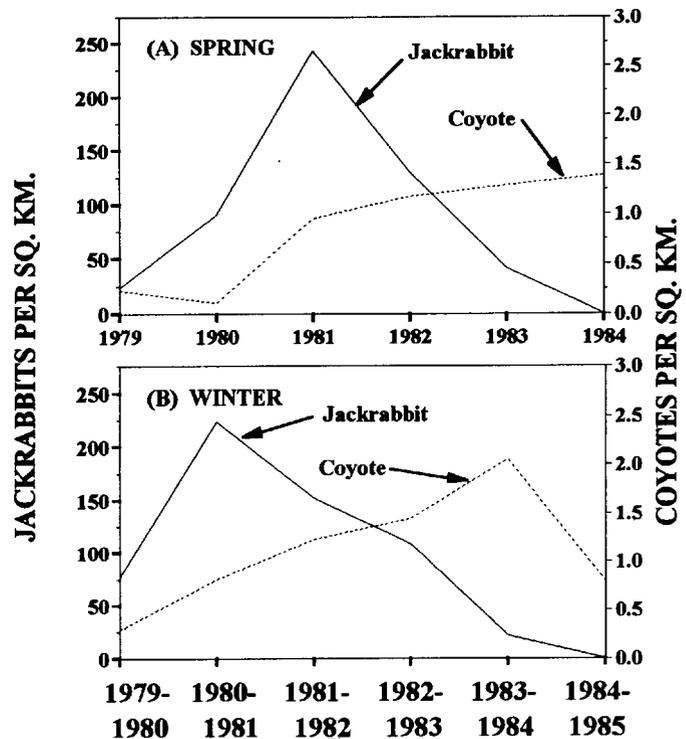


Fig. 1. Estimates of jackrabbit and coyote densities (numbers per km²) in spring (A) and winter (B).

Coyote Responses

Coyotes responded both numerically and functionally to changes in jackrabbit abundance; their numbers increased coincident with increasing numbers of jackrabbits and composition of their diet included a much higher percentage of jackrabbit (MacCracken and Hansen 1987). From 1975 to 1978 coyote density was relatively low and constant at about 0.25 coyotes km⁻² (L. C. Stoddart unpublished report). The population began to increase in 1979, peaked at 2.1 coyotes km⁻² in winter 1983–84, and declined to 0.79 coyotes km⁻² the following winter (Fig. 1). The cycles we observed in abundances of coyotes and jackrabbits on the INEL are characteristic of coyote-jackrabbit cycles reported for northern Utah (Gross et al. 1974, Knowlton and Stoddart 1983, 1992). In northern Utah the proportion of jackrabbit in coyotes' diet changed markedly with changing jackrabbit abundance (Clark 1972, Hoffman 1979). Similarly, MacCracken and Hansen (1987), in a study concurrent with ours, reported the fraction of jackrabbit in the diets of INEL coyotes increased 15-fold from low to high jackrabbit density, and during the latter, was the major source of coyote food. Changes in coyote abundance appeared to lag that of jackrabbits by 2–3 years (Fig. 1). Although the mechanics of changes in coyote abundance in response to changes in food base are not well understood, the lag may have resulted, in part, from a threshold effect (Wagner 1981). We suspect the functional response curve developed by Hoffman (1979) depicting coyote feeding patterns in relation to jackrabbit abundance in Curlew Valley, Utah (Fig. 2) is a more reasonable approximation of the form of this relationship. This suggests jackrabbit density in this area must reach 20–30 jackrabbits km⁻² before the coyote population responds with increased density, and

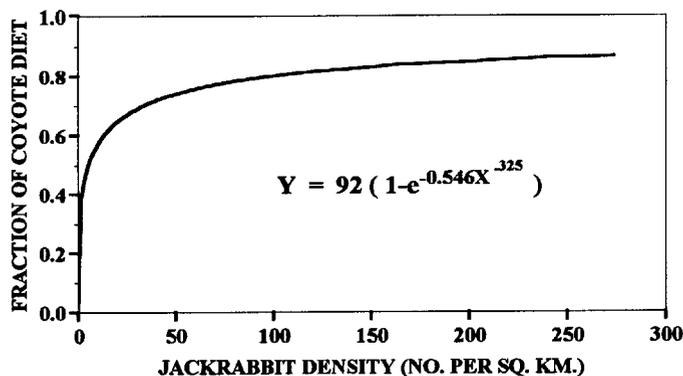


Fig. 2. Functional feeding response of coyotes to jackrabbit abundance (from Hoffman 1979) as the hypothesized buffering jackrabbits provide to sheep.

Table 1. Number of ewes and lambs grazed and mean number of days grazed per sheep in spring and winter on the Idaho National Engineering Laboratory.

Season: Year	No. of operators reporting	Animals grazed		\bar{x} days grazed per sheep
		Ewes	Lambs	
----- (No.) -----				
Spring:				
1979	5	14,500	20,780	27
1980	7	13,343	19,838	30
1981	8	17,692	20,186	32
1982	9	21,986	27,296	45
1983	6	14,029	20,291	30
1984	5	11,482	15,662	26
Mean	7	15,505	20,676	32
Winter:				
1979–80	10	26,945		63
1980–81	10	33,800		57
1981–82	6	16,324		56
1982–83	10	30,237		44
1983–84	9	18,069		38
1984–85	6	17,592		47
Mean	9	23,828		51

must decline to about the same level before the coyote population initiates a decline phase.

Reported Sheep Losses

Thirteen producers grazed sheep on the INEL during this study. Not all grazed the INEL each season and not all returned questionnaires for all seasons they did graze there. On average, spring estimates are based on reports from 7 producers, involving 15,505 ewes and 20,676 lambs, grazing for 32 days. Winter estimates were typically based on larger samples, on average involving 9 producers with 23,828 ewes grazed for 51 days (Table 1). Total sheep loss estimates and predation loss estimates are presented in Figure 3. In open range grazing situations, total loss estimates are considered more accurate than coyote predation estimates (Wagner 1988) because typically they are based upon counts of flocks entering and leaving grazing units. Estimates of predation loss-

es incorporate difficulties in locating carcasses as well as producer judgements in assigning causes of deaths. Predator killed carcasses are particularly difficult to locate on the open range (Lindzey and Wilbert 1989), and generally only a fraction are found by herders (Scrivner et al. 1985, Wagner 1988).

Reported Coyote Predation Rates

The weighted mean loss rates indicate the reported coyote predation rates of ewes and lambs on the INEL averaged 18 and 37% respectively of total loss rates of ewes and lambs. These values are generally lower than those reported in a variety of field studies of causes of sheep mortality (Wagner 1988). Also, the reported coyote predation rates on the INEL do not account for apparent systematic changes in total loss rates reported (Fig. 3). Unless mortality factors other than predation were varying in concert with changing coyote and jackrabbit numbers, which we consider unlikely, producers markedly underestimated true coyote predation rates on the INEL.

Total Losses of Ewes and Lambs

To circumvent problems associated with locating and properly assigning causes of death to sheep mortalities, we reasoned that if significant, systematic changes occurred in true coyote predation rates as coyote and jackrabbit densities fluctuated, they would be reflected by parallel changes in reported total loss rates. Consequently, we used reported total loss rates of ewes and lambs to estimate changes in predation rates rather than the reported predation rates themselves. The following discussion is based upon our

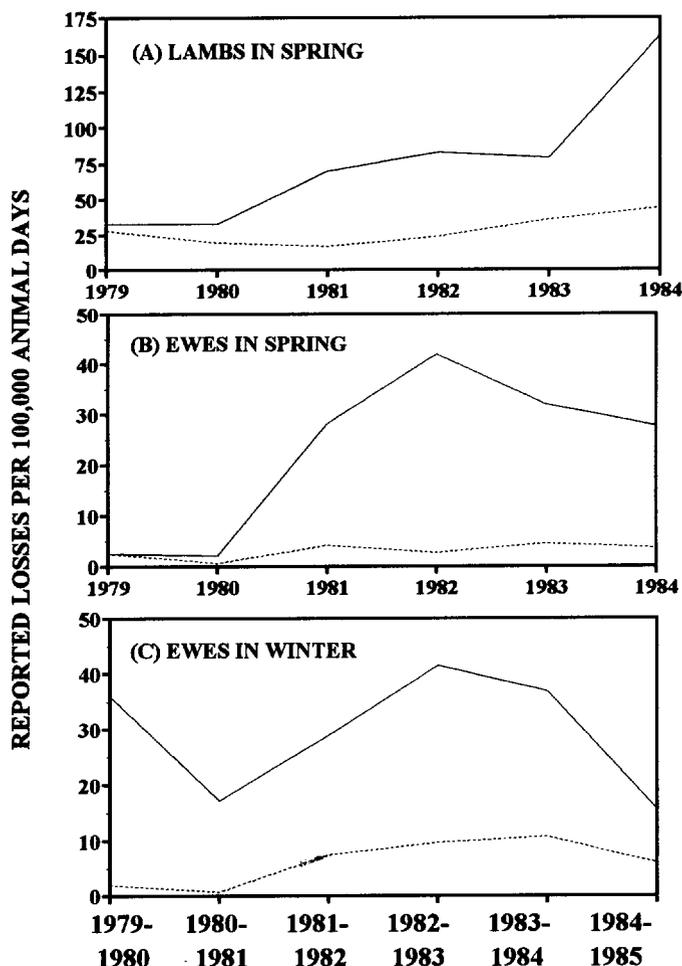


Fig. 3. Total and coyote predation loss rates (numbers lost per 100,000 sheep-days) for lambs (A) and ewes in spring (B) and winter (C) reported by ranchers grazing on INEL, 1979–1985.

analyses of total reported losses of ewes and lambs.

During this study, the weighted mean total loss rates (sheep lost per 10^5 sheep-days grazed) ranged between 3 and 40 for ewes and 30 and 160 for lambs (Fig. 3). These are consistent with losses reported to the USDA Statistical Reporting Service (SRS) over 11 western states during the years of this study who reported average total postdocking losses of ewes and lambs of about 8 and 12% respectively (Wagner 1988). These would convert to loss rates (losses per 10^5 animal days) of 22 and 80, about mid-range for the total loss rates reported for the INEL.

Frequency distributions of loss rates of ewes and lambs, by individual ranchers and grazing season, pooled over the 6 years of study were skewed. These patterns are similar to that reported by Balser (1974), Nass et al. (1984), and others for predator losses, i.e. many ranchers report few or no losses while others report relatively high losses. In our study, individual

ranchers did not always hold similar positions within the frequency distribution. The skewed pattern prevailed whether overall losses were low or high. Our single point value for abundances of coyotes and jackrabbits on the INEL for each season of each year precluded further assessment of potential causes. Uneven distributions of coyotes or natural prey on the area, proximity of other sheep, or the relative efficacy with which Wildlife Services personnel resolved specific depredation problems could contribute to a skewed frequency distribution.

The reported winter loss rate of 25 ewes per 10,000 ewe-days by 1 rancher was identified as an outlying estimate ($\alpha = 0.01$) and was subsequently dropped from further analyses. Contingency table (2 x 2) analysis indicated that high individual rancher loss rates of ewes ($\alpha = 0.005$) and lambs ($\alpha = 0.025$) in spring occurred disproportionately at higher coyote densities. A similar test involving ewes in winter was not significant.

Since we did not measure parameters for individual ranches and could not account for individual loss rates, we pooled loss rates by age and season and used the weighted means for further analyses. Weighted means of reported total loss rates of ewes in spring and winter changed systematically from relatively low values early in the study, peaked in 1982, and declined the next 2 years (Fig. 3). A similar trend was noted in reported total lamb loss rates except for the last year of study (1984) when the total lamb loss rate escalated markedly (Fig. 3). The ratio of lamb loss rate to ewe loss rate changed systematically except for 1984. Trends in predation rates reported for both ewes and lambs approximated those for total loss rates but generally at much lower rates (Fig. 3).

Total Loss Rates

The weighted mean total loss rate of ewes on the INEL in spring and winter was linearly correlated ($r^2 = 0.75$, $P < 0.001$) with estimated coyote density (Fig. 4). Inclusion of jackrabbit density as a second independent variable did not significantly improve the regression model ($P > 0.18$) for ewes. The weighted mean total loss rate of lambs was also linearly correlated ($r^2 = 0.68$, $P < 0.05$) with estimated coyote density (Fig. 5a), but the regression fit of the data was significantly improved with the addition of a term for the functional feeding response of coyotes to jackrabbit density (Fig. 5b). Although this model is supported by only 1 point, it is reasonable to expect a supersaturated coyote population to shift to alternate prey when its primary prey is no longer available. We approximated this by using the functional feeding response of coyotes to jackrabbit abundance (Fig. 2) developed by Hoffman (1979) to calculate the fraction of buffering jackrabbits might provide to sheep. This was achieved by dividing each estimate of coyote density by the functional feeding response of coyotes to jackrabbit abundance for that period and plotting this against reported lamb losses (Fig. 5b).

In the ewe and lamb total loss rate models (Figs. 4, 5), non-predation loss rates are inferred by the Y intercepts, with coyote predation accounting for losses above the intercept values. These models suggest total losses attributable to coyote predation ranging from 0 to 95%; percentages consistent with sheep mortality studies where ranges or pastures were routinely searched on a periodic basis for dead sheep and the causes of death determined by trained personnel. In those studies coyote predation was generally implicated in the death of

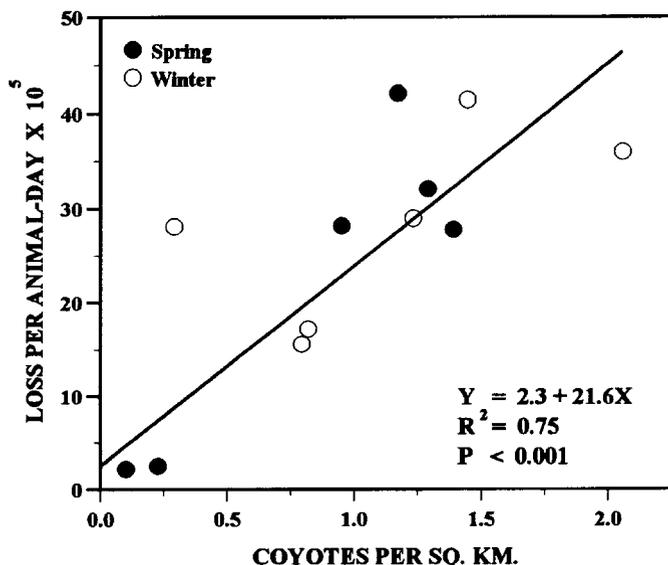


Fig. 4. Relationship between total loss rates of ewes (animals lost per 100,000 animal-days) and coyote density in spring (closed circles) and winter (open circles). Data point for winter 1979-80 ($x = 0.29$, $y = 28.1$) excluded from regression equation calculation.

30-90% of the postdocking ewe and lamb carcasses found (see reviews by O'Gara et al. 1983 and Wagner 1988). Neither coyote density nor abundance of prey were determined for those studies.

Buffering by Jackrabbits

The degree to which coyotes feed on natural prey when sheep are present represents buffering by natural prey. Although jackrabbits were an important part of the INEL natural prey base, marked changes in jackrabbit density during this study apparently did not affect the overall level of natural prey buffering of sheep as indicated by the linear relationships in Figures 4 and 5. We hypothesize that buffering is not linearly related to abundance of natural prey, but likely of the form in Fig. 2 (Hoffman 1979). As prey abundance increases from low levels, buffering of sheep approaches an asymptotic level with the coyotes response to sheep unaffected by additional increases in natural prey. In spring 1984 jackrabbits virtually disappeared from the study site. For the first time during this study total prey abundance apparently fell below the level necessary to provide buffering of lambs at the asymptotic level. Although coyote density remained nearly unchanged from 1983 to 1984, the reported total lamb loss rate doubled (Fig. 5). Because the total loss rate of ewes did not respond to the disappearance of jackrabbits in 1984, we believe the buffering curves for ewes and lambs are different and that a lower natural prey base is needed before reduced buffering occurs for ewes. More studies are necessary to clarify this buffering hypothesis.

While recent theoretical models of predator foraging behavior generally regard energetics as the most important factor in a predator's selection of prey items (Krebs et al. 1981), there also appears to be a foraging component that motivates predators to continually sample available food items, presumably to assess future optimum feeding strategies (Orians 1981). This may explain why coyotes on the INEL continued to kill sheep at a constant rate per coyote even when jackrabbits reached extremely high densities.

Management Implications

From the linear relationships between reported total loss rates of ewes and lambs and coyote density (Fig. 4, 5), we infer that predation rates on ewes and lambs are directly proportional to coyote abundance. From a management perspective, this suggests that reductions in coyote predation rates on ewes and lambs can be achieved

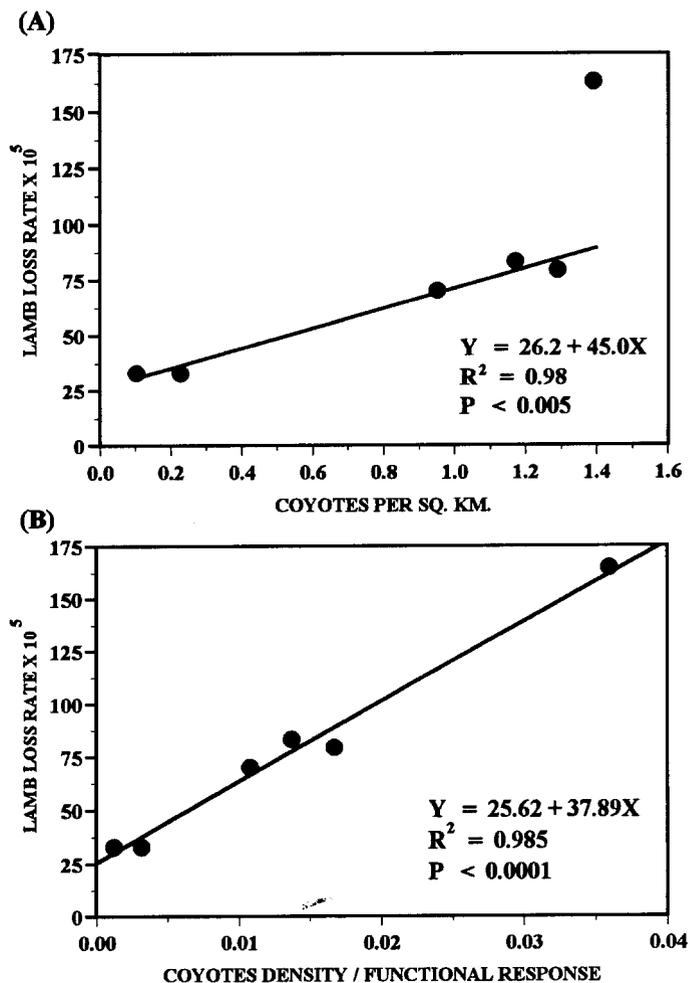


Fig. 5. Relationship between total loss rates of lambs (animals lost per 100,000 animal-days) and coyote density in spring on INEL, 1979-84, (A) without considering buffering by natural prey (data point for 1984 [$x = 1.39$, $y = 163$] excluded from regression calculations), and (B) with inclusion of the functional feeding response of coyotes (from Hoffman 1979) as a measure of buffering provided by jackrabbits.

in direct proportion to reductions in coyote abundance.

One alternative to coyote removal is reduction of coyote density through reduction in natural prey and carrion. This would be a preventive measure in which food reduction must be maintained. Some researchers (Weaver 1977, Todd and Keith 1976) suggest there is a critical period during the year, when food availability is lowest, that determines general coyote abundance on an area. Artificial reduction of the food base might be most effective in influencing coyote numbers if accomplished during such a critical period. The efficacy and feasibility of reducing food base as a means of depredation control in various habitats is currently unknown.

Because coyote density in the Great Basin fluctuates in response to cycles in jackrabbit abundance, changes in coyote predation on domestic sheep in this area are predictable. Application of this information can help sheep producers and depredation control personnel anticipate changing requirements to protect livestock and has the potential for substantially increasing the efficacy of depredation control programs. The most obvious aspect involves planning for the allocation of management resources. Generalization of this concept to other areas would depend on characteristics of the natural prey base and the relationship of coyote density to changes in prey abundance.

Conclusions

Coyote density on the INEL changed in direct response to a long-term cycle in jackrabbit abundance. Coyote predation rates on both ewes and lambs were linearly related to coyote density and were generally independent of jackrabbit abundance. However, when jackrabbits virtually disappeared from the study site, and availability of natural prey declined below the asymptotic level of our hypothesized prey buffering curve, predation rates on lambs increased beyond the level predicted by coyote density. Sheep producers on the INEL appear to have markedly underestimated coyote predation rates on ewes and lambs during the 4 years of this study when coyote density was relatively high. While conventional wisdom indicating a dramatic loss of natural prey results in increased predation on domestic stock appears correct, that same wisdom apparently does not recognize that numerical responses by coyotes associated with increased abundance of natural prey also results in increased predation on livestock.

Literature Cited

- Atwood, N.D. 1970.** Flora of the National Reactor Testing Station. Brigham Young University Science Bull., Biol. Series 11(4).
- Balsler, D.S. 1974.** An overview of predation-livestock problems with emphasis on livestock losses. Trans. 39th N. Am. Wildl. Nat. Resour. Conf. 79:292-300.
- Burnham, K.P., D.R. Anderson, and J.L. Laake. 1980.** Estimation of density from line transect sampling of biological populations. Wildl. Monogr. 72:1-202.
- Clark, F.W. 1972.** Influence of jackrabbit density on coyote population change. J. Wildl. Manage. 36:343-356.
- Davison, R.P. 1980.** The effect of exploitation on some parameters of coyote populations. Ph.D. Diss., Utah State Univ., Logan, Ut.
- Gee, C.K., R.S. Magleby, W.R. Bailey, R.L. Gum, and L.M. Arthur. 1977.** Sheep and lamb losses to predators and other causes in the western United States. USDA Agr. Econ. Rep. 369.
- Gober, D.R. 1979.** Factors affecting domestic sheep losses to predators in Trans-Pecos, Texas. Ph.D. Diss., Texas A&M Univ., College Station, Tex.
- Gross, J.E., L.C. Stoddart, and F.H. Wagner. 1974.** Demographic analysis of a northern Utah Jackrabbit population. Wildl. Monogr. 40:1-68.
- Guthery, F.S. 1977.** Efficacy and ecological effect of predator control in South Texas. Ph.D. Diss., Colorado State Univ., Fort Collins, Colo.
- Harniss, R.O. and N.E. West. 1973.** Vegetation patterns of the National Reactor Testing Station, southeastern Idaho. Northwest Sci. 47:30-43.
- Hoffman, S.W. 1979.** Coyote-prey relationships in Curlew Valley during a period of low jackrabbit density. M.S. Thesis, Utah State Univ., Logan, Ut.
- Johnson, M.K. and R.M. Hansen. 1979.** Coyote food habits on the Idaho National Engineering Laboratory. J. Wildl. Manage. 43:951-956.
- Kauffeld, J.D. 1977.** Availability of natural prey and its relationship to coyote predation on domestic sheep. M.S. Thesis, Univ. of Nev., Reno, Nev.
- Knowlton, F.F. 1984.** Feasibility of assessing coyote abundance on small areas. Unpubl. rpt. of Work Unit 909.01, Denver Wildl. Res. Ctr., Denver, Colo. 14pp.
- Knowlton, F.F. and E.M. Gese. 1995.** Coyote population processes revisited. In: D. Rollins, C. Richardson, T. Blankenship, K. Cannon, and S. Henke (eds.), Symposium Proc. Coyotes: a compendium of our knowledge. Texas A&M Univ. Ext. Serv.
- Knowlton, F.F., E.M. Gese, and M.M. Jaeger. 1999.** Coyote depredation control: An interface between biology and management. J. Range Manage. 52:398-412.
- Knowlton, F.F. and L.C. Stoddart. 1983.** Coyote population mechanics: Another look, p. 93-111. In: F.L. Bunnell, D.S. Eastman, and J.M. Peek (eds.), Symposium of Natural Regulation of Wildlife Populations, Proc. No. 14, For. Wildl. Range Exp. Sta., Univ. Idaho, Moscow, Ida.
- Knowlton, F.F. and L.C. Stoddart. 1992.** Some observations from two coyote-prey studies. Pages 101-121 In: A. Boer, ed., Ecology and Management of the Eastern Coyote. Wildl. Res. Unit, Univ. New Brunswick, Fredericton.
- Krebs, J.R., A.I. Houston, and E.L. Charanov. 1981.** Some recent developments in optimal foraging, p. 3-18. In: A.C. Kamil and T.D. Sargent (eds.), Foraging behavior: ecological, ethological, and psychological approaches. Garland Publishing Inc. New York.
- Li, J.C.R. 1964.** Statistical inference. Vol. I. Edwards Brothers, Inc., Ann Arbor, Mich.
- Lindzey, F.G. and C. Wilbert. 1989.** Estimating domestic sheep losses to mountain lions, p. 27-31. In: A.J. Bjugstad, D.W. Uresk, and R.H. Hamre (eds.), Ninth Great Plains Wildl. Damage Control Workshop Great Plains Agr. Council Pub. 127/USDA Forest Service Gen. Tech. Rpt. RM-171.
- MacCracken, J.G. and R.M. Hansen. 1987.** Coyote feeding strategies in southeastern Idaho: Optimal foraging by an opportunistic predator? J. Wildl. Manage. 51:278-285.
- McAdoo, J.K. 1975.** Predation on domestic sheep in northwestern Nevada. M.S. Thesis, Univ. of Nev., Reno, Nev.
- Nass, R.D., G. Lynch and J. Theade. 1984.** Circumstances associated with predation rates on sheep and goats. J. Range Manage. 37:423-426.
- Nielsen, D.B. 1977.** High/low predation—some why factors. Utah Sci. 38:82-86.
- O'Gara, B.W., K.C. Brawley, J.R. Munoz, and D.R. Henne. 1983.** Predation on domestic sheep on a western Montana ranch. Wildl. Soc. Bull. 11:253-264.
- Orians, G.H. 1981.** Foraging behavior and the evolution of discriminatory abilities, p. 389-405. In: A.C. Kamil and T.D. Sargent (eds.), Foraging behavior: ecological, ethological, and psychological approaches. Garland Publishing Inc. New York.
- Scrivner, J. H., W. E. Howard, A. H. Murphy, and J. R. Hays. 1985.** Sheep losses to predators on a California range, 1973-1983. J. Range. Manage. 38:418-421.
- Todd, A.W. and L.B. Keith. 1976.** Responses of coyotes to winter reduction in agricultural carrion. Alberta Rec., Parks, Wildl. Dept. Fish Wildl. Div., Wildl. Tech. Bull. 5.
- Wagner, F.H. 1981.** Role of lagomorphs in ecosystems, p. 668-694. In: K. Myers and C.D. MacInnes (eds.), 1979 Proceedings of the world lagomorph conference, Univ. Guelph, Ontario, Canada.
- Wagner, F.H. 1988.** Predator control and the sheep industry. Regina Books, Claremont, Calif.
- Wagner, F.H. and L.C. Stoddart. 1972.** Influence of coyote predation on black-tailed jackrabbit populations in Utah. J. Wildl. Manage. 36:329-342.
- Weaver, J.L. 1977.** Coyote-food base relationships in Jackson Hole, Wyoming. M.S. Thesis, Utah State Univ., Logan, Ut.
- Wywiałowski, A.P. and L.C. Stoddart. 1988.** Estimation of jackrabbit density: methodology makes a difference. J. Wildl. Manage. 52:57-59.

Assessing independence of animal locations with association matrices

KEITH T. WEBER, MILO BURCHAM, AND C. LES MARCUM

Authors are GIS director, Idaho State University, Pocatello, Idaho 83209-8130; and research biologist, The University of Montana, School of Forestry, Missoula, Mont. 59812; and professor of Wildlife Biology, The University of Montana, School of Forestry, Missoula, Mont. 59812. At the time of the research, the senior author was research assistant, The University of Montana, School of Forestry, Missoula, Mont. 59812.

Abstract

We developed and used association matrix, association pattern, and pattern recognition software (ASSOC1) to investigate the spatio-temporal association of individual radio-collared elk with other radio-collared elk in a study area in western Montana. These procedures were used to approximate the amount of time each individual spent with another individual, and assess the level of independence at which these elk acted. The results of this study will allow wildlife biologists to better understand animal movements and herd dynamics, and evaluate the independence of animal locations for home range calculation and habitat use-availability analysis.

Key Words: elk, wildlife, herds, home range, similarity

Independence of animal observations is paramount to any home range calculation (Hayne 1949, Metzgar 1972, Dunn and Gipson 1977, Swihart and Slade 1985a, 1985b, Worton 1989). Yet, relatively few tests of independence exist that are available to field biologists (cf. Cole 1949, Hurlbert 1969, Knight 1970, Swihart and Slade 1985b, 1997). Two issues of independence are of concern, 1) auto-correlation: independence of consecutive locations of the same individual (Swihart and Slade 1985a, 1985b, 1997, White and Garrott 1990), and 2) pseudoreplication: independence of individuals that are associated in groups (Hurlbert 1984). This paper deals strictly with understanding and evaluating the latter concern.

An important delineation between traditional statistics and spatial statistics is that no assumption of independence can be made because, to some degree, every location on the earth's surface is related (Cressie 1991, Wong 1995). The degree to which the data are dependent upon other data in the data set is the essence of independence relative to spatial statistics. Locations that show nominal dependence are typically treated as independent observations.

In the past, elk herds have been considered social groups with a high degree of group constancy (Darling 1937, Altmann 1952, 1956, 1960). As a result, when >1 radio-collared elk was found at

This study was part of a cooperative research effort entitled *The influence of forest fragmentation on vulnerability, habitat selection, and distribution of elk in western Montana*. Cooperators include USD1 Bureau of Land Management, USDA Forest Service Intermountain Research Station, The University of Montana School of Forestry, Rocky Mountain Elk Foundation, Plum Creek Timberlands LP, Boone & Crockett Club, and the Montana Department of Fish, Wildlife and Parks.

Manuscript accepted 19 Mar. 2000.

Resumen

Desarrollamos y utilizamos matrices de asociación, patrones de asociación y programas computacionales de reconocimiento de patrones (ASSOCI) para investigar la asociación espacio-temporal de individuos de alces portadores de radio-collares con otros individuos de alce también de radio-collar en un área de estudio del oeste de Montana. Estos procedimientos fueron utilizados para estimar aproximadamente la cantidad de tiempo que cada individuo pasa con otro individuo y evaluar el nivel de independencia con el que actúan estos alces. Los resultados de este estudio permitirán a los biólogos de fauna silvestre a tener un mejor entendimiento de los movimientos de los animales y la dinámica del hato y a evaluar la independencia de los sitios animal para el cálculo del área de apacentamiento y el análisis de uso-disponibilidad del hábitat.

the same location, field biologists often used only 1 of these locations in home range estimation, because using all locations may violate the assumption of statistical independence. The potential error in this logic is it treats all animals in the herd as a single discrete unit, and assumes any observed spatio-temporal association among individuals should be attributed to a lack of independence. Alternatively, if each individual in the herd was assumed to act independently, all points could be used in home range estimation. Thus, establishing independence for as many observations as possible would allow more accurate delineation of core use areas.

Historical Methodology

One approach to address statistical independence has been the use of an association test. An association index was described by Dice (1945) that calculated the percent of occurrences where animal A was found with animal B. Cole (1949) and Knight (1970) described a coefficient of association that was calculated by doubling the number of observations where animal A and B were found together, and dividing that value by the sum of observations for animal A and B. Cole's coefficient of association was intended to measure interspecific association. Later, Knight (1970) and Schoen (1977) applied the equation to intraspecific association. Similarly, Shoemith (1980) based a test of intraspecific association (joint occurrence) on the methods described by Cole (1949) and Hurlbert (1969). Each method involves numerous calculations and/or database manipulations on the part of the biologist. Further, these techniques only provide an association

Table 1. Sample matrices illustrating spatial association frequency (left^a) and proportion (right^b) among S radio collared elk.

n =	AN	1	2	3	4	5	AN	1	2	3	4	5
50	1	50					1	1.00	0.57	0.08	0.75	0.14
49	2	28	49				2	0.56	1.00	0.60	0.70	0.23
25	3	2	15	25			3	0.04	0.31	1.00	0.50	0.43
40	4	30	28	20	40		4	0.60	0.57	0.80	1.00	0.29
35	5	5	8	7	10	35	5	0.10	0.16	0.28	0.25	1.00

AN = Animal Number

^aFrequency of association among 5 individual elk (Animal Numbers 1–5). In this example, spatial association was defined as a radio–telemetry location occurring within 200 m of another individual elk during the same flight.

^bThe proportion of association among the same 5 individual elk. Note: these values have been corrected for sample size variation.

index or coefficient of association (which may not be sufficient to address the concern of pseudoreplication) and fail to assess any association patterns (cf Darling 1937, Altmann 1952) that may exist between individuals.

The majority of literature dealing with independence of animal locations concerns the potential for auto-correlation between consecutive observations of an individual (Hayne 1949, Metzgar 1972, Dunn and Gipson 1977, Swihart and Slade 1985a, 1985b, 1997, Worton 1989, White and Garrott 1990, Loft et al. 1991). All association tests reviewed concerning pseudoreplication were created prior to the advent and widespread use of radio-telemetry (Forbes 1907, Michael 1920, Dice 1945, Cole 1949, Hurlbert 1969). Many of these tests have been modified and applied to intraspecific association (Knight 1970, Schoen 1977, Shoesmith 1980), but none were designed specifically for this purpose. Statistical analyses of telemetry data (e.g., home range analysis, utilization distribution functions, and habitat use-availability tests) have placed unique demands on the methods and techniques used by biologists. Earlier researchers could not have foreseen the requirements of statistical independence under the circumstances encountered with telemetry studies. Thus, a technique to specifically address pseudoreplication in telemetry studies is required.

Methods

Prior to performing an association test, we first selected spatial and temporal threshold values. Spatial threshold is the maximum distance at which any 2 individuals can be separated and still considered associated. By definition, pairs of individuals separated by an Euclidean-distance that exceeds the spatial threshold are considered non-associated. When choosing a spatial threshold (using Euclidean-distance) the biologist should consider the species, its known or reported movement potential, size of the study area and/or

herd home range, and telemetry error. Temporal threshold is the minimum amount of time 2 associated individuals spent together over the sampling period. Pairs of individuals showing a temporal association less than the temporal threshold are considered non-associated. When choosing a temporal threshold (1–100%), the user should consider the objectives of the study, frequency and number of observations, and the desired scale of definition (e.g., primary herd units, sub-herd units, etc.). Using a large spatial threshold and low temporal threshold will result in the most liberal test of association.

A matrix was created containing the frequency each individual was found within the spatial threshold of another individual during a telemetry flight. A second matrix was used to convert frequency to proportions to account for variation in sample size (Table 1).

The matrices were then examined using 2 criteria; (1) Individuals having <10 observations or <10% of the maximum number of observations were not analyzed for association pattern (e.g., if the maximum number of observations for any individual was 500, any individual having <50 observations would not be analyzed for association pattern). (2) Pairs of individuals that failed to demonstrate association exceeding the temporal threshold were considered non-associated and were not included in the association pattern procedure (Table 2). The association pattern

Table 2. The resulting matrix after applying the temporal threshold^a to sample data for 5 individual elk (cf. Table 1).

n =	AN	1	2	3	4	5
50	1	yes	yes	no	yes	no
49	2	yes	yes	yes	yes	no
25	3	no	no	yes	yes	no
40	4	yes	yes	yes	yes	no
35	5	no	no	no	no	yes

AN = Animal Number

^aCells containing 'yes' indicate the pair of individual elk have demonstrated association that exceeds the temporal threshold (e.g., 50%) and are considered associated. Cells containing 'no' indicate the pair of individuals are considered non-associated. This table corresponds to Table 1 and the grid cell illustration shown in Fig. 1.

procedure consists of creating a grid for each individual with each cell of the grid representing 1 individual. The cells that correspond to the Animal Number of each individual with which the given individual had associated were shaded (Fig. 1). We then compared the association grid created for each individual with the association grid of each other individual, and calculated the percent similarity between the association grid patterns. Close examination of these patterns allowed us to categorize individuals into herd or sub-herd units based on the similarity observed among the association grid patterns.

Description of Association Software

We developed software (ASSOC1¹) that used association matrices, association patterns (cf. Darling 1937, Altmann 1952, Shoesmith 1980), and pattern recognition, to approximate the amount of time each individual radio-collared elk spent with each other radio-collared elk. The software also assessed the level of independence at which these elk acted, and categorized individual elk into herd or sub-herd units.

To categorize individuals into herds, sub-herds, or associated groups ASSOC1 was designed to select >1 association grids to act as template grids, against which all other individual association grids would be compared. Selection of a template grid was based on the number of other individuals a given individual associated with. The individual showing association with the largest set of other individuals had the highest probability of being selected as a template grid (e.g., Fig. 1, Animal Number 4). In addition, each template grid was

¹ASSOC1 was developed using Microsoft Visual Basic version 5 for Windows NT and Windows 95/98 PC's. Help documentation accompanies the 32-bit application. The software is available free of charge at

<http://giscenter.isu.edu/software/software.htm>.

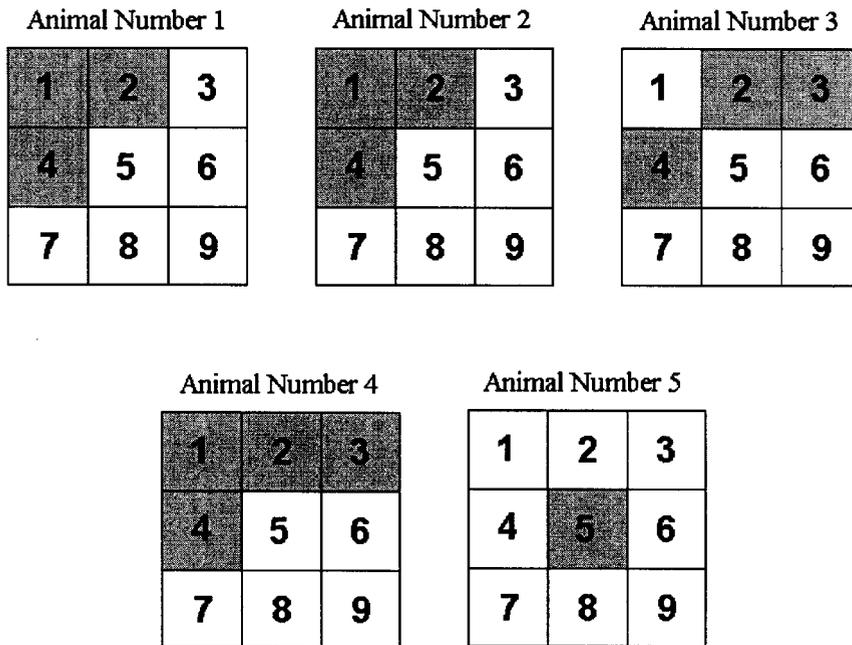


Fig. 1. Example of association pattern grids for 5 individual elk where the temporal threshold was 50% (i.e., to be considered associated, individual elk were required to have been found together (within 200 m of one another) in $\geq 50\%$ of all radio telemetry locations). Each shaded cell represents an individual elk that is considered associated with the animal listed above the grid cell. This figure corresponds with data given in Tables 1 and 2 (e.g., Animal number 3 is considered associated with Animals Numbered 2, 3 (itself), and 4).

required to identify a mutually exclusive set of individuals. When a template grid could not be selected without overlapping the set of individuals already identified by a previously selected template grid; the selection process was terminated. Each individual association grid was then compared to the template grid(s) to determine percent similarity. Individuals demonstrating a similarity to the template grid exceeding the temporal threshold were grouped into the same herd/sub-herd.

This test of association can be performed using any number of individuals. All matrices are saved in a data file for user review and, regardless of the assigned thresholds, the actual association for each individual is reported in the output from ASSOC1.

Chamberlain Creek Case Study

Two elk herds (henceforth referred to as the Chamberlain and Greenough elk herds) were identified and analyzed in this study using radio-telemetry locations. The study area was located approximately 56 km east of Missoula, Mont. in the Garnet Mountains. We radio-collared approximately 10% of the estimated elk population. Of those radio-collared elk, 80% were cows and spike bulls that were considered members of herd units (Franklin

and Lieb 1979, Geist 1982). Radio-telemetry locations for each individual were recorded in UTM coordinates (± 100 m) and obtained weekly using a 5-element Yaggi antenna mounted on fixed-wing aircraft. We ran several iterations of ASSOC1 software using various spatial and temporal thresholds. All elk locations were first divided into known primary herd units (the Chamberlain and Greenough elk herds) and then analyzed for association within herds. We defined the spatial threshold as any 2 radio-collared elk within 200 m of each other during a telemetry flight, and set the temporal threshold at 70%. This particular spatial threshold was chosen to account for our telemetry error of ± 100 m and our method of recording joint occurrences as duplicates of the first elk located. The temporal threshold of 70% was chosen so that only closely associated individuals were used in the association pattern, and pattern similarity analyses.

The overall mean association (corrected for annual variation in sample size) between individual elk within a herd was found to be only 16% for the Chamberlain elk herd, and 11% for the Greenough elk herd. This indicates these elk act independently of one another, and do not move across the landscape as a discrete unit. More importantly, the highest association

observed between any 2 individuals throughout this study was 57%. These results suggest that the structure and composition of elk herds are relatively dynamic over even brief time periods. However, any 2 radio-collared elk were found together 64% of the time. Based on this result, it seems safe to assume that a given cow elk can be found with another elk nearly 100% of the time. This observation describes the gregarious nature of elk (Craighead and Shoemith 1966), and does not address independence. It must be remembered that $< 20\%$ of an individual cow elk's time was spent with the same individual. Therefore, elk herds should be viewed as gregarious aggregations and not discrete social groups. The aggregations observed were probably due more to forage availability, family unit fidelity, and predator-prey relationships (cf. herd effect, Hamilton 1971) than dependent movement patterns.

It should be clear that absolute independence does not exist. Elk movements are influenced by forage availability (which is influenced by weather, slope, aspect, elevation, etc.), disturbance from predators and human activity (Marcum 1975), the location of other elk, weather, and each individual's response to these influences. Based on these results, home range estimations for this study were calculated using all elk observations.

Two additional iterations of ASSOC1 were performed using different thresholds (Table 3). When the temporal threshold was decreased and the spatial threshold was held constant, the frequency of association among herd members increased. Similarly, when the temporal threshold was held constant and the spatial threshold was increased the frequency of association increased. However, because spatial threshold determines the percent association, increasing the spatial threshold also increases the percent association. The affect of varying thresholds on the number of herd members identified (the number of individuals associated with template individuals) is shown in Table 3. As the association percent and association frequency increases, so does the number of

Table 3. Resulting frequency and percent association for the Chamberlain Creek Case Study using 3 alternative thresholds.

Threshold	Temporal	Association		
		Frequency	Mean %	Maximum %
200	70	1.0	9.5	56.9
200	15	7.0	9.5	56.9
5000	15	12.8	21.0	87.6

herd members associated with a herd template individual.

At coarse scales, where the spatial threshold was high (e.g., 10,000 m), we were able to distinguish between primary herd units, but were not able to discern sub-herd units that may have existed. At fine scales (e.g., 200 m) we were capable of distinguishing not only primary herd units, but sub-herd units as well. However, due to the complex procedure used to select template grids, this technique gave the best resolution when analyzing individuals that had been previously categorized into primary herd units.

Other studies that have addressed elk associations have reported similar findings (Craighead and Shoesmith 1966, Knight 1970, Schoen 1977, Shoesmith 1980), concluding that elk herds are best described as aggregations instead of social groups. Still, the question of statistical independence persists, requiring the biologist to determine the degree of association among the radio-collared animals used in the study. We feel that use of the association index (Dice 1945) is inadequate because it does not account for disproportionate sample sizes between individual animals, and like the coefficient of association, it was designed to measure interspecific association. Further, neither technique incorporates any landscape variable such as spatial threshold.

Discussion

Potential applications of this technique include not only assessing independence of herd animal locations, but distinguishing herd and sub-herd (within herd) units as well. By adjusting the spatial threshold (the maximum distance between associated individuals), biologists can vary the scale of assessment. By adjusting the temporal threshold (the minimum amount of time spent together by associated individuals), the fidelity of herd units can be described.

This technique utilizes a crisp logic system (McNeill and Freiberger 1993). If an individual is found within the spatial threshold of another individual, and spends an adequate amount of time with that individual (exceeding the temporal threshold), those individuals are considered associated. However, another individual may show very similar association yet not meet the thresholds set by the user. Hence, those individuals are considered non-associated. For this reason, we urge biologists to use this technique with several different thresholds and scales, and to report the thresh-

olds used with any results derived from this software. ASSOC1 software was not developed to provide a rigorous statistical test with critical values and a probability statement. Rather, this software acts as a spatial analysis tool that provides the biologist with a set of measures, upon which, a decision of association or independence can be more easily determined.

Many biologists have applied the recommendations from earlier studies of autocorrelation (Swihart and Slade 1985a, 1985b, White and Garrott 1990), interspecific association (Cole 1949, Hurlbert 1969), or treatments of pseudoreplication (Hurlbert 1984) to the issue of independence of herd animals. This paper differentiates these issues (auto-correlation and pseudoreplication) and addresses the question of independence of herd animals with ASSOC1 software. An advantage of this technique is the user can review each step in the procedure by examining the output association matrices (frequency and proportion), association pattern similarity, and herd assignment tables. The flexibility of this software allows ASSOC1 to handle any number of individuals at any scale by varying the user-defined spatial and temporal thresholds. Further, this technique is relatively simple, allowing the user to readily comprehend and critically examine each procedure used to produce the output. Over-complicated tests and techniques may not provide any additional information, and tend to mask errors in logic with complexity.

Literature Cited

- Altmann, M. 1952.** Social behavior of elk *Cervus canadensis nelsoni*, in the Jackson Hole area of Wyoming. *Behav.* 4(2):116-143.
- Altman, M. 1956.** Patterns of herd behavior in free ranging elk of Wyoming. *Zool.* 41(2):65-71.
- Altman, M. 1960.** The role of juvenile elk and moose in the social dynamics of their species. *Zool.* 45(1):35-39.
- Cole, L.C. 1949.** The measure of interspecific association. *Ecol.* 30(4):41 1-24.
- Craighead, J.J. and M. Shoesmith 1966.** An intensive study of elk behavior on the Mirror Plateau summer range, Yellowstone National Park. *Quart. Rpt. Mont. Coop. Wildl. Res. Unit* 1 7(2):6-8.
- Cressie, N.A. 1991.** *Statistics for spatial data.* John Wiley and Sons, Inc. New York. 900 pp.
- Darling, F.F. 1937.** *A herd of Red Deer: A study in animal behavior.* Oxford University Press, London, 215 pp.
- Dice, L.R. 1945.** Measures of the amount of ecological association between species. *Ecol.* 26:297-302.
- Dunn, J.E. and P.S. Gipson. 1977.** Analysis of radio telemetry data in studies of home range. *Biometrics.* 33:85-101.

- Forbes, S.A. 1907.** On the local distribution of certain Illinois fishes. An essay in statistical ecology. *Bull. Illinois State Lab. Nat. Hist.* 7:273-303.
- Franklin, W.L. and J.W. Lieb. 1979.** The social organization of a sedentary population of North American elk: a model for understanding other populations. Pages 185-195 *In:* M. S. Boyce and L. D. Hayden-Wing, eds. *North American elk: Ecology, behavior and management.* Univ. of Wyoming, Laramie, Wyo.
- Geist, V. 1982.** Adaptive behavioral strategies. Pp 219-277 *In:* J. W. Thomas and D. E. Toweill, eds. *Elk of North America: Ecology and management.* Wildl. Manage. Institute, Harrisburg, Penn.
- Hamilton, W.D. 1971.** Geometry for the selfish herd. *J. Theor. Biol.* 31:295-311.
- Hurlbert, S.H. 1969.** A coefficient of interspecific association. *Ecol.* 50:1-9.
- Hurlbert, S.H. 1984.** Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* 54(2):187-21 1.
- Knight, R.R. 1970.** The Sun river elk herd. *Wildl. Monogr.* 23:66 pp.
- Loft, E.R., J.W. Menke, and J.G. Kie. 1991.** Habitat shifts by mule deer: the influence of cattle grazing. *J. Wildl. Manage.* 55(1):16-26.
- Marcum, C.L. 1975.** Summer-fall habitat selection and use by a western Montana elk herd. Ph.D. Thesis, The Univ. of Montana, Missoula, Mont. 188 pp.
- McNeill, D. and P. Freiberger. 1993.** *Fuzzy Logic.* Simon and Schuster, New York, N.Y. 319 pp.
- Metzgar, L.H. 1972.** The measurement of home range shape. *J. Wildl. Manage.* 36:643-645.
- Michael, E.L. 1920.** Marine ecology and the coefficient of association; a plea in behalf of quantitative biology. *J. Anim. Ecol.* 8:54-59.
- Schoen, J.W. 1977.** The ecological distribution and biology of Wapiti (*Cervus elaphus nelsoni*) in Cedar River watershed, Washington. Ph.D. Diss., The Univ. of Washington, Seattle, Wash. 405 pp.
- Shoesmith, M.W. 1980.** Seasonal movements and social behavior of elk on Mirror Plateau, Yellowstone National Park. Pp 185-195 *In:* M. S. Boyce and L. D. Hayden-Wing, eds. *North American elk: Ecology, behavior and management.* Univ. of Wyoming, Laramie, Wyo.
- Swihart, R.K., N.A. Slade. 1985a.** Testing for independence of observations in animal movements. *Ecol.* 66:1176-1184.
- Swihart, R.K. and N.A. Slade. 1985b.** Influence of sampling interval on estimates of home-range size. *J. Wildl. Manage.* 49:1019-1025
- Swihart, R.K. and N.A. Slade. 1997.** On testing for independence of animal movements. *J. Agr., Biol., and Environ. Statistics.* 2(1): 48-63.
- White, G.C. and R.A. Garrott. 1990.** *Analysis of Wildlife Radio-Tracking Data.* Academic Press, San Diego, Calif. 383 pp.
- Wong, D. 1995.** Aggregation effects in geo-referenced data. Pp 83-106 *In:* S. L. Arlinghaus and D.A. Griffith, eds. *Practical handbook of spatial statistics.* CRC Press.
- Worton, B.J. 1989.** Kernel methods for estimating the utilization distribution in home range studies. *Ecol.* 70:164-168.

Sheep grazing spotted knapweed and Idaho fescue

BRET E. OLSON AND ROSEANN T. WALLANDER

Authors are associate professor and research associate, Department of Animal and Range Sciences, Montana State University, Bozeman, Mont. 59717-2900.

Abstract

Spotted knapweed (*Centaurea maculosa* Lam.), an Eurasian perennial forb, is replacing many native perennial grasses, such as Idaho fescue (*Festuca idahoensis* Elmer.), throughout the Northern Rocky Mountain region. Our objective was to determine sheep use of spotted knapweed and Idaho fescue during 3 consecutive summers (1991–1993). Each summer, 3 small spotted knapweed infested pastures were grazed for 5–8 days in mid-June, 2–6 days in mid-July, and 1–6 days in early September. Nutritive value of spotted knapweed leaves and flowerheads were consistently higher than of Idaho fescue. Nutritive value for both species declined as the summer progressed. The sheep readily grazed spotted knapweed, but they also grazed other plants, including the native Idaho fescue. They did not consistently graze 1 species more than another, which may have reflected daily weather patterns, slight differences in forage nutritive value, or cyclic grazing patterns which are often associated with plants containing secondary compounds, such as spotted knapweed. At the end of many grazing periods, heights of grazed spotted knapweed plants were greater than those of Idaho fescue, which reflected how the sheep grazed leaves and avoided fibrous stems of mature spotted knapweed plants, whereas they were not selective when grazing Idaho fescue. Although the sheep did not graze spotted knapweed exclusively, probably because animals seek diverse diets, their use of this noxious weed may help restore a balance in competitive relations between this noxious weed and native grasses.

Key Words: weed, *Centaurea maculosa*, *Festuca idahoensis*, utilization, nutritive value

Spotted knapweed (*Centaurea maculosa* Lam.), an aggressive, introduced perennial forb, is replacing native perennial grasses throughout the Northern Rocky Mountain region (Tyser and Key 1988, Lacey et al. 1995). Herbicides, fire, and biocontrol insects and pathogens are not containing the spread of this noxious weed. Large herbivores rarely graze spotted knapweed, possibly because it contains cyanin, a bitter tasting compound (Watson and Renny 1974, Kelsey and Locken 1987, Locken and Kelsey 1989). Where large herbivores such as cattle and horses avoid spotted knapweed, this noxious weed can outcompete native grasses for water and nutrients.

In contrast to large herbivores, the anatomy and morphology of small ruminants are more conducive for foraging on broad-leaved

We thank Kathrin Olson-Rutz for reviewing the manuscript. This study was supported by the Montana Department of Agriculture (Noxious Weed Trust Fund MDA 91-13a) and the Montana Agricultural Experiment Station.

Manuscript accepted 19 Mar. 2000.

Resumen

El "Spotted knapweed" (*Centaurea maculosa* Lam.) es una hierba perenne originaria de Eurasia que en la región norte de las montañas Rocallosas esta remplazando muchos de los zacates nativos, como el "Idaho fescue" (*Festuca idahoensis* Elmer.). Nuestro objetivo fue determinar durante tres veranos consecutivos (1991–1993) el consumo de "Spotted knapweed" y "Idaho fescue" por borregos. Cada verano 3 potreros pequeños infestados de "Spotted knapweed" se apacentaron durante 5–8 días a mediados de Junio, 2–6 días a mediados de Julio y 1–6 días a principios de Septiembre. El valor nutritivo de las hojas e inflorescencias del "Spotted knapweed" fue consistentemente más alto que el del "Idaho fescue". El valor nutritivo de ambas especies disminuyó a medida que el verano avanzó. Los borregos apacentaron con gusto el "Spotted knapweed", pero también apacentaron otras plantas, incluyendo el pasto nativo "Idaho fescue". Los borregos no apacentaron en forma consistente una especie mas que otra, lo cual pudo haber reflejado patrones climáticos diarios, ligeras diferencias en el valor nutritivo del forraje o patrones cíclicos de apacentamiento que a menudo son asociados con plantas que contienen compuestos secundarios, tal como el "Spotted knapweed". Al final de muchos períodos de apacentamiento la altura de las plantas apacentadas de "Spotted knapweed" fue mayor que la de "Idaho fescue", lo cual refleja que los borregos consumieron hojas evitando los tallos fibrosos de las plantas maduras de "Spotted knapweed" mientras que no fueron selectivos cuando apacentaron el "Idaho fescue". Aunque los borregos no apacentaron exclusivamente "Spotted knapweed", porque ellos probablemente buscan dietas diversificadas, el consumo de esta planta nociva por los borregos puede restablecer el balance en las relaciones competitivas entre esta especie nociva y los zacates nativos.

plants containing secondary defense compounds, such as spotted knapweed (Hofmann 1989). In general, sheep prefer broad-leaved herbs to grasses and shrubs (Hanley 1982), possibly because broad-leaved herbs tend to be more nutritious and digestible than grasses (Shipley 1999). Conversely, the native bunchgrass Idaho fescue (*Festuca idahoensis* Elmer.) "increases" with sheep grazing (USDA 1983), presumably because sheep prefer broad-leaved herbs and certain grasses to Idaho fescue.

In a greenhouse study, a single defoliation did not affect spotted knapweed, whereas defoliations at monthly intervals reduced root and crown weights, and carbohydrate concentrations in roots, crowns, and stems (Kennett et al. 1992, Lacey et al. 1994). This sequence of multiple defoliations was duplicated in a field study, where we assessed impacts of sheep grazing a spotted knapweed-infested community for 3 consecutive summers (Olson and Wallander 1997, Olson et al. 1997). This community was

grazed repeatedly by sheep, in mid-June when spotted knapweed was bolting, in mid-July when the native bunchgrass Idaho fescue (*Festuca idahoensis* Elmer.) was dormant, and in early September before the Idaho fescue resumed fall growth.

Our objective was to assess use of spotted knapweed and Idaho fescue by sheep during these 3 periods during the summers of 1991–1993. If sheep graze spotted knapweed more than the associated native grasses, this may help restore a balance to the plant community (Olson 1999).

Methods and Materials

The study site was 14 km south of Bozeman, Mont. (45° 36' N 111°4'W) at an elevation of 1,570 m. Soil was a shallow to moderately deep, silty clay loam over sand and gravel Typic Argiboroll class, Beaverton series on an alluvial fan (USDA 1995). The 30-year precipitation average for the nearest weather station (Bozeman, Mont.) was 487 mm. Precipitation for 1991–1993 was 99, 115, and 123% of the 30-year average, respectively. The summer (June–August) of 1991 was drier and warmer than the 30-year average, whereas the summers of 1992 and especially 1993 were cooler and wetter than the long term average (Table 1). In mid-June 1991, standing crop aver-

(*Geranium viscosissimum* F. & M.).

Three 0.1-ha pastures enclosed with Electronet[®] fencing were randomly located within a 3-ha area. The area had previously been grazed by horses for 10 years, which had encouraged the spread of spotted knapweed. Other than our sheep, domestic herbivores did not graze in or adjacent to our small pastures during the study.

Four, 10-m permanent transects were established inside each small pasture. Permanent plots (0.5-m²) were established at 1-m intervals along each transect. The nearest spotted knapweed and Idaho fescue to each corner of the 0.5-m² plots were marked with colored wire before grazing each year. Heights of these marked plants were recorded immediately before the sheep grazed each period (day 0).

Each pasture was grazed by 5 Targhee yearling ewes during the summers of 1991–1993. New animals which had never been exposed to spotted knapweed were used each year. Each pasture was grazed for 5 to 8 days in mid-June, 2 to 6 days in mid-July, and 1 to 6 days in early September. Duration of the grazing periods depended on available forage. When not in the study pastures, the sheep were grazed nearby in areas with 10–20% spotted knapweed cover.

When the sheep were in the study pastures, use of marked spotted knapweed and Idaho fescue plants was recorded

plants of similar diameter. Finally, grazed and ungrazed heights were recorded.

To determine nutritive value, ungrazed and regrowth from previously grazed spotted knapweed and Idaho fescue plants were harvested while the sheep were grazing each study pasture. All ungrazed spotted knapweed plants were air-dried, and separated into leaves, stems, and flower buds. Regrowth from previously grazed spotted knapweed plants was sorted into leaves and stems. Idaho fescue plants were separated into leaves (culmless stems) and flowering stems (culmed stems). All plant parts were ground to pass through a 1-mm screen in a Wiley mill. Crude protein (%N x 6.25; CP) was determined by a standard method (AOAC 1984). Neutral detergent fiber (NDF) and acid detergent fiber (ADF) were determined by the procedures of Goering and Van Soest (1970). In vitro dry matter disappearance (IVDMD) was determined after Tilley and Terry (1963).

Within each grazing period (June, July, September) each year (1991–1993), grazed plant frequency, percent canopy removed, and grazed plant heights were analyzed with a repeated measures analysis of variance (day 0, day 2, etc.) as a randomized-complete-block design (n = 3; GLM, SAS 1988). Plant species was the between treatment effect; day within grazing period was the within treatment effect. Analyses of grazed plant frequency and percent canopy removed were based on observations after day 0. Analyses of grazed plant heights included day 0. Because some of the distributions were not spherical, we used Huynh-Feldt adjusted P-values. Because of inherent variability in field studies such as this one, P-values less than 0.15 are presented (Gill 1981).

Table 1. Thirty-year averages and 1991–1993 mean temperatures and total precipitation for May through August, Bozeman, Mont.

Month	Temperature				Precipitation			
	30-year average	1991	1992	1993	30-year average	1991	1992	1993
	----- (°C) -----				----- (mm) -----			
May	10.8	10.0	13.5	13.5	81	134	70	84
Jun.	15.6	15.0	16.8	14.2	73	48	140	108
Jul.	19.6	20.6	16.9	14.7	34	13	43	125
Aug.	18.8	21.4	17.9	16.0	38	12	23	73

aged 1,580 kg ha⁻¹; the plant community was dominated by Idaho fescue (41%) and spotted knapweed (25%). In mid-June 1992, standing crop averaged 2,201 kg ha⁻¹; again, the plant community was dominated by Idaho fescue (50%) and spotted knapweed (16%). Standing crop was not measured in 1993. Other common species at the site were bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) Love), Kentucky bluegrass (*Poa pratensis* L.), arrowleaf balsamroot (*Balsamorhiza sagittata* (Pursh) Nutt.), lupine (*Lupinus senceus* Pursh), and sticky geranium

every 48 hours (day 2, day 4, etc.). First, impact to the marked plant was recorded as none, grazed, trampled, or grazed and trampled. "Grazed" and grazed and trampled" categories were combined to determine grazed plant frequency. This included any evidence of grazing in the preceding 2 day interval. Lack of any necrotic tissue at grazed leaf tips indicated recent grazing compared with necrotic tissue at leaf tips which indicated grazing during the previous grazing period. Second, percent canopy removed of grazed plants was estimated by comparing with ungrazed

Results

Nutritive value

Crude protein in leaves from ungrazed and previously grazed spotted knapweed plants was consistently greater than those from Idaho fescue (Tables 2,3). Crude protein in stems from ungrazed and previously grazed spotted knapweed plants was similar to levels in flowering stems of Idaho fescue. Neutral- and acid detergent fiber of leaves from ungrazed and previously grazed spotted knapweed plants was consistently lower than those from Idaho fescue. Neutral- and acid detergent fiber of stems from ungrazed and previously grazed spotted knapweed plants was similar to or slightly lower than the fiber con-

Table 2. Nutritive value (crude protein, neutral detergent fiber, acid detergent fiber, in vitro dry matter disappearance) of leaves (L), stems (S), and flower heads (F) collected from ungrazed (U) and regrowth from previously grazed (G) spotted knapweed plants during the June (JUN), July (JUL), and September (SEP) grazing periods 1991–1993. Values represent means from samples collected from each pasture (n = 3). "na" indicates not available.

		1991			1992			1993		
		JUN	JUL	SEP	JUN	JUL	SEP	JUN	JUL	SEP
crude protein		----- (%) -----								
U	L	12	6	na	13	10	5	13	12	9
	S	na	3	3	5	3	2	4	3	3
	F	na	na	8	20	11	8	na	13	9
G	L	na	18	18	na	19	18	na	21	13
	S	na	5	3	na	na	2	na	na	3
neutral detergent fiber										
U	L	24	29	na	20	21	27	22	22	28
	S	na	65	77	55	61	71	58	57	58
	F	na	na	42	26	45	56	na	27	50
G	L	na	26	29	na	24	21	na	na	22
	S	na	65	73	na	na	78	na	na	61
acid detergent fiber										
U	L	23	28	na	20	21	27	20	20	26
	S	na	50	60	45	47	57	46	44	47
	F	na	na	33	21	34	42	na	27	36
G	L	na	21	25	na	19	18	na	na	21
	S	na	53	58	na	na	64	na	na	47
in vitro dry matter disappearance										
U	L	68	61	na	60	68	45	66	60	52
	S	57	37	19	56	43	29	52	46	38
	F	na	na	43	51	54	43	na	55	46
G	L	na	48	52	na	68	56	na	60	77
	S	na	38	24	na	na	21	na	na	11

tent of flowering stems of Idaho fescue. In vitro dry matter disappearance of leaves from ungrazed and previously grazed spotted knapweed plants was consistently greater than those from Idaho fescue. Similarly, in vitro dry matter disappearance of stems from ungrazed and previ-

ously grazed spotted knapweed plants was greater than those from flowering stems of Idaho fescue.

1991

During the 6 day June grazing period (15 June to 21 June), grazed plant frequen-

cies of spotted knapweed and Idaho fescue increased similarly (day, $P = 0.002$, Fig. 1). Percent canopy removed from spotted knapweed and Idaho fescue also increased similarly (day, $P = 0.02$). Within this period, we did not measure grazed plant heights until the last day.

Table 3. Nutritive value (crude protein, neutral detergent fiber, acid detergent fiber, in vitro dry matter disappearance) of leaves (L) and flower stems (FS) collected from ungrazed (U) and regrowth from previously grazed (G) Idaho fescue plants during the June (JUN), July (JUL), and September (SEP) grazing periods 1991–1993. Values represent means from samples collected from each pasture (n = 3). "na" indicates not available.

		1991			1992			1993		
		JUN	JUL	SEP	JUN	JUL	SEP	JUN	JUL	SEP
crude protein		----- (%) -----								
U	L	9	8	7	7	5	4	6	6	5
	FS	na	na	2	5	3	1	4	4	1
G	L	na	na	8	na	12	6	na	na	8
	FS	na	na	2	na	na	1	na	na	1
neutral detergent fiber										
U	L	64	65	68	60	62	68	62	65	68
	FS	na	na	84	72	75	82	73	71	84
G	L	na	na	71	na	na	70	na	na	69
	FS	na	na	83	na	na	84	na	na	84
acid detergent fiber										
U	L	40	40	43	38	40	47	38	40	45
	FS	na	na	56	46	48	58	46	45	58
G	L	na	na	44	na	na	45	na	na	42
	FS	na	na	57	na	na	58	na	na	58
In vitro dry matter disappearance										
U	L	52	45	26	53	30	27	40	29	25
	FS	na	na	11	47	25	15	27	28	12
G	L	na	na	23	na	na	25	na	na	29
	FS	na	na	12	na	na	12	na	ba	11

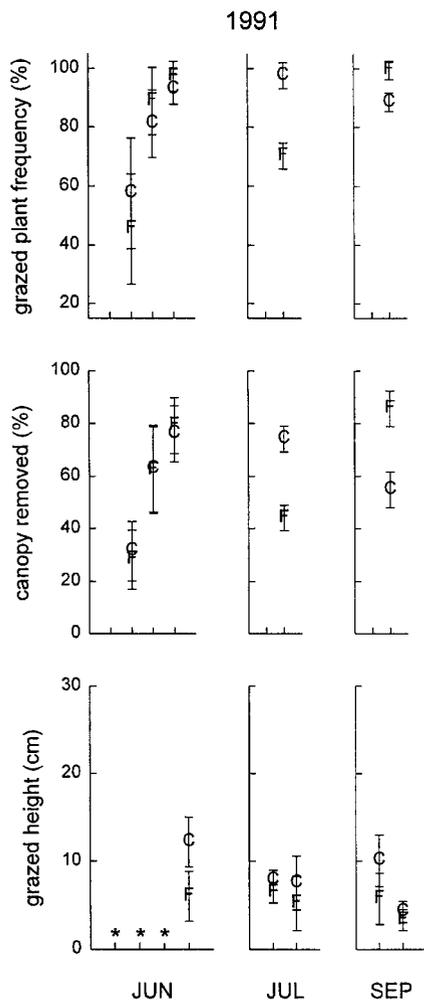


Fig. 1. Grazed plant frequency (%), canopy removed (%), and grazed plant heights (cm) of spotted knapweed (C - *Centaurea maculosa*) and Idaho fescue (F - *Festuca idahoensis*) within grazing periods in mid-June, mid-July, and early September of 1991. Grazing periods varied based on available forage. Error bars represent ± 1 S.E. The "*" indicates we did not measure heights of grazed plants these first 3 intervals.

During the 2 day July grazing period (16 July to 18 July), grazed plant frequency of spotted knapweed was greater than of Idaho fescue (species, $P = 0.01$). Percent canopy removed from spotted knapweed was greater than that removed from Idaho fescue (species, $P = 0.03$). Heights of grazed spotted knapweed plants did not change whereas heights of grazed Idaho fescue plants decreased (day by species, $P = 0.008$).

For the 1 day September grazing period (1 September to 2 September), grazed plant frequency of spotted knapweed was lower than of Idaho fescue (species, $P = 0.07$). Percent canopy removed from spotted knapweed was lower than that

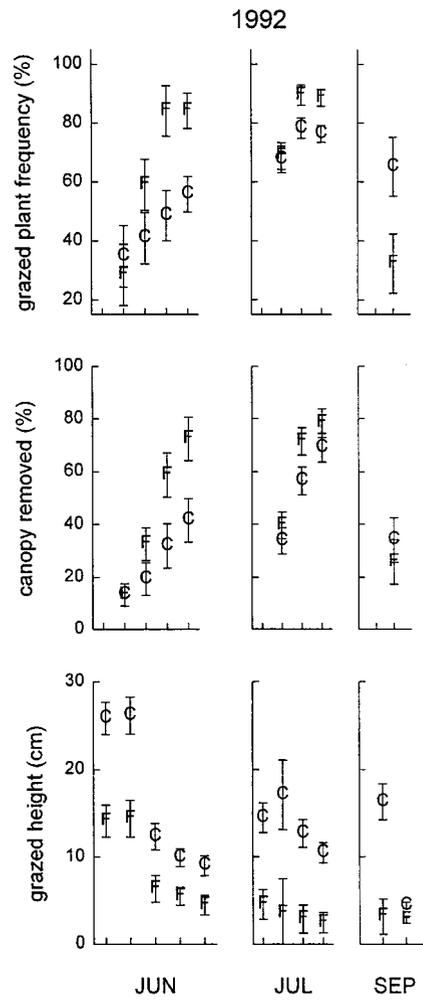


Fig. 2. Grazed plant frequency (%), canopy removed (%), and grazed plant heights (cm) of spotted knapweed (C - *Centaurea maculosa*) and Idaho fescue (F - *Festuca idahoensis*) within grazing periods in mid-June, mid-July, and early September of 1992. Grazing periods varied based on available forage. Error bars represent ± 1 S.E.

removed from Idaho fescue (species, $P = 0.03$). Grazed plant heights of both species declined (day, $P = 0.03$).

1992

During the 8 day June grazing period (18 June to 26 June), grazed plant frequency of Idaho fescue increased at a faster rate than grazed plant frequency of spotted knapweed (day by species, $P = 0.001$, Fig. 2). Percent canopy removed from both species was similar on day 2, but increased at a greater rate for Idaho fescue through day 8 (day by species, $P = 0.0004$). Heights of grazed Idaho fescue plants declined more than heights of

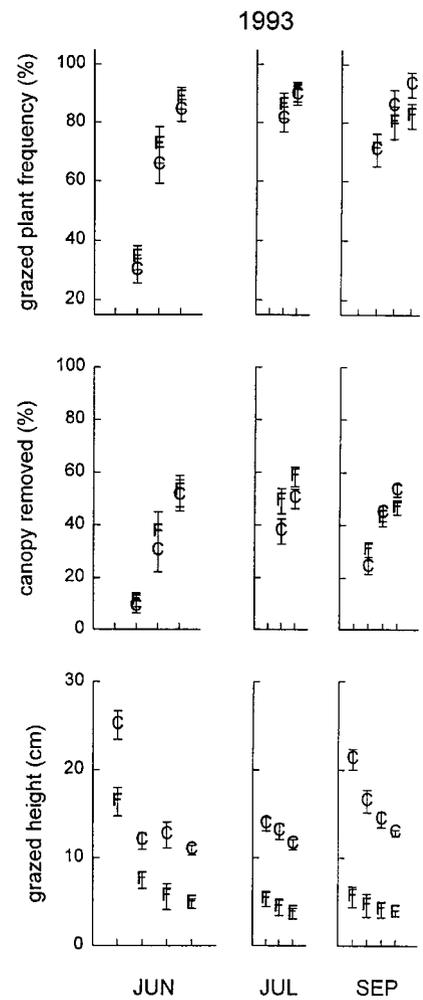


Fig. 3. Grazed plant frequency (%), canopy removed (%), and grazed plant heights (cm) of spotted knapweed (C - *Centaurea maculosa*) and Idaho fescue (F - *Festuca idahoensis*) within grazing periods in mid-June, mid-July, and early September of 1993. Grazing periods varied based on available forage. Error bars represent ± 1 S.E.

grazed spotted knapweed plants (day by species, $P = 0.03$).

During the 6 day July grazing period (19 July to 25 July), grazed plant frequencies of these 2 species were similar on day 0, but were greater for Idaho fescue than spotted knapweed on day 4 and day 6 (day by species, $P = 0.12$). Percent canopy removed from spotted knapweed and Idaho fescue increased similarly (day, $P < 0.0001$). Heights of grazed Idaho fescue and spotted knapweed plants declined similarly (day, $P = 0.15$).

By the end of the 2 day September grazing period (10 September to 12 September), grazed plant frequency of spotted knapweed was greater than of

Idaho fescue (species, $P = 0.08$). Percent canopy removed from both species was similar (species, $P = 0.53$). Heights of grazed spotted knapweed plants declined more than 50%, whereas the decline was less for the short-statured Idaho fescue (day by species, $P = 0.01$).

1993

During the 5 day June grazing period (20 June to 25 June), grazed plant frequency of spotted knapweed and Idaho fescue increased similarly (day, $P = 0.0001$, Fig. 3). The increase in percent canopy removed from spotted knapweed and Idaho fescue was similar (day, $P = 0.0001$). Heights of grazed Idaho fescue plants declined more, on a percentage basis, than heights of grazed spotted knapweed plants (day by species, $P = 0.12$).

During the 4 day July grazing period (14 July to 18 July), grazed plant frequency of spotted knapweed and Idaho fescue increased similarly (day, $P = 0.008$), and percent canopy removed increased similarly (day, $P = 0.002$). Heights of grazed spotted knapweed and Idaho fescue plants declined similarly (day, $P = 0.0008$).

During the 6 day September grazing period (3 September to 9 September), grazed plant frequency of spotted knapweed and Idaho fescue was similar on day 2, but was greater for spotted knapweed than Idaho fescue on day 4 and 6 (day by species, $P = 0.02$). Percent canopy removed from spotted knapweed was initially lower than that removed from Idaho fescue (day 2), but similar on day 4 and 6 (day by species, $P = 0.04$). Heights of grazed spotted knapweed plants declined more than of grazed Idaho fescue plants (day by species, $P = 0.003$).

Discussion

By the traditional measures of forage nutritive value (CP, NDF, ADF, IVDMD), spotted knapweed is more nutritious than Idaho fescue, so sheep should graze it readily. Yet despite spotted knapweed's high nutritive value, it was not consistently grazed more than Idaho fescue. Cnicin, a sesquiterpene lactone, in spotted knapweed may have limited grazing of this weed. Sheep rumen microbial populations are negatively affected when a sheep's diet contains 70% or more spotted knapweed, especially when the diet consists of mature leaves or flower heads which have high cnicin concentrations (Olson and Kelsey 1997). High cnicin concentrations in leaves and flowerheads of spotted knap-

weed may offset the potential benefits associated with its high crude protein and low fiber content.

Sheep grazed the spotted knapweed, but they also grazed the native bunchgrasses, including Idaho fescue. Herbivores desire mixed diets containing a variety of nutrients (Provenza 1996). Even when presented with ad lib amounts of a food that meet their nutritional needs, lambs select a varied diet (Provenza et al. 1996). Animals may select varied diets for 1 or more of the following reasons: 1) animals are inherently curious and often sample foods, 2) a diverse diet often represents a balanced diet, or 3) a diverse diet may counter toxic effects associated with secondary compounds, such as cnicin in spotted knapweed.

Grazing patterns among periods differed slightly each of the 3 summers. By using a new set of "inexperienced" ewes each summer, there was no opportunity to acquire a long term preference for or aversion to spotted knapweed. In the first summer (1991), numerous standing stems of the previous year's spotted knapweed were present, but they did not deter use of the new growth at the base of the plant. With their relatively small muzzles, sheep grazed new growth surrounded by the previous year's stems. In the summers of 1992 and 1993, there were few ungrazed stems remaining from the previous year.

Use patterns within grazing periods often varied among the 2 day observation intervals. This could simply reflect responses to weather or cyclic patterns of grazing (Pfister et al. 1997). Weather patterns differed considerably between years; the summer (June–August) of 1991 was drier and warmer than the 30-year average, whereas the summers of 1992 and especially 1993 were cooler and wetter than the long term average. These could have influenced forage nutritive value, and therefore grazing patterns within each summer and among summers. Cyclic grazing, varying the intake of toxic plant compounds from day-to-day, may limit the potential cumulative effects of certain secondary compound (Pfister et al. 1997).

We used 3 different measures of utilization: grazed plant frequency, percent canopy removed, and grazed plant heights. Grazed plant frequency and plant heights are quantitative, whereas percent canopy removed is a visual estimate of how much was removed during a grazing period relative to an estimate of the intact canopy at the beginning of each grazing period. Grazed plant frequencies are usually greater than percent canopy removed,

because only a small bite from a plant constitutes "grazed" for grazed plant frequency. Our grazing system mimicked an intensive grazing system which counters an animal's ability to select preferred forages. Grazed plant frequencies were often in the 80 and 90 percent range, indicating that the sheep were sampling most plants.

The estimate "percent canopy removed" often tracked "grazed plant frequency", although the values were considerably less. Both variables are measured rapidly, yet percent canopy removed is more meaningful ecologically, representing material remaining for subsequent foraging or for protecting soil from erosion. It is an estimate, though, and may vary from observer to observer, or even within an observer during the day as fatigue sets in. We recorded heights of ungrazed and grazed plants. Instead of averaging ungrazed and grazed heights, we report only grazed plant heights. Averaging the 2 would provide an overall estimate of use, but this estimate is greatly influenced by grazed plant frequency, one of our variables. Further, the average could be influenced by a few tall plants. In contrast, grazed plant heights indicate to what extent individual plants were grazed, which influences their ability to compete for water and nutrients (Briske and Richards 1995).

Grazed plant heights were usually taller on spotted knapweed than Idaho fescue plants, especially at the end of the July and September grazing periods. This does not necessarily indicate greater use of Idaho fescue for 2 reasons. First, most of the aboveground biomass of Idaho fescue, like most bunchgrasses, is close to the soil surface; the relatively few, flexible flowering stems are readily grazed. In contrast, flowering stems of spotted knapweed bolt in mid- to late June. After bolting, a greater percentage of spotted knapweed's biomass is in the upper part of the plant compared with Idaho fescue. In addition, spotted knapweed stems are thicker and more fibrous (Kelsey and Mihalovich 1987) than Idaho fescue stems. Our sheep would often remove the developing flowerheads and stem leaves of spotted knapweed, but would not graze much of the stem, resulting in "taller" heights of grazed spotted knapweed plants. Second, based on leaf heights, ungrazed spotted knapweed plants are inherently taller than ungrazed Idaho fescue plants in mid-summer (60 cm versus 29 cm, respectively). Thus, these taller, more rigid stems of spotted knapweed explain the greater grazed plant heights of this noxious weed.

Based on grazed plant frequency, sheep often grazed Idaho fescue more than spotted knapweed which may partly reflect the plants we marked to determine use. In this study, most of our marked plants were moderate in size (mean stem basal area: spotted knapweed 4 cm² Idaho fescue 22 cm²). In our companion study, we found that sheep grazing altered the age-class distribution of spotted knapweed plants (Olson et al. 1997). Apparently, the sheep selected younger (< 3 years-old), smaller, presumably more palatable spotted knapweed plants. We had marked few plants in these age classes to estimate use. By grazing younger, more nutritious spotted knapweed along with mature plants, a long-term commitment to sheep grazing has the potential to restore a balance to infested plant communities (Olson 1999).

Conclusion

Sheep readily grazed spotted knapweed, but they also grazed other plants, including the native Idaho fescue. It is unlikely that we will identify an herbivore which would only graze a certain species, such as spotted knapweed, because animals seek diverse diets. Nonetheless, sheep grazing spotted knapweed-infested communities may help restore a balance in competitive relations between this noxious weed and native grasses, compared with communities grazed by large herbivores which avoid spotted knapweed.

Literature Cited

- AOAC. 1984.** Official methods of analysis (14th ed.). Association of Official Analytical Chemists. Washington, D.C.
- Briske, D.D. and J.H. Richards. 1995.** Plant responses to defoliation: a physiologic, morphologic and demographic evaluation, p. 635–710. *In*: D.J. Bedunah and R.E. Sosebee (eds.), *Wildland plants: physiological ecology and developmental morphology*. Soc. Range Manage., Denver, Colo.
- Gill, J.L. 1981.** Evolution of statistical design and analysis of experiments. *J. Dairy Sci.* 64:1494–1519.
- Goering, H.K. and P.J. Van Soest. 1970.** Forage fiber analysis (apparatus, reagents, procedures, and some applications). *ARS, USDA Agr. Handb.* 379.
- Hanley, T.A. 1982.** The nutritional basis for food selection by ungulates. *J. Range Manage.* 35:146–151.
- Hofmann, R.R. 1989.** Evolutionary steps of ecophysiological adaptation and diversification of ruminants: A comparative view of their digestive system. *Oecologia* 78:443–457.
- Kelsey, R.G. and U. Locken. 1987.** Phytotoxic properties of cnicin, a sesquiterpene lactone from *Centaurea maculosa* (spotted knapweed). *J. Chem. Ecol.* 13:19–33.
- Kelsey, R.G. and R.D. Mihalovich. 1987.** Nutrient composition of spotted knapweed (*Centaurea maculosa*). *J. Range Manage.* 40:277–281.
- Kennett, G.A., J.R. Lacey, C.A. Butt, K.M. Olson-Rutz, and M.R. Haferkamp. 1992.** Effects of defoliation, shading and competition on spotted knapweed and bluebunch wheatgrass. *J. Range Manage.* 45:363–369.
- Lacey, J.R., K.M. Olson-Rutz, M.R. Haferkamp, and G.A. Kennett. 1994.** Effects of defoliation and competition on total nonstructural carbohydrates of spotted knapweed. *J. Range Manage.* 47:481–484.
- Lacey, C.A., J.R. Lacey, P.K. Fay, J.M. Story, and D.L. Zamora. 1995.** Controlling knapweed on Montana rangeland. *Mont. State Univ. Ext. Ser. Circ.* 311, Bozeman, Mont.
- Locken, L.J. and R.G. Kelsey. 1989.** Cnicin concentrations in *Centaurea maculosa*, spotted knapweed. *Biochem. Syst. Ecol.* 15:313–320.
- Olson, B.E. 1999.** Grazing and weeds. p. 85–96. *In*: R.L. Sheley and J.K. Petroff (eds.), *Biology and management of noxious rangeland weeds*. Oregon State University Press, Corvallis, Ore.
- Olson, B.E. and R.G. Kelsey. 1997.** Effect of *Centaurea maculosa* on sheep rumen microbial activity and mass in vitro. *J. Chem. Ecol.* 23:1131–1144.
- Olson, B.E. and R.T. Wallander. 1997.** Biomass and carbohydrate status of spotted knapweed and Idaho fescue after repeated grazing. *J. Range Manage.* 50:409–412.
- Olson, B.E., R.T. Wallander, and J.R. Lacey. 1997.** Effects of sheep grazing on a spotted knapweed-infested Idaho fescue community. *J. Range Manage.* 50:386–390.
- Pfister, J.A., F.D. Provenza, G.D. Manners, D.R. Gardner, and M.H. Ralphs. 1997.** Tall larkspur ingestion: can cattle regulate intake below toxic levels? *J. Chem. Ecol.* 23:759–777.
- Provenza, F.D. 1996.** Acquired aversions as the basis for varied diets of ruminants foraging on rangelands. *J. Anim. Sci.* 74:2010–2020.
- 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.
- SAS. 1988.** Statistical analysis system. SAS Institute Inc. Raleigh, N.C.
- Shiple, L.A. 1999.** Grazers and browsers: how digestive morphology affects diet selection. pp. 20–27. *In*: K.L. Launchbaugh, J.C. Mosley and K.D. Sanders (eds.), *Grazing behavior of livestock and wildlife*. Idaho Forest, Wildlife and Range Exp. Stat. Bull. #70, Univ. Idaho, Moscow, Ida.
- 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.
- Tyser, R.W. and C.H. Key. 1988.** Spotted knapweed in natural area fescue grasslands: An ecological assessment. *Northwest Sci.* 62:981–987.
- U.S.D.A. 1983.** Soil Conservation Service. Technical Guide. Bozeman, Mont.
- U.S.D.A. 1995.** Natural Resources Conservation Service. Gallatin County Soil Survey. Bozeman, Mont.
- Watson, A.K. and A.J. Renny. 1974.** The biology of Canadian weeds. *Centaurea diffusa* and *C. maculosa*. *Can. J. Plant Sci.* 54:687–701.

Range condition, tenure, management, and bio-physical relationships in Sonora, Mexico

JOSE A. CORONADO-QUINTANA AND MITCHEL P. McCLARAN

Authors are professor of Management, University of Sonora, Reforma y Colosio, Hermosillo, Son., México 83100 and associate professor of Range Management, University of Arizona, Tucson, Ariz. USA 85721.

Abstract

The objective of this study was to describe the relationship among range condition scores, tenure system, management practices and bio-physical variables for 107 communal *ejido* ranches and 373 private ranches in Sonora, Mexico. The data was obtained from assessments of range condition and recommended carrying capacity for individual ranch units that were completed between 1973 and 1993 by the Comisión Técnica para la Determinación de Coeficientes de Agostadero. Variables measured were range condition, land tenure (communal *ejido* or private ranch), management characteristics (human density, live-stock stocking rate, ranch size, and infrastructure condition), and bio-physical characteristics (rangeland site quality and precipitation in the year of assessment). We used a combination of simple, univariate chi-square analyses and more complex, multivariate ordered logistic regression analyses to assess the relationships among these variables. There was no evidence from the logistic regression analysis that range condition of ranches in Sonora was related to the *ejido* or private tenure systems. Infrastructure condition was different between the 2 tenure systems, and infrastructure condition was positively related to range condition for both *ejido* and private ranches. Based on the univariate and multivariate analyses, precipitation amounts in the year of assessment was less for private ranches, and range condition on private ranches was more sensitive to precipitation than *ejido* ranches. Compared to estimates made in the 1960's and 1970's in other parts of Mexico, we found there to be less of a difference in stocking rate between the more lightly stocked private ranches and more heavily stocked *ejido* ranches, and generally good condition infrastructure on all ranches. The important relationship between precipitation and range condition implies that range condition assessments should be done over many years to produce estimates of trend that can be compared across wet and dry years.

Key Words: communal resources, *ejido*, infrastructure, precipitation

The relationship between rangeland conditions and land tenure systems, particularly private versus non-private tenure systems, has long been viewed as a basic element in the management of rangeland uses (e.g. Smith 1898, Worster 1992). The articulation

Resumen

El objetivo de este estudio fue describir la relación entre condición del pastizal y el sistema de tenencia de la tierra, variables biofísicas y de manejo de 107 ejidos y 373 propiedades privadas. Los datos fueron obtenidos de los estudios de condición y determinación de carga animal realizados de 1978 a 1993 en el estado de Sonora, México por la Comisión Técnica para la Determinación de Coeficientes de Agostadero. Las variables consideradas fueron condición del pastizal, tipo de propiedad (*ejido* ó propiedad privada), características de manejo (densidad humana, carga animal, tamaño de la unidad y condición de la infraestructura), y variables biofísicas (calidad del pastizal y precipitación durante el año de estudio). La información fue analizada usando tabulaciones simples y modelos de regresión logística en la búsqueda de relaciones entre las variables. Mediante regresión logística, no se encontró relación entre condición y tenencia de la tierra. La condición de la infraestructura fue diferente entre ambos tipos de propiedad y positivamente relacionado con la condición del pastizal. En base a la tabulación y regresión logística, la cantidad de precipitación durante los años de estudio fue menor para las propiedades privadas y, la condición de los pastizales en las propiedades privadas fue mas sensible a la precipitación que en los *ejidos*. Comparado con estudios hechos en los 1960's y 1970's, en otras partes del país, se encontró menos diferencia entre carga animal aplicada en los ejidos y las propiedades privadas y en general, mejor infraestructura en ambos tipos de propiedad. La relación importante entre condición del pastizal y precipitación, indica que los estudios de evaluación de condición de los pastizales deben hacerse durante muchos años para poder obtener estimaciones de tendencias que permitan hacer comparaciones entre años de baja y alta precipitación.

of this relationship for Mexican rangelands became more important after 1991, when amendments to article 27 of the Mexican Constitution permitted the alienation (sale of property rights) of communal lands known as *ejidos* with the goal of improving the productive output of these lands (Solidaridad 1992). In this paper, we evaluate the relationships among land tenure system (private vs. *ejido*), rangeland conditions, management practices (e.g. stocking rate and infrastructure conditions) and bio-physical rangeland characteristics (e.g. rangeland site quality and precipitation) in the state of Sonora, Mexico.

Since Hardin's (1968) Tragedy of the Commons publication, various non-private tenure systems have been characterized according to rules governing access to resources (Ostrom et al. 1999). For example, Hardin (1968) described an open-access

Special thanks are given to Dr. David King and Dr. Lamar Smith from the University of Arizona for their advice and to the Consejo Nacional de Ciencia y Tecnología (CONACYT) for its financial support to complete this research project.

Manuscript accepted 25 Apr. 2000.

communal system where individuals' unlimited access to pasture resources resulted in a decline in the productive condition of the pasture. In contrast, limited-access communal systems use cultural norms and social systems to establish rules for the individual's access to resources while maintaining a non-private property rights tenure system (e.g. Feeny et al. 1990). Beyond the access-exclusion contrasts, there are different expectations concerning the willingness to invest in resource management among tenure systems. Some argue that market forces will act to foster greater investment under private ownership (e.g. Baden and Stroup 1977). In contrast, Wilson and Thompson (1993) found that limited-access *ejido* communal systems in the Northern Altiplano of Mexico were better able to withstand the risks of rangeland livestock production if costs of enforcing limited access were not prohibitive, and if human and financial capital were available to perform sustainable management practices.

In the context of tenure systems, we ask if different levels of management are observed across tenure systems, and whether these differences are manifest as differences in the condition of resources. A basic tenet of rangeland management is that management practices will influence resource condition, and therefore, we expect a negative relationship between grazing intensity (i.e. stocking rate) and resource conditions (albeit, not necessarily a linear relationship; e.g. Hart et al. 1993), and we expect the development of fence and water infrastructure to foster an improvement of rangeland conditions (e.g. Vallentine 1990). An alternative hypothesis is that differences in management practices transcend tenure systems, and, therefore, resource conditions are more strongly related to management than tenure system.

We ask if there is a consistent pattern in the inherent quality of rangeland sites according to land tenure system, and whether these differences are manifest as differences in rangeland condition. For example, the role of bio-physical characteristics in determining a potential for rangeland condition is expressed through the classification of rangeland sites (ecological sites) that vary in their soils, climate, vegetation and primary productivity (Humphrey 1949, Anderson and Fly 1955), and therefore, different rangeland sites may possess different potentials to respond to management practices (e.g. Launchbaugh et al. 1990). The distribution of different range sites may vary among land tenure systems (e.g. Loring

and Workman 1987), and such variation could account for some of the variation in resource condition among tenure systems. We ask if there is a relationship between tenure systems and the amount of precipitation occurring during the year of the condition assessment, and if these differences are manifest as differences in the condition of resources. Assessing the role of management on rangeland conditions is contingent on a rating system where the influences of management are independent of (or at least distinguishable from) other factors such as precipitation. In fact, precipitation pattern has been specified as an explicit agent of transition in the state-and-transition model (Westoby et al. 1989), and precipitation is considered a primary driving force in the abundance of vegetation in arid ecosystems (Ellis and Swift 1988). Therefore, our analysis of the role of precipitation addresses fundamental issues concerning the utility of the rangeland condition metric in identifying the agents responsible for different resource conditions.

Our objective is to inform the debate on the role of tenure systems in determining rangeland conditions by describing for 480 ranches in Sonora, Mexico the relationship among rangeland condition scores measured from 1973 to 1993, tenure system, management practices and bio-physical variables.

Methods

Study Area

Since the Mexican Revolution of 1910, the term *ejido* has been applied to all types of land distributed to groups of 20 or more persons (Coronado-Quintana 1998). *Ejido* is a type of land tenure where property rights are assigned to the group, each group member enjoys the right to use a specific resource, and that use is regulated by rules imposed by the property right holders and government authorities. With amendments in 1991 to article 27 of the Mexican Constitution that permitted alienation of property rights, the government intended to eliminate paternalism and increase flexibility in order to improve the ability of the *ejido* to meet changing economic conditions (Solidaridad 1992).

In 1988, there were 95.1 million hectares of *ejidal* land in Mexico (49 percent of the land area), which was distributed among 28,058 *ejidos* and agrarian communities and 3,070,906 *ejidatarios* (Instituto Nacional de Estadística, Geografía y Informática 1990). The majority of these lands are rangelands

(54.2 million ha) dedicated to the production of livestock. Located in northwestern Mexico, the state of Sonora covers 18.5 million ha, with nearly 91% of the land area used for livestock production. *Ejidal* land covers 5.2 million ha (28% of the area) and is distributed among 889 communal *ejidos*, of which 594 are engaged in some kind of livestock production (Instituto Nacional de Estadística, Geografía y Informática 1994). These livestock producing *ejidos* accounted for nearly 12% of the 5,188 properties producing livestock in Sonora (Instituto Nacional de Estadística, Geografía y Informática 1997).

Data

The data for this study was obtained from assessment of range condition and recommended carrying capacity for individual ranch units completed by the Comisión Técnica para la Determinación de Coeficientes de Agostadero (COTECOCA) from 1973 to 1993. The full data set described 739 ranches, including *ejidos*, Indian communities, and private properties. However, due to missing variables for some ranches in the data set, our analysis used only the 480 ranches without missing data.

For the purpose of this study, a ranch unit is a piece of land managed by an individual (normally private properties) or a group of individuals (*ejidos* or Indian communities) in a contiguous geographic area. If more than 1 property was managed by a single individual or *ejido*, the 2 or more properties were treated as separate ranches if they were located in different areas of Sonora.

A total of 107 *ejido* ranches were included in the sample of 480 ranches. These *ejidos* represent 26% of the ranches and 58% of the land in the 480 ranch sample. These proportions are about twice as high as the representation of *ejidos* ranches and land area in Sonora, as described above. However, given the total sample size, this over-representation should not adversely influence our analysis of the relationships among range condition, tenure system, management practices, and bio-physical resources for these ranches.

In our analysis, we used COTECOCA measurements of range condition, land tenure, management characteristics (human density, livestock stocking rate, ranch size, and infrastructure condition), and bio-physical characteristics (rangeland site quality and precipitation).

Range Condition

The COTECOCA used a modified climax plant community approach (Dyksterhuis 1949) to estimate range condition, where

plant cover (basal cover for grasses and herbs and foliar cover for shrubs and trees) was measured as the vegetation parameter. Most COTECOCA studies used the Canfield Line Intercept or Step Point methods to estimate plant cover (Evans and Love 1957). As modified by COTECOCA, the condition rating was biased toward plants contributing to livestock diets and production, and therefore, if a rating was excellent, it did not necessarily equate to a climax composition. Furthermore, range condition rating was lowered if there were signs of accelerated erosion.

The COTECOCA studies determined range condition for each range site (ecological site) on each ranch unit. Four range condition categories were used to organize the condition ratings based on the proportion of plant cover measured for excellent species: greater than 75% cover contributed by excellent species equated to excellent condition, 51 to 75% equated to good condition, 25 to 50% equated to regular condition, and less than 25% equated to poor condition (Comisión Técnica para la Determinación de Coeficientes de Agostadero 1974).

We developed a composite range condition score for each ranch unit by calculating a weighted average according to the proportion of the property covered by each range site,

$$\frac{\sum(\text{condition score}_i \times \text{hectares}_i)}{\text{total ranch hectares}} \quad (1)$$

where condition scores were 1, 2, 3, and 4 for poor, regular, good and excellent condition, respectively, and the subscript *i* designates the area of each range site found on the ranch unit. A ranch unit with a weighted average of 1 through 1.49 was classified in poor condition, a 1.5 through 2.49 weighted average was classified in regular condition, a 2.5 through 3.49 weighted average was classified in good condition, and a weighted average greater than 3.49 was classified in excellent condition. Because only 4 ranch units were in excellent condition, they were grouped with those found to be in good condition.

Land Tenure

Land tenure was represented as a dummy variable with a value of 0 if the ranch was *ejido* or Indian community property and a value of 1 if the ranch was private property. In the original sample, *ejidos* and Indian communities were described as separate categories, but because the Indian community properties were few and were managed in the same manner as *ejidos*, they were grouped as one type of property called *ejido*.

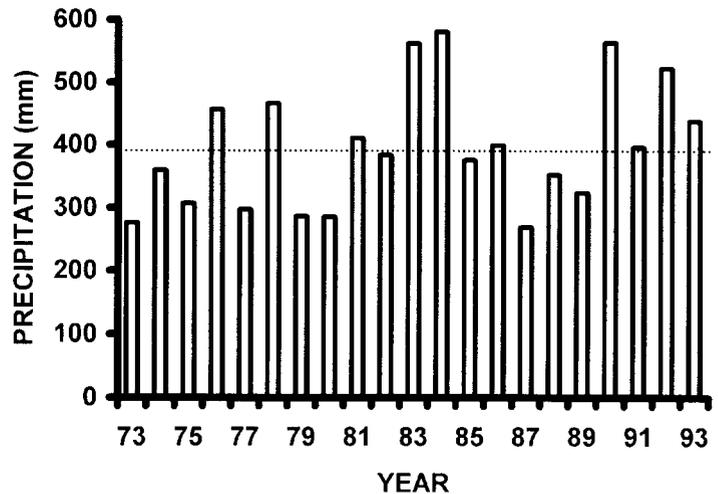


Fig. 1. Annual (bars) and average (dotted line) precipitation for Sonora, Mexico, 1973–1993.

Management Characteristics

Human density is the number of hectares per property right holder (hectares/person). A property right holder was considered a person who had a legal right to use the land. Normally, and according to the law, *ejidos* have a minimum of 20 members. Most of the private properties have just 1 legal owner.

The COTECOCA estimated the livestock stocking rate as the normal number of animal units per hectare grazing on the ranch unit during an entire calendar year, based on forage samples and complimentary information from ranchers and previous ranch studies (Comisión Técnica para la Determinación de Coeficientes de Agostadero 1974).

Ranch unit size was measured in hectares; excluding irrigated and cultivated pastures, cropping areas, and places considered unsuitable for livestock grazing. In the establishment of ranch size for *ejidos*, we ignored the presence of any internal subdivisions that *ejidatarios* may have made to divide a pasture.

The COTECOCA personnel used 3 categories (poor, regular, and good) to describe the condition of livestock management infrastructure (e.g. fences, corals, and watering places) for the entire ranch unit. We coded the condition classes as 1 = poor, 2 = regular, and 3 = good.

Bio-physical Characteristics

The COTECOCA applied the range site concept (Anderson and Fly 1955) to distinguish 4 classes of rangeland quality based on the potential for biomass production. These classes recognize that the productivity potential of a range site is a function of soil, slope, climate and potential vegetation.

Similar to the composite range condition score, we also calculated a composite rangeland site quality score for each ranch unit by calculating a weighted average according to the proportion of the property covered by each of 4 site quality classes established by COTECOCA. Site quality scores were 1, 2, 3, and 4 for poor, regular, good and excellent quality, respectively. A ranch unit with a weighted average of 1 through 1.49 was classified as poor quality, a 1.5 through 2.49 weighted average was classified as regular quality, a 2.5 through 3.49 weighted average was classified as good quality, and a weighted average greater than 3.49 was classified as excellent quality. Because only 24 ranch units were in the excellent quality category, they were grouped with those found to be in the good quality category.

The amount for precipitation associated with each ranch unit was based on the average precipitation in Sonora during the year that the range condition survey was completed by COTECOCA (Fig. 1). The weighted average precipitation value was estimated by Comisión Nacional del Agua for the State of Sonora (1996), where precipitation readings are obtained from different points in 7 watersheds, and then the average of the records from the 7 watersheds represents the precipitation for the State in a given year.

Data Analysis

We used a combination of simple, univariate chi-square contingency analyses and more complex, multivariate ordered logistic regression analyses to assess the relationship among the variables. The chi-square analysis provides a clear presentation of the actual values of the parameters

and is easily understood, but this approach does not assess the strength of relationships between more than 2 variables at a time. The logistic regression describes the relative strengths of the relationship of all the independent variables with the dependent variable simultaneously, but it is difficult to visualize the distribution of the actual values of these variables because of the logistic transformation. Finally, chi-square analysis was used to express the actual values for some variables found to have significant relationships in the multivariate analyses.

The univariate approach used the chi-square method (Kohler 1988) to evaluate differences in the distribution of range condition, management variables, and bio-physical variables between land tenure systems and among range condition classes. The multivariate approach used the ordered logistic regression method (Hosmer and Lemeshow 1989, Greene 1993) to compare the relative importance of independent variables in distinguishing among classes of land tenure system (*ejido* and private) and among ordered classes of range condition (poor, regular, and good).

To distinguish between *ejido* and private ranches, we used an analysis where the dependent variables were *ejido* and private ranches and the independent variables were the categorical variables of infrastructure condition and range quality, and the continuous variables of range condition, hectares per person, hectares per animal unit, and precipitation. Ranch size was not included in this analysis because it was greatly different between tenure types and thus other independent variables would not be needed to differentiate between *ejido* and private ranches.

To distinguish among the ordered categories of poor, regular and good range condition, we performed 3 separate regression analyses. The first analysis used all ranches and all independent variables were included (categorical variables were tenure system, infrastructure condition, and range quality, and the continuous variables were ranch size, hectares per person, hectares per animal unit and precipitation). The second and third regression analyses were restricted to ranches in each tenure category: *ejido* only or private only. The comparison between these 2 restricted analyses provides a simple assessment of the interaction between tenure system and the other independent variables.

Ordered logistic regression is a better framework to analyze ordinal dependent variables like land tenure and range condition than using linear regression. With ordinal dependent variables, it is unlikely that the linear regression assumption of normally distributed errors will be met,

and the coefficients can not be interpreted as probabilities for classifying cases into the ordinal categories. In contrast, the ordered logistic regression method calculates coefficients that can be interpreted as the odds ratio that there will be a change in the dependent variable category with a change in the independent variable. For example, if we find a negative coefficient for the independent variable of ranch size in relation to land tenure (0 = *ejido* and 1 = private), then we interpret this to mean that it is less likely that a ranch will be privately owned as ranch size increases. If the coefficient is positive, then it is more likely

that the ranch will be private as ranch size increases. If the coefficient is 0, then we expect no relationship between tenure and ranch size (Hosmer and Lemeshow 1989, Greene 1993, Menard 1995).

In all these analyses, we used a $p < 0.05$ criteria to reject the null hypotheses.

Results

The distribution of ranch units in the 3 range condition categories was different between *ejido* and private property types,

Table 1. Distribution of management characteristics (human density, stocking rate, ranch size, and infrastructure condition) and bio-physical characteristics (range site quality and precipitation) within categories of property type and range condition rating. Probabilities (p values) represent chi-square probabilities that there is no difference in the distribution of the proportions between property types or among range condition classes.

	Property Type (percent of ranches)		Range Condition Rating (percent of ranches)		
	<i>Ejido</i> (n=107)	Private (n=373)	Poor (n=153)	Regular (n=249)	Good (n=78)
Range Condition	----- (%) -----				
<i>Ejido</i>			16.8	78.5	4.7
Private			36.2	44.2	19.6
			p < 0.001		
Human Density (ha/person)					
≤ 100	66.4	1.6	10.5	22.5	6.4
> 100 to ≤ 500	29.9	13.7	22.9	15.3	12.8
> 500 to ≤ 1000	3.7	27.1	22.2	20.1	26.9
> 1000 to ≤ 2000	0.0	25.5	22.2	17.7	20.5
> 2000 to ≤ 3000	0.0	15.0	9.2	11.2	17.9
> 3000	0.0	17.2	12.4	13.3	15.4
	p < 0.001		p = 0.006		
Stocking Rate (ha/AU)					
< 6	29.9	16.6	22.8	20.5	10.3
> 6 to ≤ 12	43.9	52.8	51.0	45.8	66.7
> 12 to ≤ 18	15.0	17.7	13.7	20.9	11.5
> 18	11.2	12.9	12.4	12.9	11.5
	p < 0.001		p = 0.03		
Ranch Size (ha)					
< 1000	7.5	41.8	44.4	26.1	39.7
> 1000 to ≤ 2000	10.3	25.7	24.8	20.5	23.1
> 2000 to ≤ 3000	13.1	15.3	11.1	15.3	20.5
> 3000 to ≤ 4000	13.1	7.5	5.9	12.0	3.8
> 4000	56.1	9.7	13.7	26.1	12.8
	p < 0.001		p = 0.001		
Infrastructure Condition					
Poor	18.7	7.2	13.7	8.4	6.4
Regular	62.6	48.8	57.5	54.2	33.3
Good	18.7	44.0	28.8	37.4	60.3
	p < 0.001		p = 0.001		
Range Site Quality					
Poor	14.0	19.3	30.1	14.1	7.7
Regular	55.1	44.5	29.4	54.2	57.7
Good	28.0	30.6	33.3	28.1	29.5
Excellent	2.8	5.6	7.2	3.6	5.1
	p < 0.19		p = 0.001		
Precipitation (mm)					
< 287	17.8	31.4	39.2	20.5	32.1
287– 376	7.5	28.1	40.5	16.5	12.8
377– 409	22.4	22.0	12.4	27.7	23.0
> 409	52.3	18.5	7.9	35.3	32.1
	p < 0.001		p = 0.001		

Table 2. Coefficients, z-scores, and probabilities (p values) for the logistic regression analysis to distinguish *ejido* and private Sonoran ranches.

Independent Variable	Coefficient	z-score	p > z
Range Condition	-0.25	-0.62	0.54
Human Density	0.01	7.38	< 0.01
Livestock Stocking Rate	1.47	2.69	< 0.01
Poor Infrastructure	-0.44	0.53	0.59
Regular Infrastructure	0.37	0.65	0.52
Poor Rangeland Quality	-0.11	-0.15	0.88
Regular Rangeland Quality	-0.78	-1.41	0.16
Precipitation	-0.01	-4.23	< 0.01

revealing a greater proportion of private ranch units with good and poor condition ratings than *ejido* ranch units (Table 1).

The distribution of ranch units in the 2 property type categories was different for all the management and bio-physical variables except range site quality (Table 1), revealing respectively, a) a higher proportion of *ejido* ranches with the fewest hectares per person, b) a higher proportion of *ejido* ranches with the fewest hectares per animal unit (i.e. higher stocking rate), c) a higher proportion of *ejido* ranches in the largest ranch size category, d) a higher proportion of private ranches in the good infrastructure category, and e) a greater proportion of *ejido* ranches in the highest precipitation category.

The distribution of ranch units in the 3 range condition categories was different for all management and bio-physical variables (Table 1), revealing respectively a) a higher proportion of regular condition ranches with the fewest hectares person, b) a lower proportion of good condition ranches with the fewest hectares per animal unit (i.e. higher stocking rate), c) a lower proportion of regular condition ranches in the smallest sizes classes, d) a greater proportion of good condition ranches with good infrastructure, e) a lower proportion of poor range condition ranches in the highest site quality category, and f) a lower proportion of poor condition ranches received the highest amount of precipitation.

Only human density, livestock stocking rate, and precipitation were significantly related to land tenure system (*ejido* or private) in the logistic regression analysis (Table 2). The results accounted for a large portion of the variability between tenure system types (pseudo $r^2 = 0.77$). The direction (+ or -) of the coefficients show that hectares per human and hectares per animal unit were greater for private ranches, but precipitation during the assessment was greater for *ejido* ranches.

Only infrastructure condition, range quality and precipitation were significantly related to range condition in the analy-

sis that included all ranches (Table 3). These independent variables accounted for a small, but significant portion of the variability among range condition categories (pseudo $r^2 = 0.11$). The direction (+ or -) of the coefficients show that a) ranches with regular and good range condition ratings were more likely to have received higher precipitation amounts, b) ranches in good condition were less likely to have poor than regular or good condition infrastructure, and c) ranches in good condition were more likely to have regular rangeland quality. For *ejido* ranches only, the distinction among ranches in the 3 categories of range condition was slightly better than the analysis with all ranches (pseudo $r^2 = 0.17$), and only infrastructure condition was significantly related to

range condition; where the proportion of ranches in poor condition was greater for poor infrastructure than good or regular infrastructure (Table 3). In the analysis for private ranches only, the distinction among ranches in the 3 categories of range condition was nearly the same as the analysis with all ranches (pseudo $r^2 = 0.13$), and only infrastructure condition and precipitation were significantly related to range condition; where the proportion of ranches in poor condition was greater for poor infrastructure than good or regular infrastructure, and the proportion of ranches in poor condition was greater in years with less precipitation (Table 3).

The range condition distributions were different between *ejido* and private ranches for 3 of the 4 precipitation categories; they were not different in the 377–409 mm category (Fig. 2). The proportion of private ranches in poor condition was greater than *ejido* ranches in the drier years of assessment, the proportion of private ranches in good condition was greater than *ejido* ranches in the wetter years of assessment, and the proportion of *ejido* ranches in regular condition was greater than private ranches in nearly all types of rainfall conditions.

Table 3. Coefficients, z-scores, and probabilities (p values) for the ordered logistic regression analyses for all ranches, *ejido* ranches only, and private ranches only to distinguish Sonoran ranches in poor, regular, and good range condition.

Independent Variable	Coefficient	z-score	p > z
<u>All Ranches</u>			
Tenure System	-0.16	-0.52	0.60
Human Density	< 0.01	1.21	0.23
Livestock Stocking Rate	0.03	0.07	0.95
Ranch Size	> -0.01	-1.95	0.05
Poor Infrastructure	-1.35	-3.88	<0.01
Regular Infrastructure	-1.03	-4.88	<0.01
Poor Rangeland Quality	-0.52	-1.92	0.06
Regular Rangeland Quality	0.49	2.36	0.02
Precipitation	< 0.01	6.50	<0.01
<u>Ejido Ranches Only</u>			
Human Density	> -0.01	-0.51	0.61
Livestock Stocking Rate	-0.37	-0.47	0.64
Ranch Size	> -0.01	-1.76	0.08
Poor Infrastructure	-2.37	-2.54	0.01
Regular Infrastructure	-0.08	-0.11	0.92
Poor Rangeland Quality	0.31	0.38	0.70
Regular Rangeland Quality	0.85	1.41	0.16
Precipitation	< 0.01	1.87	0.06
<u>Private Ranches Only</u>			
Human Density	< 0.01	1.34	0.18
Livestock Stocking Rate	0.57	0.92	0.36
Ranch Size	> -0.01	-1.31	0.19
Poor Infrastructure	-0.94	-2.25	0.03
Regular Infrastructure	-1.20	-5.24	< 0.01
Poor Rangeland Quality	-0.59	-1.93	0.05
Regular Rangeland Quality	0.43	1.86	0.06
Precipitation	< 0.01	6.54	< 0.01

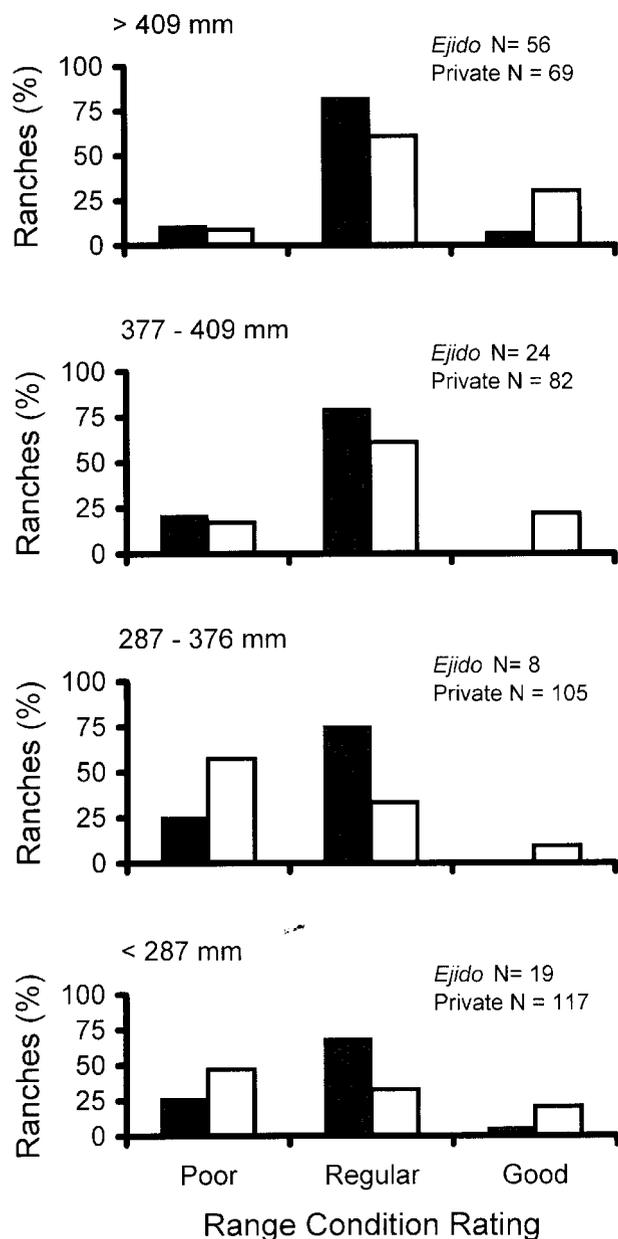


Fig. 2. Comparisons of *ejido* (solid bar) and private (open bar) ranch distributions of range conditions classes for four levels of precipitation during the year of range condition assessment. Distributions between *ejido* and private ranches are different ($p < 0.05$) for all levels of precipitation except 287–376mm ($p = 0.06$).

Discussion

Management, Tenure System and Range Condition

For Sonoran ranches assessed by COTECOCA between 1973 to 1993, we found different levels of management between the tenure systems, but there was little evidence to support the hypothesis that these differences in management were associated with different range conditions between *ejido* and private tenure systems. All management variables were different

between tenure systems when we used the univariate chi-square analysis, but human density and livestock stocking rate were the only management variables significantly related to tenure system in the multivariate ordered logistic regression (note that ranch size was not included in the multivariate analysis because it was dramatically different between tenure systems). We found different distributions of range condition between tenure systems using the univariate chi-square analysis, but tenure was not significantly related to range condition in the logistic regression

analysis for all ranches. Infrastructure condition was the only management variable significantly related to range condition in the analysis of all ranches. These results support an interpretation that the management practice of developing infrastructure to improve range conditions transcends these tenure systems. However, one must be cautious, and not place too much emphasis on these multivariate results distinguishing range condition categories because they accounted for only a small, but significant, amount of the variation in range condition.

The differences in ranch size and human density between *ejido* and private ranches are not surprising because they are inherent in the nature of these systems. Even though the univariate analysis indicated a non-uniform relationship between ranch size and range condition categories, there was no general trend where range condition increased with ranch size, unlike previous findings of a positive relationship between size and condition (e.g. Passmore and Brown 1992, Young 1985). Ranch size was not significantly related to range condition in the logistic regression analysis. The different results between the univariate and multivariate methods may arise from a) size being organized as a continuous and categorical variable in the multivariate and univariate analyses, respectively, and b) less consistency in the relationship between size and condition than for the precipitation and infrastructure variables that were significantly related to range condition.

Generally, the more dense stocking of livestock on *ejido* than private ranches follows the pattern reported by LaBaume and Dahl (1984) and Yates (1981) in Mexico, and by Ward et al. (1998) in Namibia. However, the differences in stocking rate are not as large for these ranches surveyed in 1973-1993 in Sonora, compared to those in 1960-1970 for other parts of Mexico (LaBaume and Dahl 1984, Yates 1981). Although stocking rate varied among range condition classes in the univariate analysis, it was not included in the multivariate analyses that distinguished the 3 range condition classes. The absence of a significant relationship between range condition and stocking rate in these multivariate analyses is contrary to most expectations (e.g. Hart et al. 1993), but is consistent with the comparison of range condition between communal and private land in Namibia (Ward et al. 1998). Again, these differences between univariate and multivariate results may arise from the same causes as discussed for ranch size.

The absence of a significant relationship between infrastructure condition and tenure systems in the multivariate analyses is different than the univariate results illustrating a generally better condition of infrastructure on private than *ejido* ranches. The univariate results are consistent with the differences noted in Mexico by Yates (1981), but the differences between univariate and multivariate results may arise from less consistency in the relationship between infrastructure condition and tenure system than for precipitation, stocking rate, and human density which are significantly related to tenure type. In contrast, infrastructure condition was positively related to range condition in all univariate and multivariate analyses. The generally good condition of infrastructure on these Sonoran ranches is in sharp contrast to Yates' (1981) assessment in the 1970s when two-thirds of all ranches had poor infrastructure conditions.

Bio-physical Characteristics, Tenure System, and Range Condition

We found no evidence for different levels of rangeland quality between the land tenure systems with either the univariate or multivariate analyses, but there was evidence to support the hypothesis that the relationship between rangeland quality and range condition transcends tenure system. Rangeland quality was significantly related to range condition in the logistic regression analysis for all ranches but it was not significantly related to range condition in the separate analyses for *ejido* and private ranches. We found evidence that there was a difference in the precipitation received during the year of assessment between the tenure systems, and there was evidence to support the hypothesis that the difference in precipitation between tenure systems was associated with different range conditions between *ejido* and private ranches. The detailed univariate chi-square analyses describing the relationship between tenure system and range condition at 4 levels of precipitation revealed a stronger relationship between precipitation and range conditions for private ranches than *ejido* ranches. These results support an interpretation that the relationship between range conditions and rangeland quality transcends these tenure systems, but the relationship between precipitation and range condition does not transcend these tenure systems. However, one must be cautious and not place too much emphasis on these multivariate results distinguishing range condition categories because they accounted for

a small, but significant, amount of the variation in range condition.

The positive relationship between rangeland quality and range condition was not consistent with expectations (e.g. Launchbaugh et al. 1990), also, the absence of a tenure related difference in range site is different from patterns in the United States where better sites are often under private ownership (e.g. Starrs 1998).

The relationship between precipitation and rangeland vegetation conditions is inherent in models of vegetation dynamics where transitions from one state of vegetation to another can be more influenced by precipitation amounts and timing than by livestock management (Westoby et al. 1989), and similar patterns can be seen when examining vegetation production in arid regions (Ellis and Swift 1988). A finding that is unique to our study is the greater sensitivity of range condition on private ranches to variation in precipitation than was found on *ejido* ranches. Our data does not permit an examination of the mechanisms for this intriguing relationship.

Implications

Our results identify 2 critical issues in management and evaluation of rangelands that apply to all tenure systems: a) encouraging investment in and proper use of infrastructure, and b) developing range condition assessment strategies that are more sensitive to management and less sensitive to precipitation.

The strong relationship between infrastructure condition and range condition, that transcended these 2 tenure systems supports Wilson and Thompson's (1993) proposition that communal properties are as likely to benefit from investment in infrastructure as private ranches. Furthermore, the apparently higher condition of infrastructure in this Sonora sample compared to earlier assessments in Mexico, suggests that *ejido* ranches have been as likely to invest in infrastructure as private ranches. Finally, these results are consistent with findings suggesting that investment in management transcends the influence of tenure on range condition (Loring and Workman 1987).

The current renaissance in range condition assessment (e.g. Task Force on Unity in Concepts and Terminology 1995, National Research Council 1994, Natural Resource Conservation Service 1997) has focused on parameters and metrics to distinguish management influences from precipitation or other bio-physical influences, and to represent a variety of resource values in addition to livestock forage. While

the COTECOCA range condition method can be criticized for adherence to Clementian-based metrics, a more critical area of improvement would be the institution of regular and repeated assessments that would document the trend of conditions. The current COTECOCA data precludes an estimate of the trend in conditions because there was only a one-time assessment for each ranch, and not all ranches were assessed in the same year. The availability of trend information for these Sonoran ranches would have permitted comparisons of ranch performance across the inter-annual variations in weather, rather than the less revealing comparison among ranches assessed in only 1 year. We encourage the measurement of range condition trend on these rangelands to assist in the evaluation of the current privatization opportunity, and to provide criteria for the qualification and assessment of capital assistance programs.

Literature Cited

- Anderson, K.L. and C.L. Fly. 1955. Vegetation-soil relationships in Flint Hills bluestem pastures. *J. Range Manage.* 8:163-169.
- Baden, J. and R. Stroup. 1977. Property rights, environmental quality and the management of national forests. p. 229-240. *In:* G. Hardin and J. Baden (eds.). *Managing the commons*, W.H. Freeman and Company, San Francisco, Calif.
- Bails, D.G. and L.C. Peppers. 1993. *Business fluctuations: forecasting techniques and applications*. 2nd ed. Prentice Hall, Englewood Cliffs, N.J.
- Comisión Nacional del Agua. 1996. Resúmen de precipitaciones del Estado de Sonora. Pamphlet, unpublished data.
- Comisión Técnica para la Determinación de Coeficientes de Agostadero. 1974. *Coeficientes de Agostadero de la República Mexicana: Estado de Sonora*. Secretaría de Agricultura y Ganadería.
- Coronado-Quintana, J.A. 1998. Relationship between range condition and the land tenure system in Sonora. Ph.D. Diss., Univ. of Arizona, Tucson, Ariz.
- Dyksterhuis, E.J. 1949. Condition and management of rangeland based on quantitative ecology. *J. Range Manage.* 2:104-115.
- Ellis, J.E. and D.M. Swift. 1988. Stability of African pastoral ecosystems: alternate paradigms and implications for development. *J. Range Manage.* 41:450-459.
- Evans, R. A., and R.M. Love. 1957. The step-point method of sampling: A practical tool in range research. *J. Range Manage.* 10:208-212.
- Feeny, D., F. Berkes, B.J. McCay, and J.M. Acheson. 1990. The tragedy of the common: twenty-two years later. *Human Ecol.* 18:1-19.

- Greene, W. H. 1993.** *Econometric Analysis*. 2nd Ed. Macmillan Publishing Company, New York, N.Y.
- Hardin, G. 1968.** The tragedy of the commons. *Sci.* 162:1243–48.
- Hart, R. H., S. Clapp, and P. S. Test. 1993.** Grazing strategies, stocking rates, and frequency and intensity of grazing on western wheatgrass and blue grama. *J. Range Manage.* 46:122–126.
- Hosmer, D. W. and S. Lemeshow. 1989.** *Applied Logistic Regression*. John Wiley & Sons, New York, N.Y.
- Humphrey, R.R. 1949.** Field comments on the range condition method of forage survey. *J. Range Manage.* 2:1–10.
- Instituto Nacional de Estadística, Geografía y Informática. 1990.** *Estadísticas Históricas de México*, Tomo 1. INEGI, Aguascalientes, Mexico.
- Instituto Nacional de Estadística, Geografía y Informática. 1994.** *Censo Ejidal: Sonora*. INEGI, Aguascalientes, Mexico.
- Instituto Nacional de Estadística, Geografía y Informática. 1997.** *Anuario Estadístico del Estado de Sonora*. INEGI, Aguascalientes, Mexico.
- Kohler, H. 1988.** *Statistics for business and economics*. 2ed. Scott, Foreman and Company, Glenview, Ill.
- LaBaume, J.T. and B.E. Dahl. 1984.** Communal grazing: the case of the Mexican *ejido*. *J. Soil and Water Conserv.* 41:24–27.
- Launchbaugh, K.L., J.W. Stuth, and J.W. Holloway. 1990.** Influence of range site on diet and nutrient intake of cattle. *J. Range Manage.* 43:109–115.
- Loring, M.W. and J.P. Workman. 1987.** The relationship between land ownership and range condition in Rich County, Utah. *J. Range Manage.* 40:290–293.
- Menard, S. 1995.** *Applied logistic regression analysis*. Sage Univ. Series of Quantitative Appl. in the Social Sciences. Sage Press, Thousand Oaks, Calif.
- National Research Council. 1994.** *Rangeland health: new methods to classify, inventory, and monitor rangelands*. Nat. Acad. Press, Washington, D.C.
- Natural Resource Conservation Service. 1997.** *Range and pasture management handbook*. U.S. Gov. Printing Office.
- Ostrom, E., J. Burger, C.B. Field, R.B. Norgaard, and D. Policansky. 1999.** Revisiting the commons: local lessons, global challenges. *Sci.* 284:278–282.
- Passmore, J. G. I. and C. G. Brown. 1992.** Property size and rangeland degradation in the Queensland mulga rangelands. *Rangeland J.* 14(1):9–25.
- Smith, J. 1898.** Grazing problems in the Southwest and how to meet them. *USDA Bull.* 16.
- Solidaridad. 1992.** *Nueva Legislación Agraria: Artículo 27 Constitucional, Ley Agraria, Ley Orgánica de los Tribunales Agrarios*. Gaceta de Solidaridad, Mexico, D.F.
- Starrs, P.F. 1998.** Let the cowboy ride: cattle ranching in the American west. Johns Hopkins Univ. Press, Baltimore, Md.
- Task Force on Unity in Concepts and Terminology. 1995.** New concepts for assessment of rangeland condition. *J. Range Manage.* 48:271–282.
- Vallentine, J.F. 1990.** *Grazing management*. Academic Press, New York, N.Y.
- Ward, D., B.T. Ngairorue, J. Kathena, R. Samuels, and Y. Ofran. 1998.** Land degradation is not a necessary outcome of communal pastoralism in arid Namibia. *J. Arid Environ.* 40:357–371.
- Westoby, M., B. Walker and I. Noy Meir. 1989.** Opportunistic management for rangelands not at equilibrium. *J. Range Manage.* 42:266–74.
- Wilson, P.N. and G.D. Thompson. 1993.** Common property and uncertainty: compensating coalitions by Mexico's pastoral ejidatarios. *Econ. Development and Cultural Change* 41(2): 299–318.
- Worster, D. 1992.** *Under western skies: nature and history in the American west*. Oxford University Press, New York, N.Y.
- Yates, L.P. 1981.** *Mexico's agricultural dilemma*. University of Arizona Press, Tucson, Ariz.
- Young, M.D. 1985.** The influence of farm size on vegetation condition in an arid area. *J. Environ. Manage.* 21:193–203.

Rotationally stocked beef cattle responses to daily and weekly residence

N. S. BOYD, T. ASTATKIE, A. H. FREDEEN, AND R. C. MARTIN

The authors are an agronomy graduate student in the Department of Plant Science, a statistician and Associate Professor in the Department of Mathematics, Physics and Humanities, a ruminant nutritionist and Professor in the Department of Animal Science and an agronomist and associate professor in the Department of Plant Science at the Nova Scotia Agricultural College, Truro, N.S., Canada B2N 5E3.

Abstract

Rotational stocking is a component of intensive pasture management and involves the systematic movement of animals among paddocks to optimize harvest of digestible nutrients. The optimum period of residence time for beef cattle in a paddock has not been researched in Atlantic Canada. A series of experiments were conducted at the Nova Scotia Agricultural College during the 1994, 1995, and 1996 grazing seasons to determine if short residence times (1 day) or longer residence times (6 or 7 days) encouraged higher average daily gains (ADG) in beef cattle. In 1994 and 1995, Hereford steers were used, and in 1996, Hereford heifers were used to compare the effects of daily and weekly residence times. In the mid to late season of 1994, a preliminary study with fewer replicates than in 1995 and 1996 indicated that the steers with a daily and weekly residence time gained 1.18 and 1.09 kg animal⁻¹ day⁻¹, respectively. Based on these results the project was expanded with the hypothesis that daily residence times result in higher average daily gains compared with weekly residence times. In both 1995 and 1996, cattle ADG for the first part of the season was higher with weekly residence times and similar near mid-season. Near the end of the grazing season the trend reversed with the daily residence time producing a higher cattle ADG. The results of this study indicate that animal performance could be maximized by long rotation cycles during periods of rapid forage growth and short rotation cycles during periods of slow forage growth. In all years, animals were finished on pasture with no visible yellow fat.

Key Words: average daily gain, period of stay, repeated measures, rotational grazing, white clover, yellow fat

Rotational stocking involves strategical and sequential movement of livestock through paddocks to optimize use of the available forage. Some claim an increase in stocking rate without compromising weight gains of individual animals. Bertelson et al. (1993) reported a 42% increase in stocking rate without decreasing animal gains on alfalfa (*Medicago sativa* L.), fescue (*Festuca arundinacea* Schreb.), and orchard grass (*Dactylis glomerata* L.) pastures. Increased individual animal gains with increased stocking rate may be due to increased forage production or quality. While

Resumen

El apacentamiento rotacional es un componente del manejo intensivo de praderas que implica el movimiento sistemático de los animales entre los potreros para optimizar la cosecha de nutrientes digestibles. El periodo óptimo de residencia del ganado en el potrero no ha sido estudiado en la región atlántica de Canadá. Durante la estación de apacentamiento de los años 1994, 1995 y 1996 se condujo una serie de experimentos en la Universidad Agrícola de Nueva Escocia con el objetivo de determinar si tiempos cortos de residencia (1 día) o tiempos largos (6 o 7 días) fomentan mayores ganancias diarias de peso (GDP) en ganado de carne. En 1994 y 1995 se utilizaron novillos Hereford y en 1996 se utilizaron vaquillas de esta misma raza, estos animales se utilizaron para comparar los efectos de los tiempos de residencia diaria y semanal. Un estudio preliminar con menos repeticiones que los estudios de 1995 y 1996 y conducido de mediados a fines de la estación de 1994 indicó que los novillos con tiempos de residencia diaria y semanal ganaron 1.18 y 1.09 kg animal⁻¹ día⁻¹ respectivamente. Basados en estos resultados el proyecto se extendió con la hipótesis de que tiempos de residencia de un día resultan en mayores ganancias diarias de peso que los tiempos de residencia de una semana. En 1995 y 1996 la GDP durante la primer parte de la estación de apacentamiento fue mayor con los tiempos de residencia semanales e igual a mediados de la estación. Cerca del final de la estación de apacentamiento la tendencia se revertió y los tiempos de residencia diarios produjeron las mayores GDP del ganado. Los resultados de este estudio indican que el comportamiento productivo del animal pudiera ser maximizado mediante ciclos de rotación largos durante la etapa de crecimiento rápido del forraje y ciclos de rotación cortos durante los periodos de crecimiento lento del forraje. En todos los años los animales fueron finalizados en la pradera sin la acumulación visible de grasa amarilla.

some authors have reported no increase in forage quality with rotational grazing (Walker et al. 1989, Popp et al. 1997), Heitschmidt et al. (1987) reported that rotational stocking raised crude protein content and reduced litter in the sward. They attributed the difference to less mature plants, as a result of grazing pressure.

Little work has been done to determine the optimum period of time for beef cattle to remain in a given paddock. Some research suggests the longer the animals remain in a paddock the lower the forage quality with some plant species (Morrow et al. 1991). Bertelsen et al. (1993) found no significant difference in sward quality with a 3 or 6 day residence time in a mixed pasture.

Research was funded in part by Nova Scotia Department of Agriculture and Marketing Research Grants. The authors thank Ignatius Augustin and Gary Wallace for technical assistance and practical advice.

Manuscript accepted 24 Apr. 2000.

However, the paddocks where the animals remained for 3 days tended to have more available forage before grazing than the paddocks where the animals remained for 6 days.

The purpose of this research was to examine the effects of daily and weekly residence times on beef cattle average daily gains (ADG) while holding forage availability as constant as possible by adjusting paddock size according to forage height. Secondary objectives were to determine the presence or absence of yellow fat on the carcasses of cattle, the seasonal forage yield, and the white clover proportion of forage.

Materials and Methods

Study site

The study was conducted from 1994 to 1996 at the Nova Scotia Agricultural College in Truro, Nova Scotia, Canada (45°, 14'N, 63°, 19'W). The pasture was composed mostly of Kentucky bluegrass (*Poa pratensis* L.), meadow fescue (*Festuca pratensis* Huds.), meadow foxtail (*Alopecurus pratensis* L.), and common white clover (*Trifolium repens* L.) grown on a Woodville Sandy loam soil (orthic humo-ferric podzol).

Field design

The experiment was designed to examine the effect of daily versus weekly residence time (every 6 days in 1994 and 1995 and every 7 days in 1996) in a paddock on average daily gain (ADG) and weight of cattle. In 1994, preliminary research was conducted with 6 cattle per treatment and 2 replications of each treatment. In 1995 and 1996, each treatment was replicated 4 times with 4 animals allocated to each treatment, within each replicate.

A 6.4 ha field was divided into 4 strips, 50 m by 320 m, using a high tensile power fence. Within each strip or replicate, each treatment was randomly allocated to one end or the other. The paddocks were formed within the strips with strands of polywire, perpendicular to the high tensile wires forming the experimental unit. Mineral supplement and water was provided within each paddock.

Paddock Rotation

The experiment began on 19 July in 1994, 24 May in 1995, and 28 May in 1996. At the beginning of each season, animals moved daily had a paddock 6m by 50m, and the animals moved weekly had a

paddock 40m by 50m. Before moving cattle to a new paddock, its size was determined according to forage regrowth since the previous grazing cycle, as indicated by forage height. Paddock size was increased if the residual forage was less than 5 cm tall or if the forage in the new paddock was less than 20 cm. The paddock size was reduced if the residual forage exceeded 7 cm or the available forage was more than 25 cm in the new paddock. Every 6 meters, sward heights were measured with a meter stick. Six heights were taken from the daily residence time paddocks and 30 heights taken from the weekly residence time paddocks. All dung patches or excessively tall grass due to urination were avoided to prevent measuring forage that animals typically will not consume.

The 2 treatments were randomly allocated to each end of a strip and the cattle moved through progressive paddocks toward the centre of the strip. Forage heights in the first paddock were monitored consistently while the animals continued to move towards the centre. When the forage in the first paddock was between 20 and 25 cm the animals returned to that paddock initiating a new rotation.

Animal Weights

In 1994, 24 Hereford crossbred steers were weighed on 19 July and 6 October. In 1995, 32 male crossbred Hereford steers were weighed on the 23 and 24 of May and averaged to obtain their initial weight before the start of the pasture project. Animals were weighed 2 weeks prior to the initial weighing in the field while in the barn to determine the effects of the transition from silage to pasture. The herd was sorted into groups of 4 with all groups having similar total group weights. The animals were weighed once monthly during the summer and on 2 consecutive days before slaughter. The same procedure was used in 1996, except that Hereford crossbred heifers were used instead of steers. The grazing season ended when forage regrowth had slowed to the point that forage heights were too low for cattle to graze.

All animals were slaughtered directly off pasture to determine whether they would be down-graded for yellow fat. Many Maritime farmers will feed grain to cattle before slaughter regardless of age, genetics, fatness, or animal gender.

Forage Production

Forage mass was estimated by clipping 0.2 x 0.5 m quadrats to ground level. Forage from a 0.15 m x 0.15 m area within the quadrat was sorted into grass and

white clover to determine composition. Six samples were taken from the daily residence time paddock and 12 from the weekly residence time paddock. All samples were oven dried at 80°C for at least 48 hours to determine forage mass dry matter at time of entrance. In 1995, forage samples were taken from every seventh paddock from the daily residence time treatment. In the weekly residence time paddocks, samples were taken in every second paddock and a total of 8 samples were taken with the small and large quadrats. Samples from the daily and weekly residence time treatments were not taken on the same day, therefore, they could not be compared statistically but general seasonal patterns could be observed. In 1996, forage samples were taken every 2 weeks from daily and weekly residence time treatments just before cattle entered the assigned paddocks.

Statistical methods

Weight response of cattle was measured on 5 occasions between May and September in both years. Forage dry matter was measured on 7 occasions between May and August in 1995 and on 6 occasions in 1996. Treatment effects over the growing season were estimated as repeated measures, using the GLM procedure of SAS (SAS institute Inc., 1990). For comparing the actual weight responses from daily and weekly residence times, measured at the various weighing times, the initial weights (in the barn just before the animals were taken to pasture) were used as covariates. For the average daily gain (ADG) response, to account for the differences in the initial weight of the animals, the analysis was done on weight changes between 5 July and 24 May, 2 August and 5 July, etc. This procedure amounts to using initial weight as a covariate for each measurement time. In all the analyses, the residuals were examined as described by Montgomery (1997) to verify the normal distribution and constant variance assumptions needed for the validity of the statistical tests.

Results

Animal Weights

In 1994 between late July and late September, the average daily gain (ADG) was 1.18 and 1.09 kg gain day⁻¹ for daily and weekly residence times, respectively ($p < 0.05$). Given this result, the project was expanded and continued in 1995 and 1996 to examine whether animals moved

Table 1. Least squares means (LSM) of actual weights (kg) along with P-values for testing the equality of the weights from daily residence times (DRT) and weekly residence times (WRT). These values were obtained by using their initial (barn) weight as a covariate.

Year	Date	LSM-DRT	LSM-WRT	P-value
1995	24 May	290	294	0.341 ¹
	5 July	349	368	0.001
	2 Aug.	370	398	0.002
	29 Aug.	393	423	0.001
	20 Sept.	414	433	0.005
1996	28 May	289	289	0.972
	25 June	334	342	0.003
	23 July	352	364	0.019
	8 Aug.	364	379	0.009
	11 Sept.	386	384	0.866

¹P-values less than 0.05 suggest significant difference at the 5% level.

daily continued to obtain greater gains than the animals moved on a weekly basis.

In 1995 and 1996, the initial weights of the cattle in both treatments were similar (Table 1). In 1995, the animal weights of the cattle with a weekly residence time were significantly higher at each subsequent weighing. These responses were repeated in 1996 except for the final weights that were not significantly different.

In 1995, the animals lost weight during the transition period from feedlot to pasture. The animals moved weekly lost 0.47 kg day⁻¹ compared with a loss of 0.67 kg day⁻¹ for the daily residence time (p = 0.11) (Table 2). Weight gains were significantly higher for the weekly residence time at 2 of the subsequent three weighings. Thereafter the trend reversed with the daily residence time treatment gaining significantly more between August 29 and September 20 (p = 0.003).

From 24 May to 5 July there was a significant weight gain (p = 0.0001) for both treatments with the difference between the magnitude of ADG due to the 2 treatments remaining constant between the 2 time points (p = 0.123) (Table 2). The ADG for both treatments declined (p = 0.0001) between 5 July and 2 August. Between 2 August and 29 August, however, ADG

was similar (p = 0.189) and the treatment effect between time points did not differ (p = 0.418). Between 29 August and 20 September, ADG for the weekly residence time declined (p = 0.005). The ADG for the daily residence time increased slightly, which resulted in a significantly higher ADG for the daily residence time than the weekly residence time (p = 0.003). Over the grazing season, the ADG for the weekly residence time was significantly higher (p = 0.009).

Similar trends were noted in 1996 (Table 3). The ADG dropped between 25 June and 23 July (p = 0.000) for both treatments giving a non-significant treatment x time interaction effect (p = 0.526). Between 23 July and 8 August, ADG did not increase significantly for either treatment (p = 0.093) and the treatment x time interaction effect remained constant (p = 0.991). Between 8 August and 11 September rate of gain of heifers with a daily residence time was over 2.5 times greater than heifers on weekly residence time (p = 0.002). The ADG for both treatments fell significantly (p = 0.006), more abruptly for weekly than for daily residence time (p = 0.03). Unlike the result in 1995, over the grazing season, the ADG of both treatments were equal (p = 0.428).

Without exception, in both years, the carcasses of cattle (64 steers and heifers) from this experiment were not down-graded for the presence of yellow fat (data not shown).

Pasture Production

The available biomass varied between treatment and year. During the first year of the project there was a seasonal average of 3,292 and 3,435 kg ha⁻¹ of dry matter mass before each grazing event in daily and weekly residence time paddocks, respectively. The available dry matter was extremely high because the animals did not begin grazing until late in the season. The seasonal average of available biomass dropped, in 1995, to 1,466 in the daily residence time paddocks and 1,292 kg ha⁻¹ in the weekly residence time paddocks (Table 4). The exceptional increase of forage biomass from 24 May to 29 May can be attributed to the movement of cattle from areas of low biomass to those with higher biomass and to improving seasonal growth. In 1996, there were 1,394 and 1,544 kg ha⁻¹ of dry matter available in daily and weekly residence time paddocks, respectively. Due to an oversight, in 1995 the available dry matter and percent clover in a paddock before grazing were not measured at the same time and hence could not be compared statistically. However, daily residence time paddocks tended to have more forage available within the paddocks than weekly residence time paddocks.

The white clover content of the pasture also declined over the 3 year period (Table 4). In 1994, there was approximately 56.7 and 52.3% clover in daily and weekly residence time paddocks, respectively. The clover content declined in 1995 to a seasonal average of 16.3% in daily residence paddocks and 13.3% in weekly residence paddocks. The decline continued in 1996 with a seasonal average of 12.3% for both treatments. The percent clover was not dif-

Table 2. Summary of the 1995 repeated measures analysis results on average daily gains (ADG) of cattle with a daily residence time (DRT) and a weekly residence time (WRT). A p-value (shown in italics) of less than the level of significance (say, 5%) suggests significant difference.

Source	24 May-barn ¹ (1)	5 July-24 May (2)	2 Aug.-5 July (3)	29 Aug.-2 Aug. (4)	20 Sept.-29 Aug. (5)	Over the season
Treatment	<i>0.113²</i>	<i>0.0001</i>	<i>0.291</i>	<i>0.004</i>	<i>0.003</i>	<i>0.009</i>
ADG-DRT	-0.67	2.12	0.79	0.83	0.90	0.79
ADG-WRT	-0.47	2.64	0.95	1.11	0.45	0.94
Difference between time points		(2)-(1)	(3)-(2)	(4)-(3)	(5)-(4)	
Mean		<i>0.0001³</i>	<i>0.0001</i>	<i>0.189</i>	<i>0.005</i>	
Treatment		<i>0.123⁴</i>	<i>0.123</i>	<i>0.418</i>	<i>0.0001</i>	

¹Cattle were weighed in barn in 1995 prior to being put on pasture

²p-value to compare DRT and WRT within a weighing time

³p-value to compare the effect of consecutive weighing times on ADG across time

⁴p-value to compare the magnitude of the difference between DRT and WRT at consecutive weighing times, i.e. the treatment x time interaction

Table 3. Summary of the 1996 repeated measures analysis results on average daily gains (ADG) of cattle with a daily residence time (DRT) and a weekly residence time (WRT). A p-value (shown in italics) of less than the level of significance (say, 5%) suggests significant difference.

Source	25 June–28 May (1)	23 July.–25 June (2)	8 Aug.–23 July (3)	11 Sept.–8 Aug.20 (4)	Over the season
Treatment	<i>0.052</i> ¹	0.320	0.265	0.002	0.428
ADG–DRT	1.71	0.55	0.80	0.70	0.94
ADG–WRT	2.03	0.75	1.00	0.27	1.01
Difference between time points		(2) – (1)	(3) – (2)	(5) – (4)	
Mean		<i>0.0001</i> ²	<i>0.093</i>	<i>0.006</i>	
Treatment		<i>0.526</i> ³	<i>0.991</i>	<i>0.030</i>	

¹p-value to compare DRT and WRT within a weighing time

²p-value to compare the effect of consecutive weighing times on ADG across time

³p-value to compare the magnitude of the difference between DRT and WRT at consecutive weighing times, i.e. the treatment x time interaction

ferent at any time in the 3 years between the 2 treatments, except on 21 August, 1996. Although the clover content progressively dropped from 1994 to 1996 the authors observed that in 1997 under similar management the clover content of the field had once again increased to original levels.

Discussion

The results of this study indicated that the effect on weight gain of daily or weekly residence times varies seasonally. During 1995 and 1996, animals moved weekly tended to have higher average daily gain (ADG) than animals moved daily and these differences were significant early in each season. In June, forages in Nova Scotia are typically at their peak growth rate and the larger area, associated with a longer residence time, may provide more opportunities for cattle to select forage. Near the end of both grazing seasons the trend observed with cattle ADG

reversed. The animals moved daily were unaffected by a drop in forage production and their ADG increased or decreased only slightly. These cattle were provided with fresh forage more frequently during the period of slow forage regrowth. The ADG of the cattle moved weekly dropped below the ADG of those moved daily. Nevertheless, the higher means of the actual weights of the cattle moved weekly were maintained until the final weighing in 1995, but in 1996 the actual weights did not differ by the final weighing.

When biomass production decreased, the paddocks were enlarged in an attempt to keep a constant amount of forage available. In 1995, the cattle with a daily residence time were given more cumulative area than the cattle with a weekly residence time but the cattle moved weekly still had higher gains. Cattle with a weekly residence time may have had higher gains earlier in the season because the larger paddocks allowed them to have a more selective diet. Hart et al. (1993) found that selectivity increased as grazing pressure

decreased. Rate of gain with weekly residence time may have declined near the end of the season because of their higher energy requirement coinciding with a requirement for more energy to obtain the forage. Near the end of the season the forage was shorter and larger paddocks were necessary to provide enough biomass which caused the animals to walk further and take more bites to obtain enough dry matter to support their rate of gain. Chacon et al. (1978) found that animals grazing a shorter sward took smaller bites and may not have been able to obtain enough dry matter regardless of the forage quality.

In both years the clover content in daily residence time paddocks tended to be higher late in the season suggesting a higher protein content. In several studies, neither continuous nor rotational stocking, nor stocking density has been found to affect pasture sward quality (Popp et al. 1997, Walker et al. 1989). Morrow et al. (1991) reported a decrease in forage quality in some pasture mixes (bromegrass and alfalfa) after the animals had been in a paddock for 3 days. Early in the grazing season forage quality may have been high and unaffected by grazing treatment. Near the end of the grazing season, when water is limiting and forage regrowth slows, short grazing periods within a paddock may maintain a higher forage quality and higher ADG.

Despite the high gains obtained on pasture, carcasses of animals raised solely on grass tend to be graded lower than animals finished in a feedlot (Bowling et al. 1977). Two major causes of the lower grading are yellow fat and lack of sufficient marbling. The amount of yellow fat on a carcass is partially due to fatness of animals, genetics, gender, and age (Walker et al. 1990). Consequently, many farmers finish their cattle on grain to increase the fat content of the carcass and reduce the incidence of yellow fat to avoid discounts on the price paid by packers (Muir et al. 1992). In this study without grain finishing, yellow fat was not

Table 4. Forage mass Dry Matter (kg ha⁻¹) and clover content (%) prior to grazing by cattle in paddocks of animals with a daily residence time (DRT) and a weekly residence time (WRT).

Year	Date	Available Dry Matter		Clover Content	
		DRT	WRT	DRT	WRT
		----- (kg ha ⁻¹) -----		----- (%) -----	
1995	24 May	126	116	13.0	12.8
	29 May	1803	1974	11.5	13.1
	13 June	2080	1974	4.7	6.7
	20 June	2071	1819	4.8	2.9
	4 July	1933	938	23.0	12.7
	7 Aug.	1631	1903	25.8	30.9
	20 Aug.	617	316	31.3	14.1
	1996	29 May	694	1012	4.6
12 June		1465	1402	8.8	11.2
26 June		2521	2255	4.5	2.3
10 July		1330*	2691	23.0	14.2
7 Aug.		815	860	9.8	15.4
21 Aug.		1540*	1042	27.2*	11.3

¹Due to the timing of data collection the values obtained in 1995 cannot be compared statistically. The date given was when DRT paddocks were sampled. WRT paddocks may have been sampled 2 or 3 days before or after.

*Means significantly different at the 5% level of significance.

apparent on carcasses, presumably because Herefords mature sooner than some larger breeds and the forage was of sufficient quantity and quality to finish the cattle before aging contributed to yellow fat.

Conclusions

Animals moved to a new paddock weekly (longer residence time) had higher average daily gain (ADG) than those moved daily (shorter residence time) in the early grazing season when forage was plentiful. At the end of each season when forage growth rate was low, cattle with a daily residence time had higher ADG. The results of this study indicate that animal performance could be maximized by long rotation cycles during periods of rapid forage growth and short rotation cycles during periods of slow forage growth. Pasture productivity remained constant in 1995 and 1996, while clover content of pasture declined throughout the experiment. In 1995 and 1996, all cattle (64 steers and heifers) were slaughtered directly from pasture without incidence of yellow fat on the carcasses.

Literature Cited

- Bertelsen, B.S., D.B. Faulkner, D.D. Buskirk and J.W. Castree. 1993.** Beef cattle performance and forage characteristics of continuous 6-paddock, and 11-paddock grazing systems. *J. Anim. Sci.* 71:1381–1389.
- Bowling, R.A., G.C. Smith, Z.L. Carpenter, T.R. Dutson, and W.M. Oliver. 1977.** Comparison of forage-finished beef and grain-finished beef carcasses. *J. Anim. Sci.* 45:209–215.
- Chacon, E.A., T.H. Stobbs, and M.B. Dale. 1978.** Influence of sward characteristics on grazing behavior and growth of Hereford steers grazing tropical grass pastures. *Aust. J. Agr. Res.* 29:89–102.
- Hart, R.H., J. Bissio, M.J. Samuel, and J.W. Waggoner JR. 1993.** Grazing systems, pasture size, and cattle grazing behavior, distribution and gains. *J. Range Manage.* 46:81–87.
- Heitschmidt, R.K., S.L. Dowhower, and J.W. Walker. 1987.** Some effects of a rotational grazing treatment on quantity and quality of available forage and amount of ground litter. *J. Range Manage.* 40:318–321.
- Montgomery, D.C. 1997.** Design and analysis of experiments, 4th edition. Wiley, New York.
- Morrow, R.E., V.G. Schulze-Tate, J.R. Gerrish, and C.R. Roberts. 1991.** Implications of daily quality changes in rotationally grazed pastures for beef cattle. *Proc. of Forage and Grassl. Conf. of Columbia.* 145–149.
- Muir, P.D., G.J. Cruickshank, N.B. Smith, K.S. MacLean, and G.J. Wallace. 1992.** A comparison of grain and pasture finishing of heavyweight cattle. *Proc. of the New Zealand Soc. of Anim. Production.* CAB Abstracts. 52:93–95.
- Popp, J.D., W.P. McCaughey, and R.D.H. Cohen. 1997.** Effect of grazing system, stocking rate and season of use on diet quality and herbage availability of alfalfa-grass pastures. *Can. J. Anim. Sci.* 77:111–113.
- SAS Institute Inc. 1990.** SAS/STAT user's guide, version 6, 4th edition, Vol.2, Cary, N.C: SAS Institute Inc.
- Walker, J.W., E.A. DeMoraes, R.K. Heitschmidt, M.M. Kothmann, and S.L. Dowhower. 1989.** Quality and botanical composition of cattle diets under rotational and continuous grazing treatments. *J. Range Manage.* 42(3):239–242.
- Walker, P.J., R.D. Warner, and C.G. Winfield. 1990.** Sources of variation in subcutaneous fat colour of beef carcasses. *Proc. of the Aust. Soc. of Anim. Prod.* CAB Abstracts. 18:416–419.

Variations in soil moisture content in a rangeland catchment

ROHIT SALVE AND BARBARA ALLEN-DIAZ

Authors are geological scientist, Earth Sciences Division, Lawrence Berkeley National Laboratory, 1 Cyclotron Road, Berkeley, Calif. 94720 and associate dean for research and extension at the Environmental, Science, Policy and Management, 101 Giannini Hall, University of California, Berkeley, Calif. 94720-3100. At the time of the research, the senior author was a Ph.D candidate, Department of Environmental, Science, Policy and Management, University of California, Berkeley, Calif.

Abstract

Soil water studies for California rangelands have focussed on near-surface hydrologic processes, limiting our understanding of spatial-temporal dynamics of the water regime below the root zone. Soil moisture content and potential were monitored for 16 months in 12 locations in an annual grass dominated 20 ha catchment. The data collected were analyzed by ANOVA to determine significant spatial and temporal differences in soil moisture. Further analysis identified variables that influenced the amount of moisture present at a particular subsurface location. It was determined that there were significant differences in the amount of soil moisture present along the vertical profile of each site and between sites. Soil texture, type of vegetation cover, and elevation were the significant variables that influenced the soil moisture status.

Key Words: California rangelands, subsurface hydrology

The circulation of water between ocean, atmosphere and land is called the hydrologic cycle (Freeze and Cherry 1979). Within the context of rangeland hydrology, the land-based portion of the cycle as it may be operative on an individual watershed is of primary importance. This component of the cycle enters the system through precipitation and exits as streamflow or evapotranspiration. Overland flow is generated when rainfall intensities exceed infiltration rates (Horton 1933). In situations where soils are heterogeneous, overland flow is observed in certain portions of the watershed. This describes the partial-area-contribution concept as presented by Betson (1964).

Seasonal changes in the land components of the hydrological cycle cause important variations in the surface and subsurface flow dynamics in rangeland catchments in California. Examination of surface and subsurface flow dynamics is one step towards better understanding vegetation composition, productivity and growing season dynamics, as well as potentially elucidating possible watershed pollution flow paths.

Subsurface flow has been observed to be a significant source of runoff in certain situations (Whipkey 1966, Dunne 1969, Hewlett and Nutter 1970). Hewlett and Hibbert (1963) showed the feasibility of such flow experimentally. The prime requirement is a shallow horizon of high permeability at the surface (Freeze and Cherry 1979). Dunne and Black (1970), working on an experimental watershed in Vermont, developed the concepts for the mecha-

Resumen

Los estudios del agua del suelo en los pastizales de California se han enfocado en los procesos hidrológicos cercanos a la superficie, limitando nuestro entendimiento de las dinámicas espacio-temporal del régimen del agua abajo de la zona de raíces. El contenido de humedad en el suelo y el potencial se monitorearon durante 16 meses en 12 sitios de un área de captación dominada por zacates anuales. Los datos colectados se analizaron por ANOVA para determinar diferencias significativas espacio-temporal de la humedad del suelo. Análisis adicionales identificaron variables que influyeron en la cantidad de humedad del subsuelo presente en un sitio particular. Se determinó que hubo diferencias significativas en la cantidad de humedad presente a lo largo del perfil vertical de cada sitio y entre sitios. La textura del suelo, tipo de cobertura de la vegetación y la elevación fueron variables significativas que influyeron en el estado de humedad del suelo

nisms of saturated overland flow. Here surface saturation was found to occur because of a rising water table, and ponding and overland flow occurred when no soil moisture storage was available. A comprehensive understanding of the hydrochemical response of catchments is limited because of the complexity of the hydrology.

Infiltration rates and sediment production on a rangeland have been assumed to integrate the complex interactions of soil and vegetation factors for use as indicators of hydrologic conditions (Thurrow et al. 1986). Compaction of surface soil and the removal of plant cover have been identified as the major impacts of grazing on the hydrologic cycle. While these conclusions are common to a large body of literature concerned with the hydrology of rangelands (e.g. Thurrow et al. 1986, Rauzi and Hanson 1986, Wood and Blackburn 1981a, 1981b), insights to the subsurface hydrology of these systems have not been investigated.

The objective of this study was to determine the influence of catchment features such as soil texture, topography, and vegetation on the seasonal changes in soil moisture content in a rangeland. This paper provides a description and results of a statistical analysis used to identify variables (i.e. soil texture, elevation, vegetation type, precipitation and evapotranspiration) significantly influencing the spatial and temporal dynamics of soil moisture in a California rangeland catchment.

Methods

The study site was a 20-hectare (ha) watershed located 10 km west of Walnut Creek, in Contra Costa County, California (37° 54' N, 122° 03' W) (Fig. 1). Changes in soil moisture content and

Thanks to Dan Hawkes and 2 anonymous reviewers for review of this manuscript. Manuscript accepted 8 May 2000.

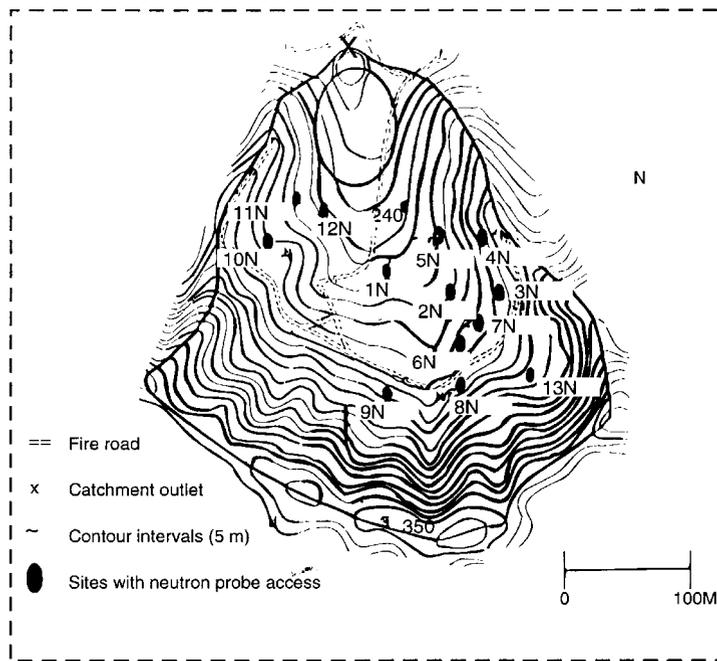


Fig. 1. Topographic map of Russell Tree Farm showing location of sites monitored for changes in soil moisture content.

matric potential were monitored along the vertical soil profile in 12 locations (Salve and Tokunaga 2000). These sites represented the 3 dominant vegetation types found in the catchment (annual grasses, shrubs, and trees) and 3 broad elevation categories (low, medium, and high) (Table 1).

Soil moisture content was determined by the neutron-probe method (Gardner 1986) and soil water potentials were determined using nested tensiometers. Soil removed during auguring of the 13 access holes for the neutron probe measurements, was collected in 0.15 m intervals and analyzed for soil particle size distribution. Soil moisture content was measured with a neutron probe at 0.15-m intervals at monthly intervals while water potential were measured at weekly intervals during the wet period and monthly intervals late in the summer. Soil moisture content data were analyzed to determine significant spatial and temporal differences and to identify variables that influenced the amount of moisture present at a particular location within the catchment slopes.

Results

The study period started at the end of the 1992–93 rainfall season, a season in which precipitation totals for the region were greater than the average for the last

decade (Fig. 2a). During the first 7 months of monitoring (May–November, 1993) there was negligible precipitation. Measurable rainfall was recorded in a single event in November, and then for a number of events between December and early March, 1994 (Fig. 2b).

The moisture content profiles in each site, up to a depth of ~1.0 m showed similar patterns of wetting and drying during the entire monitoring period (Fig. 3). Early in May 1993, a period which coincided with the start of the summer, all the sites recorded large amounts of soil moisture (e.g. at Site 6N the volume of water per unit volume of soil was between 0.17 and 0.32) at all depths. Over the next month all the shallow soil profiles lost a significant

amount of moisture (e.g. at Site 6N the volumetric moisture content fell by ~50%), and in the ensuing months moisture losses from the profiles continued, but at decreasing rates. With the start of the winter rains, the amount of water in the soil profiles began increases during the first wet month (i.e. December 1993). In the next 2 months, when the bulk of the seasons' rain occurred, small increases were detected in all profiles, but these were much smaller than those observed early in the winter. Shortly after the wet season ended in early March 1994, the shallow profiles showed small losses in soil moisture content. The largest decreases were observed in April, and significantly smaller reductions occurred in the following months. This drying pattern was similar to that of the previous year, with the exception that the drying process in 1994 began almost 60 days earlier.

In the shallow soil profiles in all sites except 1N and 10N (Fig. 1), the deeper zones were wetter than the near-surface profile at any given time of year. In the case of 1N and 10N there was a period of 3 months coinciding with the wettest time of year when the shallow sections of the profiles recorded higher volumes of moisture than the deeper profiles. In each of the sites the total moisture lost from the near surface profile during the summer of 1993 was replenished during the following winter. Similar amounts of moisture were then lost from the profiles by the end of August, 1994. In essence, the shallow soil profiles (i.e. up to a depth of ~1.0 m) reached a fixed upper and lower limit in storing soil moisture towards the end of each season, irrespective of the amount of rainfall received for the 2 wet seasons.

The 5 deep monitored profiles (6N, 7N, 8N, 9N, and 13N) ranged from 3.75 to 5.70 m in depth. Large losses in moisture following a wet winter (1992–93) in 4 of

Table 1. Physical features of monitored locations at the study site.

Site	Elevation (m)*	Aspect	Soil depth (m)	Slope (%)	Vegetation	Soil texture
1N	14	West	>3.0	<9	Grass	Sandy clay loam
2N	33	West	~ 2.5	9–45	Grass/shrub	Clay loam
3N	47	West	~1.5	>45	Grass	Loam-clay loam
4N	51	West	~1.5	>45	Grass	Silty clay loam
5N	31	West	~1.5	9–45	Grass/shrub	Loam-clay loam
6N	46	Northwest	>6.0	9–45	Grass/shrub	Sandy clay loam
7N	48	Northwest	~5.0	9–45	Grass	Clay loam
8N	50	North	~5.0	9–45	Tree	Sandy loam
9N	47	North	~5.0	9–45	Tree/shrub	Sandy loam
10N	42	Northeast	~1.5	>45	Tree/grass	Sandy loam
11N	32	East	~1.5	9–45	Grass	Clay loam
12N [#]	9	East	~5.0	>45	Grass	Sandy loam
13N	66	Northeast	~5.0	>45	Grass	Sandy loam

[#]Because 12N remained submerged during most of the monitoring period it has not been included in the analysis

*Relative to catchment outlet

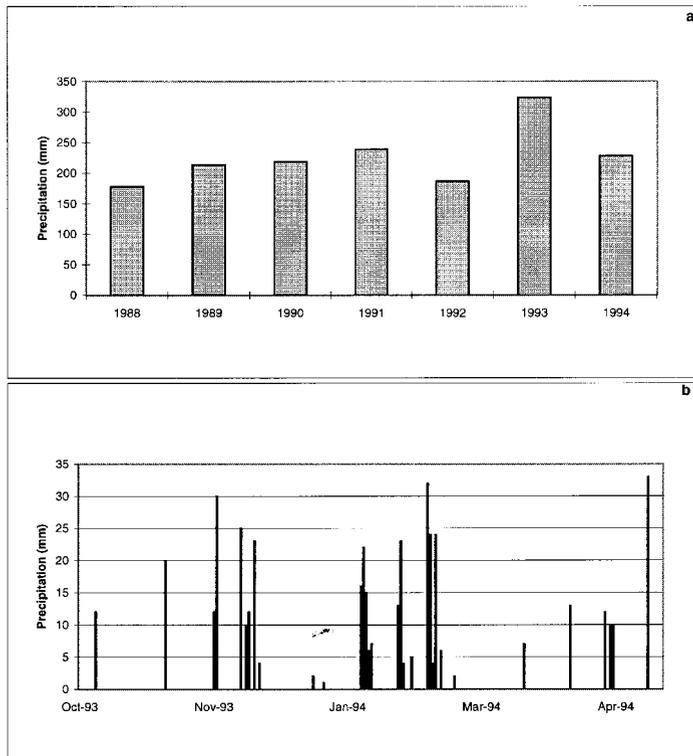


Fig. 2. (a) Annual totals of rainfall recorded at Walnut Creek located 10 km east of Russell Tree Farm. (b) Rainfall recorded at Russell Tree Farm.

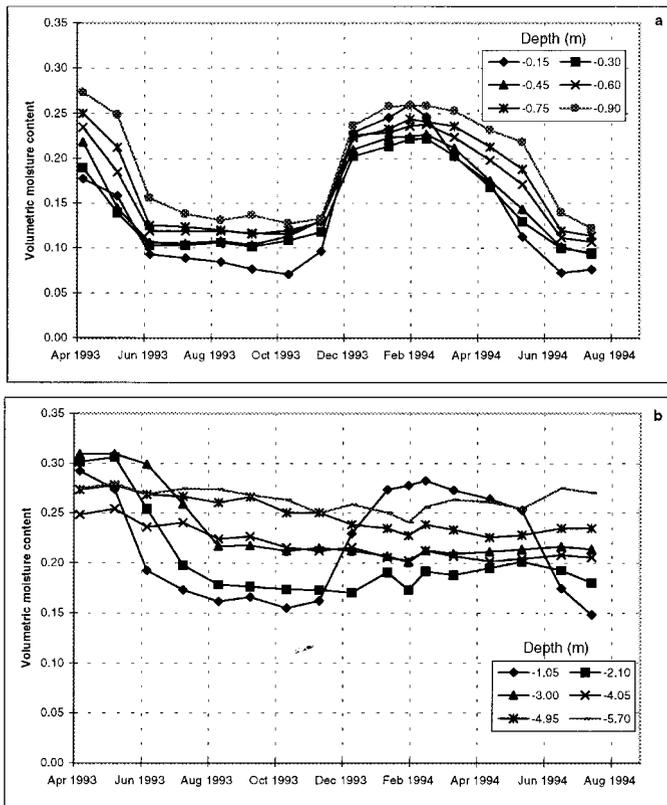


Fig. 3. Volumetric moisture content measured along the (a) shallow and (b) deep profile at site 6 N. Similar measurements were made along the vertical profiles of all the monitored sites.

the 5 sites extended beyond the 2.0 m depth. The single exception (7N) recorded losses in moisture which were largely restricted to the top 1.9 m of the profile.

Among these sites, at depths greater than 2.0 m, changes in soil moisture content varied considerably. Of the 5 deep locations, 7N consistently contained most water per unit volume of soil, while 8N was always the driest. Throughout the monitoring period the difference in wetness between these 2 sites also remained fairly constant. In the remaining deep sites the relative difference in wetness, however, continued to change at different times of year. Thus Site 13N had an average moisture content similar to 8N for the first 7 months of monitoring, but deviated for the remaining period as 8N dried at a faster rate. Site 9N initially recorded average moisture amounts similar to 7N, but dried significantly faster in the ensuing summer months. This difference continued to increase during the wet winter months, when 7N retained much higher amounts of water. Site 6N, which was drier than 9N in early May 1993, had similar rates of drying and wetting, and so maintained a near constant average difference in wetness as 9N.

In the deeper profiles moisture content tended to increase with depth. A single exception to this was 8N, where during the summer of 1993 the deepest zone in the profile was drier than the zones lying between 0.6 and 2.5 m

Data Analysis

Neutron probe data collected monthly at 0.15 m intervals over a vertical distance of 1.05 m in 12 sites was analyzed by ANOVA (SPSS 1993) to determine if there were significant spatial and temporal differences in moisture content measured at different locations within the catchment. Specifically, 3 null hypotheses were tested:

Ho: Within a vertical soil profile (i.e. each site), mean moisture content (average of 16 months) does not vary significantly by depth.

Ho: Among the 12 sites, mean moisture content (average of 16 months) does not vary significantly by depth.

Ho: At each measured depth along the 12 vertical profiles, moisture content does not vary significantly in time.

All 3 hypotheses were rejected by the ANOVA tests. These tests established that at depths between 0.15 and 1.05 m, the moisture content within the catchment changed significantly during the monitoring period. Further, these tests suggested that significant differences existed in the amount of moisture, both within 11 sites

Table 2. Multiple regression models developed for 4 seasons and for entire monitoring period.

Variable	B	SEB	Beta	T	Sig T
Very wet season	1.79E-03	1.76E-04	4.80E-01	10.21	0
Clay	-7.25E-02	7.56E-03	-4.46E-01	-9.59	0
Distance	-7.29E-04	1.86E-04	-1.88E-01	-3.92	0.0001
Elevation	-4.38E-02	5.27E-03	-3.93E-01	-8.30	0
Tree	-4.38E-02	5.27E-03	-3.93E-01	-8.30	0
(Constant)	1.88E-01	1.10E-02	1.71E+01	0.00	
			<i>Adjusted R2</i>		<i>6.43E-01</i>
Wet season					
Clay	1.36E-03	2.47E-04	2.90E-01	5.51	0
Distance	-5.98E-02	1.06E-02	-2.93E-01	-5.62	0
Elevation	-1.14E-03	2.62E-04	-2.32E-01	-4.33	0
Tree	-3.94E-02	7.42E-03	-2.82E-01	-5.30	0
(Constant)	1.95E-01	1.55E-02	1.26E+01	0.00	
			<i>Adjusted R2</i>		<i>3.28E-01</i>
Dry season					
Distance	1.21E-01	5.66E-03	-5.82E-01	-21.41	0
Elevation	-1.58E-03	1.41E-04	-3.18E-01	-11.24	0
Clay	1.02E-03	2.43E-04	2.12E-01	4.19	0
Grass	1.04E-02	4.14E-03	8.37E-02	2.51	0.0123
Sand	-3.34E-04	1.71E-04	-1.02E-01	-1.95	0.0518
Tree	-1.41E-02	5.31E-03	-9.88E-02	-2.66	0.081
(Constant)	1.56E-01	1.48E-02	1.05E+01	0.00	
			<i>Adjusted R2</i>		<i>5.80E-01</i>
Very dry season					
Clay	1.48E-03	1.54E-04	3.20E-01	9.61	0
Distance	-1.14E-01	6.62E-03	-5.66E-01	-17.19	0
Elevation	-1.70E-03	1.66E-04	-3.52E-01	-10.21	0
Grass	1.04E-02	4.85E-03	8.68E-02	2.15	0.0327
Tree	-2.53E-02	5.68E-03	-1.83E-01	-4.45	0
(Constant)	1.31E-01	9.79E-03	1.34E+01	0.00	
			<i>Adjusted R2</i>		<i>6.42E-01</i>
Overall model					
Distance	-1.01E-01	4.39E-03	-4.66E-01	-23.02	0
Elevation	-1.44E-03	1.10E-04	-2.77E-01	-13.05	0
Grass	3.50E-02	3.23E-03	2.71E-01	10.851	0
Shrub	2.50E-02	3.76E-03	1.71E-01	6.65	0
(Constant)	1.24E-01	7.29E-03	1.70E+01	0.00	
			<i>AdjustedR2</i>		<i>4.57E-01</i>

B Partial Regression Coefficients
Beta Beta Coefficients Calculated for Regression Coefficients
T T-Test

and between sites. For the single exception, i.e. Site 9, significant differences in the average moisture content along the vertical profile were not detected.

Model building

Following the 1 factor ANOVA tests a repeated measures analysis of variance was employed to detect for both spatial and temporal effects, and also to test whether there was an interaction between the 2 factors. The independent variables within the catchment for which location-specific data were collected included soil texture (Fig. 4), elevation, and vegetation type (Table 1). Climatic data (precipitation and estimates of evapotranspiration) were used from a weather station in Walnut Creek (Fig. 5).

Since the variables thought to influence the moisture content in the catchment

belonged to 2 broad categories, (i.e. weather related data that varied from month to month and time independent data), an effort was made to develop 2 predictive models.

In each case, the general form of the model was:

$$\theta_i = \beta_0 + \beta_1 X_{1i} + \beta_2 X_{2i} + \dots + \beta_p X_{pi} + e_i \tag{1}$$

Where θ_i is the predicted moisture content at a given location. The notation X_{pi} indicates the value of the p th independent variable for case i . The β terms are unknown parameters (partial regression coefficients). In the first model only time independent variables (i.e. soil texture, elevation, depth in soil profile and vegetation type) were considered while in the second model only time dependent variables (precipitation and evapotranspiration) were considered.

Model with Time-Independent Variables:

The important variables (not changing in time) that influenced the amount of moisture in the soil were isolated by first grouping the 1,328 observations of soil water content (12 sites, for 16 separate months, at 7 depths, with observations missing from a depth of 1.05 m at Site 3N)

To formally define the membership of each groups the distribution of moisture along the profile of each site, at each time period, was defined by a cubic function (since this function most accurately described the soil moisture distribution along each profile). The coefficients of the cubic function were then used to define 4 clusters for each site over the 16-month period using the between-groups linkage method, in which the similarity matrix was computed using the Euclidean distance method. The clusters from all 12 sites were then plotted to determine if all sites showed similar seasonal boundaries (Fig. 6). Observations of soil moisture content were then analyzed to determine the dominant independent variables influencing the amount of moisture. In this analysis 5 linear regression models were developed. The first included all 1,328 observations while the remaining 4 included observations from each of the 4 "seasons" (very wet, wet, dry, and very dry in Figure 6).

In all 5 linear-regression models, the 3 independent variables, clay content, distance from surface, and elevation were found to significantly influence the amount of moisture present at a given location (Table 2). From the stepwise regression procedure used to develop the regression model for each season, the adjusted correlation coefficient (Adj.R²) was highest for the 2 extreme climatic conditions, i.e., the wettest period and the driest period. The lowest Adj.R² values were detected in the period between the wet and dry seasons.

In the regression model developed for the very wet season, significant independent variables influencing the soil moisture content were clay content, trees, distance, and elevation. Of these, clay content had the highest positive correlation with moisture content followed by grass, silt content, and shrubs (Table 3). The largest negative correlations were with sand content, followed by distance, trees, and elevation. In this regression the final Adj.R² was 0.64. For the transient period between the wet season and the dry summer months, the significant variables influencing the moisture content in the soil were the same as those detected for the wet season. However, the absolute value of the

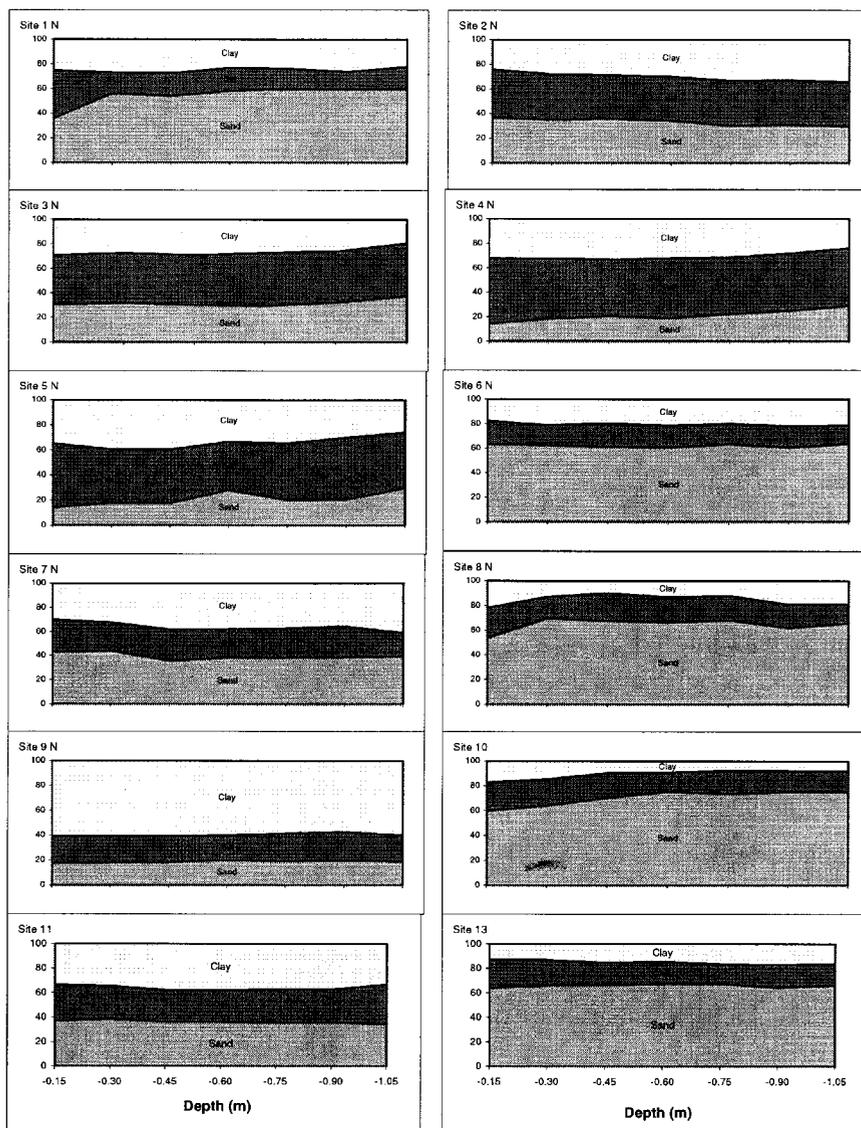


Fig. 4. Result of particle size analysis done on soils obtained from the vertical profile of the 12 monitored sites. The soil samples were collected at intervals of 0.15 m. The 'Y' axis in each plot indicated the percentage of sand, silt and clay present at each depth.

correlation coefficients for all of the independent variables (excluding trees) was reduced. Here, too, the final Adj.R² was reduced to 0.32.

In the regression equation developed from observations in the dry summer months, the independent variables significantly influencing the amount of moisture

at a given location were clay, sand, distance, elevation, trees, and grasses. The final Adj.R² was 0.58. For the regression equation developed from observations in the driest summer months, the variables found to have significant influences on the amount of moisture content included clay, distance, elevation, grasses, and trees. For this equation the final Adj.R² was 0.64.

For the regression analysis performed on observations made throughout the monitoring period, the variables significantly influencing moisture content were clay, grass, shrubs, distance, elevation, and distance. Here the Adj.R² was reduced to 0.46.

Model with Time-Dependent Variables:

The neutron-probe data collected at each site and depth in the catchment had the form of a typical time series. Since observations of moisture content at all depths indicated a sinusoidal pattern of changes over time the temporal components of the data were analyzed first. Here, an effort was made to build an autoregressive integrated moving average (ARIMA) model to explain the components of the series at each monitored depth. This model building procedure consists of 3 steps-identification, estimation and diagnosis (Box and Jenkins 1976). Identification of the model involved isolating the processes underlying the series by determining the 3 integers p, d, q in the ARIMA process generating series. Because the data were limited to 16 months of monitoring, parameters describing seasonal fluctuations were not included in the model building process. Since the identification process of the autoregressive and moving average components requires a stationary series (i.e., equal mean and variance throughout the series), all the times-series data was differenced twice and log-transformed to obtain a new stationary series. From the new series, the other ARIMA parameters p and q were developed from the autocorrelation function and partial autocorrelation func-

Table 3. Correlation coefficients between seasonal soil moisture content and independent variables.

Variable	Seasons					Independent Variables							
	Very wet	Wet	Dry	Very dry	Overall	Clay	Distance	Elevation	Grass	Sand	Shrub	Silt	Tree
Moisture	1.00	1.00	1.00	1.00	1.00	0.49	-0.43	-0.33	0.28	-0.45	0.09	0.19	-0.42
Clay	0.49	0.31	-0.57	0.35	0.32	1.00	0.02	-0.14	-0.02	-0.81	0.00	0.22	0.02
Distance	-0.43	-0.28	-0.38	-0.56	-0.46	0.02	1.00	0.00	-0.02	-0.09	0.03	0.13	-0.01
Elevation	-0.33	-0.33	0.32	-0.43	-0.35	-0.14	0.00	1.00	0.05	0.15	-0.24	-0.09	0.19
Grass	0.28	0.21	0.14	0.18	0.16	-0.02	-0.02	0.05	1.00	-0.08	-0.58	0.16	-0.56
Sand	-0.45	-0.32	-0.30	-0.33	-0.30	-0.81	-0.09	0.15	-0.08	1.00	-0.14	-0.75	0.24
Shrub	0.09	0.11	0.08	0.07	0.07	0.00	0.03	-0.24	-0.58	-0.14	1.00	0.24	-0.36
Silt	0.19	0.17	0.13	0.16	0.01	0.22	0.13	-0.09	0.16	-0.75	0.24	1.00	-0.42
Tree	-0.42	-0.32	-0.22	-0.29	0.14	0.02	-0.01	0.19	-0.56	0.24	-0.35	-0.42	1.00

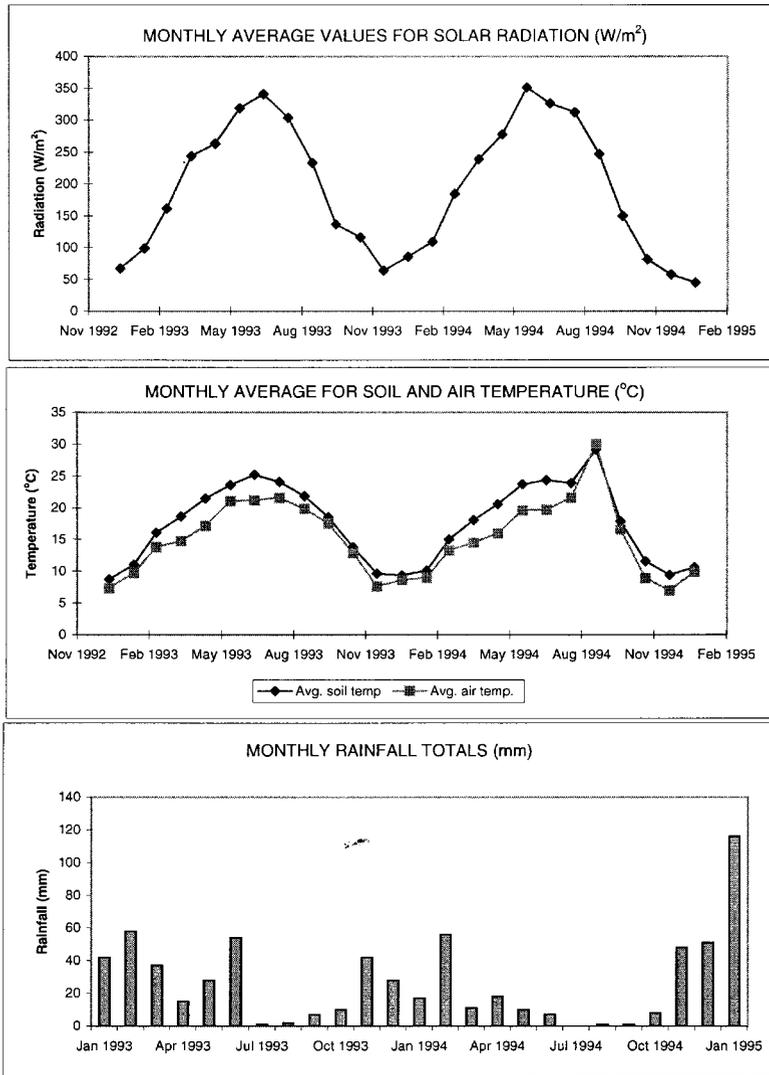


Fig. 5. Climatic data used to estimate evapotranspiration from a weather station at Walnut Creek located 10 km west of the study site.

tion. Coefficients of the ARIMA model for each series were then estimated using a statistical package (SPSS 1993), and tested to determine the maximum-likelihood

coefficients. Finally, the autocorrelation function and partial autocorrelation function of the error series were checked to see if they were significantly different from 0.

Because robust ARIMA models could not be developed for each time-series, observations from 2 depths (i.e. 0.3 and 0.9 m) from all 12 sites was differenced twice (to obtain a stationary series) and normalized as were the data of the 2 independent variables, monthly, rainfall and evapotranspiration (ET). With these normalized values, a regression analysis was done in which moisture content at a given site was regressed against the monthly rainfall and ET.

Results from the autoregression suggest that close to the surface (i.e. 0.15 m), the regression model can account for very little of the moisture response in time using the autoregression parameter, rainfall, and ET (Table 4). At greater depths, the ARIMA model shows that the autoregressive component is able to significantly explain some of the seasonal variability. However, even though this model shows that moisture content is positively correlated with rainfall and negatively with ET, the contributions of these variables in improving the model are negligible.

Discussion

An important characteristic of the climate in the region is the tremendous variability in annual precipitation amounts (Fig. 4), which consequently results in a large variability in the amount of moisture penetrating into the soil. Evidence of this was apparent during the 16-month monitoring period, when the total rainfall recorded at the end of 1993–94 wet season was significantly lower than that observed

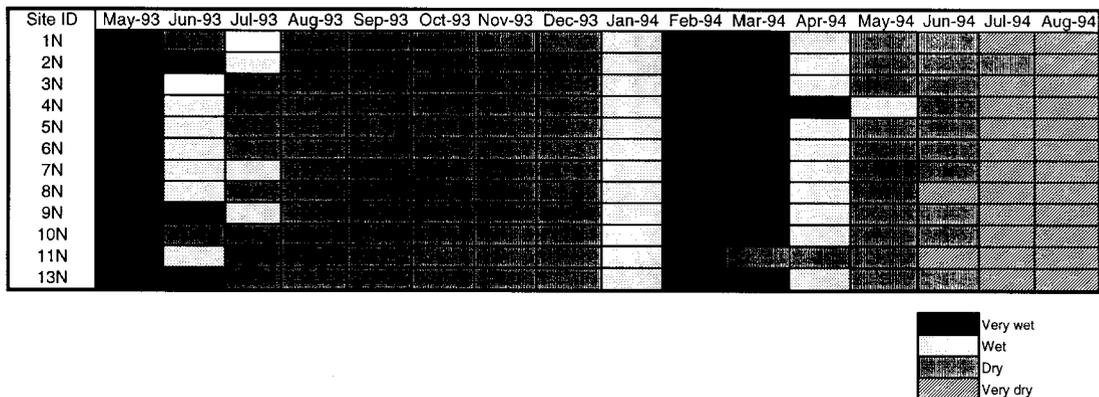


Fig. 6. Relative wetness at each site as determined by a clustering procedure.

Table 4. Results of autoregression analysis of various depths in Site 11N.

Variable	B	SEB	T-Ratio	Approx. Prob.
Depth = 0.15m				
AR1	7.17E-01	1.75E-01	4.11	1.45E-03
ET	2.43E-04	2.48E-03	0.10	9.24E-01
Rainfall	1.09E-03	2.38E-03	0.46	6.54E-01
Constant	-2.04E+00	4.14E-01	-4.94	3.44E-04
Depth = 0.30m				
AR1	7.44E-01	1.77E-01	4.20	1.23E-03
ET	-1.11E-03	1.24E-03	-0.90	3.88E-01
Rainfall	1.46E-04	1.16E-03	0.13	9.02E-01
Constant	-1.41E+00	2.12E-01	-6.67	2.30E-05
Depth = 0.45m				
AR1	7.37E-01	1.78E-01	4.14	1.37E-03
ET	-8.24E-04	1.00E-03	-0.82	4.27E-01
Rainfall	5.04E-05	9.46E-04	0.05	9.58E-01
Constant	-1.32E+00	1.70E-01	-7.78	4.99E-06
Depth = 0.60m				
AR1	7.85E-01	1.70E-01	4.63	5.80E-04
ET	-3.71E-04	8.89E-04	-0.42	6.84E-01
Rainfall	5.71E-04	8.11E-04	0.70	4.95E-01
Constant	-1.30E+00	1.61E-01	-8.12	3.24E-06
Depth = 0.75m				
AR1	7.55E-01	1.86E-01	4.07	1.58E-03
ET	-1.59E-04	7.86E-04	-0.20	8.43E-01
Rainfall	1.37E-04	7.32E-04	0.19	8.55E-01
Constant	-1.27E+00	1.36E-01	-9.28	8.00E-07
Depth = 0.90m				
AR1	7.76E-01	1.82E-01	4.25	1.12E-03
ET	8.22E-05	7.49E-04	-0.08	9.35E-01
Rainfall	-6.80E-05	6.88E-04	-0.10	9.23E-01
Constant	-1.25E+00	1.34E-01	-9.34	7.40E-07
Depth = 1.05m				
AR1	7.73E-01	1.74E-01	4.44	8.00E-04
ET	-9.05E-05	7.30E-04	-0.12	9.03E-01
Rainfall	4.34E-05	6.72E-04	0.06	9.50E-01
Constant	-1.20E+00	1.30E-01	9.25	8.30E-07

during the previous winter. The depth to which soil was moistened was consequently much shallower in the winter of 1993–94, as is apparent in the significantly greater readings recorded in the deeper profiles in May 1993 than those recorded following the rains in February 1994 (Salve and Tokunaga 2000).

While precipitation was the single source of recharge to the catchment subsurface, results from the regression analysis indicate that soil texture, vegetation cover, and elevation had significant influences in the amount of moisture at a given location. From the regression models (Table 2) it is apparent that a strong seasonal influence caused periodic changes in the significance of these variables. For example, during the very wet season, clay greatly influenced the amount of moisture present in the soil. Over the following months, when the catchment continued to dry, the relative contributions of clay content in the predictive equations continued to decrease. Distance from the surface, however, was not as significant a factor during the wet period (when large amounts of water migrated into the pro-

file) as it was in the summer months when the near-surface processes were able to reduce moisture amounts at rates faster than the deeper profiles.

The changes in moisture content in each profile represent a function of the moisture characteristic curves for each of the profiles. During the wet period, the amount of moisture retained in the soils is large, but as the matric potential in the soil decreases, there are initially significant amounts of drainage. With further decreases in soil moisture potentials, the amount of moisture lost per unit drop in pressure decreases, asymptotically approaching zero. During the wetting period, this behavior is reversed, with some differences resulting from hysteresis.

The significant positive correlation of moisture content with clay content can be explained by the general properties of clays to retain more moisture over a larger range of matric potentials than sands or silts. In the catchment where soil moisture in the near surface profile reached potentials below the functioning range of tensiometers (< -8.0 m) for a significant portion of the monitoring period, it can be

assumed that soils with higher sand content had significantly lower moisture content. While this result is not unexpected, it is important to note that the regression analysis did not account for possible lenses of either sand or clay, which could significantly influence the amount of moisture migrating along the vertical plain.

The significant correlation of moisture content with depth (i.e., greater moisture content with increasing depth) can be explained by the vertical gradient in the intensity of near surface hydrologic processes like recharge and evapotranspiration (ET). Close to the surface, recharge and ET rates are the greatest, and with increasing depth the amount of moisture recharged or lost to ET decreases. Close to the surface, therefore, the net gain in the amount of water over a hydrologic year is close to zero, because all water received is recharged or lost to ET. At the same time, with increasing depth however, the net differences between recharge and moisture loss are smaller, resulting in greater storage of moisture over the year. It is only for brief periods following rainfall events that the near-surface profile has larger moisture content than the deeper profile. The higher correlation's observed in the drier seasons and lower correlation's observed in the wet period tend to support this argument.

The effect of vegetation cover on the moisture content as interpreted from the regression results indicates that there was a negative correlation of moisture content with tree cover, and a positive correlation with the presence of grasses. In most cases, no significant correlations between moisture content and shrubs could be observed. For areas characterized by large, yearly variability in rainfall, several reasons for this relationship between vegetation type and moisture content could exist. Perhaps the most significant of these is the year-round loss of soil moisture through transpiration from trees. Grasses, on the other hand, transpire over a relatively short period (between November and May), at a time when most of the season's precipitation is received. Besides removing water throughout the year, the tree cover is able to intercept larger amounts of the low-intensity rain than annual grasses. Grasses are also likely to prevent losses of moisture through surface evaporation by providing mulch of thick, matted biomass early in the summer.

The negative correlation of moisture content with elevation perhaps results from the combination of lateral drainage and lower infiltration occurring at the higher elevations. While no strong correla-

tion between vegetation type and elevation among the monitored sites could be observed, in the higher elevations (above 300 m) of the catchment, trees are the dominant vegetation type. Consequently, greater amounts of precipitation are intercepted in the higher elevations than in the lower areas of the catchment. Further, at the lower elevations, because of the topography of the catchment, subsurface flow paths converge, resulting in increasing amounts of flow passing through reducing areas. Therefore, at higher elevations less moisture travels through the soil.

Summary

Within a rangeland catchment in California, changes in moisture content in the soil profile followed an annual cycle, increasing in the winter following the start of the rains and decreasing during the dry summer months. The magnitude of these changes varied both along the vertical soil profile and at different locations within the catchment. Along the length of a soil column, fluctuations were the largest close to the surface and gradually decreased with depth. At depths greater than 3.0 m, the seasonal changes in moisture content were small. Further, during seasons of low rainfall, the vertical migration of moisture was severely limited, resulting in little or no recharge in the deep profile.

The rainfall pattern (frequency, intensity, duration) of the semi-arid region influenced the extent to which recharge took place during a particular year. Infrequent rainfall events provided ample opportunity for evaporation losses at the surface, thereby reducing recharge to deep seepage.

The important parameters influencing the amount of moisture in the soil included seasonal rainfall, soil texture, vegetation type and elevation. Locations with annual grasses as the dominant vegetation cover retained the large amounts of moisture within the root zone, followed by shrubs and trees respectively. Soil moisture content was generally more in areas with higher clay content and decreased amounts of sand regardless of the vegetation cover. Soil moisture generally increased with depth along the vertical soil profiles.

Literature Cited

- Box, G. E. P. and G. M. Jenkins. 1976.** Time series analysis: Forecasting and control. Holden-Day, San Francisco, Calif.
- Betson, R. P. 1964.** What is watershed runoff? *J. Geophys. Res.*, 69: 1541-1551.
- Dunne, T. 1969.** The significance of "partial-area" contributions to storm runoff for the study of sources of agricultural pollutants. *Agr. Res. Ser.*, Danville, Vt.
- Dunne, T. and R. D. Black. 1970.** An experimental investigation of runoff production in permeable soils. *Water Resour. Res.*, 6: 478-490.
- Freeze, R. A. and J. A. Cherry. 1979.** *Groundwater.* Prentice-Hall Inc., New Jersey.
- Gardner, W. H. 1986.** Water Content. In *Methods of soil analysis, Part 1.* Ed. A. Klute, Agronomy Monograph No. 9, 2nd edition, Amer. Soc. Agron., Madison, Wisc.
- Hewlett, J. D. and A. R. Hibbert. 1963.** Moisture and energy conditions within a sloping soil mass during drainage. *J. Geophys. Res.*, 69: 1081-1087.
- Hewlett, J. D. and W. L. Nutter. 1970.** The varying source area of streamflow from upland basins. *Proceedings of the symposium on inter-disciplinary aspects of watershed management,* Montana State University, Bozeman, Amer. Soc. Civil Eng., pp. 65-83.
- Horton, R. E. 1933.** The role of infiltration in the hydrologic cycle. *Trans. Amer. Geophys. Union*, 14: 446-460.
- Rauzi, F. C. and C. L. Hanson. 1986.** Water intake and runoff as affected by intensity of grazing. *J. Range Manage.*, 19: 351-356.
- Salve, R. and T. K. Tokunaga. 2000.** Flows processes in a rangeland catchment in California. *J. Range Manage.* 53: 489-498.
- SPSS for Windows, 1993.** Release 6.1, SPSS Inc.
- Thurow, T. L., W. H. Blackburn, and C. A. Taylor Jr. 1986.** Hydrologic characteristics of vegetation types as affected by livestock grazing systems, Edwards Plateau, Texas. *J. Range Manage.*, 39(6): 505-509.
- Whipkey, R. Z. 1966.** Subsurface stormflow from forested slopes. *Bull. Internat. Assoc. Sci. Hydrology*, 10(2): 74-85.
- Wood, M. K. and W. H. Blackburn. 1981a.** Sediment production as influenced by livestock grazing in the Texas Rolling Plain. *J. Range Manage.*, 34: 228-231.
- Wood, M. K. and W. H. Blackburn. 1981b.** Grazing systems: their influence on infiltration rates in the Texas Rolling Plains. *J. Range Manage.*, 34: 231-335.

Spotted knapweed response to season and frequency of mowing

MATTHEW J. RINELLA, JAMES S. JACOBS, ROGER L. SHELEY, AND JOHN J. BORKOWSKI

Authors are graduate research assistant, post-doctoral research associate, and associate professor, respectively, Department of Land Resources and Environmental Science and associate professor, Department of Mathematical Sciences, Montana State University, Bozeman, Mont. 59717.

Abstract

Spotted knapweed (*Centaurea maculosa* Lam.) is a non-indigenous weed that has invaded millions of hectares of rangeland in the United States. Mowing may be useful for reducing this weed. Our objective was to investigate the response of spotted knapweed and grasses to season and frequency of mowing. Response of grass and spotted knapweed to 16 mowing treatments applied annually for 3 years was studied at 2 sites. Treatments consisted of combinations of spring, summer, and fall mowing. Treatments were arranged in a randomized-complete-block design with 4 replications (16 treatments; 4 replications; 2 sites = 128 plots). After repeating mowing treatments for 3 years, a single fall mowing when spotted knapweed was in the flowering or seed producing stage reduced its cover and adult density as much as any treatment consisting of repeated mowing. Fall mowing decreased adult density 85 and 83% below that of the control at Sites 1 and 2, respectively. Treatments reduced seedling density at Site 2, but the response was not consistent between years or among treatments. Spotted knapweed cover was decreased by several mowing treatments at each site (10–36%), while grass cover was only decreased by 3 mowing treatments (18–23%) at Site 1 in 1998. We recommend a single annual mowing, applied at the flowering or seed producing stage, for the partial control of spotted knapweed.

Key Words: *Centaurea maculosa*, density, cover, weed control

Grassland ecosystems of the western United States, once dominated by native grasses, now contain extensive areas dominated by non-indigenous weeds, such as spotted knapweed (*Centaurea maculosa* Lam.) (Roché and Talbott 1986). Spotted knapweed, a perennial in the Asteraceae family, was introduced to the Pacific Northwest around 1900 (Strang et al. 1979). This species now infests over 2.2 million hectares in 5 northwestern states and is spreading rapidly (Chicoine et al. 1985, Sheley and Rice 1995). Research suggests that weeds like knapweed may degrade soil and water resources (Lacey et al. 1989), reduce biodiversity (Tyser and Key 1988, Randall 1996), diminish wildlife habitat and livestock forage production (Spoon et al. 1983, Thompson 1996), and alter the functioning of the ecosystem (Randall 1996).

Various tools have been developed and used for controlling rangeland weeds. The most effective herbicide, picloram (4-amino-3, 5, 6-trichloropicolinic acid), can control spotted knapweed for 2 to 5 years, but the weed reestablishes after the herbicide dissipates (Davis 1990). Several species of insects have been

Resumen

El "Spotted Knapweed" (*Centaurea maculosa* Lam.) es un maleza introducida que ha invadido millones de hectáreas de pastizal en Estados Unidos. La siega puede ser útil para reducir esta maleza. Nuestro objetivo fue investigar la respuesta del "Spotted knapweed" y los zacates a la época y frecuencia de segado. Se estudio la respuesta de los zacates y el "Spotted knapweed" a 16 tratamientos de siega aplicados anualmente durante 3 años en dos sitios experimentales. Los tratamientos consistieron en la combinación de segado en primavera, verano y otoño. Los tratamientos se evaluaron bajo un diseño de bloques completos al azar con cuatro repeticiones (16 tratamientos; 4 repeticiones; 2 sitios = 128 unidades experimentales). Después de repetir los tratamientos de siega por 3 años, una sola siega en otoño, cuando el "Spotted knapweed" estaba en las etapas de floración o producción de semilla, redujo su cobertura y la densidad de plantas adulto tanto como cualquiera de los tratamientos de siega repetida. La siega en otoño disminuyó la densidad de adultos en 83 y 85% con respecto a la densidad de las parcelas control de los sitios 1 y 2 respectivamente. Los tratamientos redujeron la densidad de plántulas en el sitio 2, pero la respuesta no fue consistente entre años ni entre tratamientos. En cada sitio la cobertura de "Spotted knapweed" disminuyó (10–36%) en respuesta de algunos de los tratamientos de siega múltiple, mientras la cobertura de los zacates del sitio 1 disminuyó (18–23%) en 1998 en solo 3 de los tratamientos de siega. Para el control parcial de "Spotted knapweed" recomendamos una sola siega aplicada en las etapas de floración o producción de semilla.

released for controlling knapweed (Rees et al. 1996). In some instances, these natural enemies have reduced seed output and damaged roots (Story et al. 1989), but they have not successfully decreased plant density. Repeated grazing by sheep has resulted in reduced knapweed density and lowered reproduction (Olson et al. 1997). Also, sheep have minimal impact on associated grasses if grazing occurs when plants are dormant. More recently, revegetation of infested rangeland has shown some potential for successful weed management, but environmental and economic considerations associated with this intensive system require its thoughtful use (Lym and Tober 1997, Ferrel et al. 1998).

Mowing is a management tool that may reduce spotted knapweed. Kennett et al. (1992) found that repeated partial defoliation of spotted knapweed in a greenhouse experiment reduced root and crown weight. Decreased root and crown weight can reduce long-term survival of individual plants (Bula and Smith 1954, Menke and Trlica 1981). Watson and Renny (1974) reported that

the density of diffuse (*Centaurea diffusa* Lam.) and spotted knapweed plants that produced seed was reduced from 34.3 plants m⁻² in the control to 7.8 and 0.3 plants m⁻² when mowing occurred during the bud and flowering stage, respectively. Mowing during the flowering stage reduced seed germination to 17.9% compared to 91.1% in the control. The effects of mowing on knapweed are not fully understood (Sheley et al. 1998). Currently, mowing is not extensively used for managing knapweed. Repeated mowing within a season has not been studied, and the optimum season for mowing has not been determined.

Our objective was to determine the effect of mowing frequency and season on spotted knapweed density and knapweed, grass, litter, and bare ground cover when treatments were repeated in 3 consecutive growing seasons. We believed that frequent removal of biomass would maximize plant injury and that late-season mowing would damage plants more than early- and mid-season mowing because more biomass is removed. Because of morphological differences between forbs and grasses, we believed that mowing would remove more knapweed biomass than grass biomass as a percentage of total plant weight. If true, this suggested that mowing might affect knapweed more adversely than grasses. We hypothesized that: 1) spotted knapweed would decrease as mowing frequency increased, 2) late-season mowing would decrease spotted knapweed more than early- and mid-season mowing, and 3) mowing would decrease spotted knapweed cover more than grass cover.

Materials and Methods

Study Sites

This study was conducted at 2 sites from 1996 through 1998. Site 1 was located 1 km south of Belgrade, Mont. (45°47'N, 111°10'W) at an elevation of 1,349 m. This site was within the *Festuca idahoensis*-*Agropyron spicatum* habitat type (Mueggler and Stewart 1980) and was dominated by spotted knapweed, smooth brome (*Bromus inermis* Leyss.), and cheatgrass (*Bromus tectorum* L.). The soil is a Beaverell gravelly loam (loamy-skeletal over sandy or sandy-skeletal, mixed, Aridic Argiustoll).

Site 2 was located 15 km southwest of Bozeman, Montana (45°36'N, 111°5'W) at an elevation of 1,340 m. This site was also within the *Festuca idahoensis*-*Agropyron*

spicatum habitat type (Mueggler and Stewart 1980) and was dominated by spotted knapweed, Idaho fescue (*Festuca idahoensis* Elmer), bluebunch wheatgrass (*Agropyron spicatum* Pursh), and Kentucky bluegrass (*Poa pratensis* L.). The soil is 70% Beaverton cobbly loam (loamy-skeletal over sandy or sandy-skeletal, mixed, Typic Argiboroll) and 30% Hyalite loam (fine-loamy, mixed, Typic Argiboroll).

Monthly precipitation data were collected for both sites. Weather stations were located 1.6 and 4.5 km north of Sites 1 and 2, respectively.

Experimental Design

Treatments consisted of 15 mowing regimes and a control. The mowing treatments were: 1 spring mowing (SP1); 1 summer mowing (SU1); 1 fall mowing (F1); 2 spring mowings (SP2); 2 summer mowings (SU2); 2 fall mowings (F2); 1 spring and 1 summer mowing (SP1-SU1); 1 spring and 1 fall mowing (SP1-F1); 1 summer and 1 fall mowing (SU1-F1); 1 spring, 1 summer, and 1 fall mowing (SP1-SU1-F1); 2 spring and 2 summer mowings (SP2-SU2); 2 spring and 2 fall mowings (SP2-F2); 2 summer and 2 fall mowings (SU2-F2); 2 spring, 2 summer, and 2 fall mowings (SP2-SU2-F2); a treatment consisting of mowing at 2 week intervals throughout the growing season (2WK); and a control that received no mowing (NONMOWN). Growth stage of spotted knapweed and date were recorded at each mowing. Treatments were arranged in a randomized-complete-block design with 4 replications. A rotary gasoline-powered push mower with a 53-cm long blade set at a height of 10 cm was used for mowing, and treatments were applied to 1.8-m² plots. We believed this cutting height would maximize removal of knapweed biomass while removing relatively little grass biomass during mid- and late-season mowing. Treatments were applied in 1996 and were repeated on the same plots in 1997 and 1998.

Sampling

Data were collected 22 September through 26 September in 1997 and 28 September through 2 October in 1998 from a randomly placed 20 x 50-cm frame in each plot. Measurements included spotted knapweed seedling and adult density and knapweed, grass, bare ground, and litter cover, visually estimated as a percentage of plot surface area. Knapweed plants between the cotyledon and 2-leaf stage were counted as seedlings. Plants consist-

ing of a rosette with or without reproductive shoots were counted as adults.

Data Analysis

Data from Sites 1 and 2 were analyzed separately because of differences in species composition between sites. Data were analyzed as a split-plot in time with mowing treatment as the whole-plot factor and year as the sub-plot factor. Individual means were compared using a least significant difference test at the 5% level of confidence. In order to provide experimentwise error protection, least significant differences were not calculated unless effects were significant at the 5% level of confidence in the analysis of variance F-tests (Fisher 1960).

Results and Discussion

Precipitation was similar between sites (Table 1). It was wetter in 1997 than in 1998 with significant rainfall occurring in every month during the 1997 growing season. Late summer precipitation was lower in 1998 than in 1997. Growth stage of spotted knapweed was similar for each mowing treatment among years (Table 2).

Table 1. Monthly precipitation within growing season on 2 study sites in south central Montana.

Site	Month	1996	1997	1998
----- (mm)-----				
1	Apr.	9.86	27.93	26.70
	May	28.14	* ^a	34.92
	Jun.	22.59	58.13	79.90
	Jul.	trace	84.42	13.76
	Aug.	6.57	31.02	15.61
2	Sep.	18.90	31.43	16.02
	Apr.	34.51	47.86	27.11
	May	90.17	87.30	28.14
	Jun.	20.75	92.22	102.29
	Jul.	trace	51.14	11.30
	Aug.	14.58	41.70	21.98
	Sep.	22.18	53.61	19.72

^aMissing precipitation data.

Bare Ground and Litter Cover

Year or mowing did not affect amount of litter cover at either site (Table 3). Treatment or year did not affect amount of bare ground at Site 1, but treatment and year had a significant effect on bare ground at Site 2 (Table 3). Bare ground increased with mowing frequency at that site (Fig. 1). Amount of bare ground was higher in 1997 (22%) than in 1998 (14%) at Site 2.

Spotted Knapweed Seedling Density

Spotted knapweed seedling density was affected by mowing at both sites (Table 3). The response of seedling density to mowing varied with year only at Site 2 (Table 3). Most mowing treatments reduced seedling density below the control at Site 2, and the magnitude and consistency of seedling reductions increased with mowing frequency. No mowing regime reduced seedling density below the control at Site 1 (Table 4).

Seedling establishment can be strongly affected by the soil surface environment (Harper et al. 1965), and frequent mowing may have altered the soil microenvironment making it less suitable for seedling establishment. In this study, seedlings were too short to be cut by the mower blade, but blowing soil during mowing may have injured seedlings and enhanced seedling mortality. Watson and Renny (1974) found that mowing could reduce spotted knapweed seed production and germination. Reductions in seedling density likely resulted from reduced seed production in this study. Reduced seedling recruitment may lead to decreases in density of plants over time.

Table 2. Mowing dates and spotted knapweed growth stages for various mowing treatments repeated over years (1996-98) on 2 sites in south central Montana.

Mowing Treatments	Year					
	1996		1997		1998	
	Date	Stage	Date	Stage	Date	Stage
SP1	22/5	r ^a	15/5	r	20/5	r
SP2	22/5	r	15/5	r	20/5	r
	5/6	b	29/5	b	3/6	b
SU1	19/6	b	11/6	b	17/6	b
SU2	19/6	b	11/6	b	17/6	b
	3/7	bu	25/6	bu	1/7	f
F1	21/8	f/s	21/8	f/s	26/8	s
F2	21/8	f/s	21/8	f/s	26/8	s
	4/9	s	4/9	s	9/9	s
2WK	22/5	r	15/5	r	20/5	r
	5/6	b	29/5	b	3/6	b
	19/6	b	11/6	b	17/6	b
	3/7	b	25/6	bu	1/7	f
	17/7	f	9/7	f	15/7	f
	31/7	f/s	23/7	f	29/7	f/s
	10/8	f/s	7/8	f/s	12/8	f/s
	21/8	s	21/8	f/s	26/8	s
	4/9	s	4/9	s	9/9	s
	18/9	s	18/9	s	23/9	s

^a r=rosette, b=bolt, bu=bud, f=flowering, s=seed bearing.

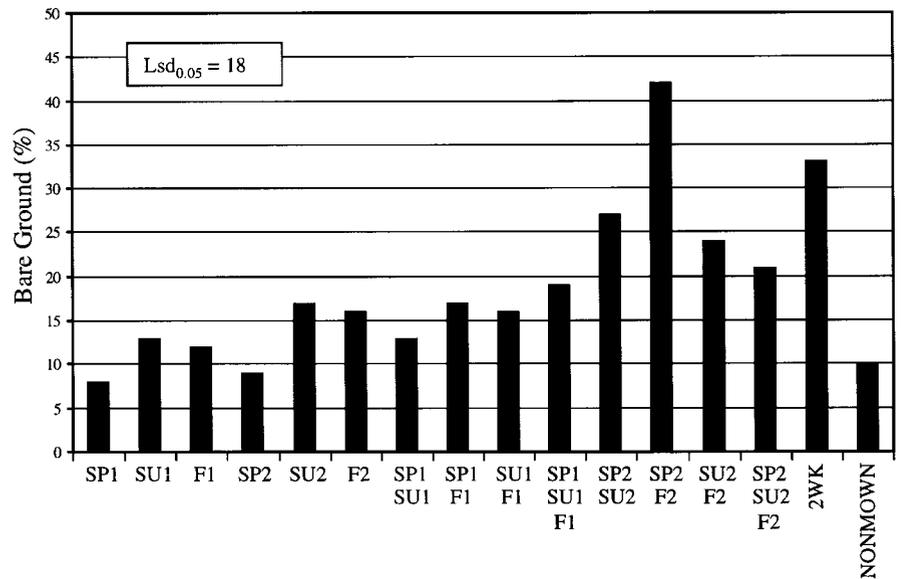


Fig. 1. Effect of various mowing treatments repeated over years (1996-98) on bare ground at Site 2 in south central Montana.

Spotted Knapweed Adult Density

The effect of mowing on spotted knapweed adult density was dependent on year at both sites (Table 3). Adult density increased during the study period in the control at Site 1 (Table 4). However, adult density did not increase during the study

period where summer and/or fall mowing occurred at this site. Mid- to late- season mowing may discourage increases in adult density. The control had similar adult densities in 1997 and 1998 at Site 2.

Every mowing regime, except the treatment consisting of 1 spring mowing, decreased spotted knapweed adult density below the control at Site 1 in 1998 (Table 4). No treatment decreased adult density below the control at Site 1 in 1997. Most treatments decreased adult density at Site 2 in both years.

Fall mowing was more effective than spring or summer mowing at Site 1 in 1997 and at both sites in 1998. Late season mowing removes more spotted knapweed biomass and may enhance knapweed mortality. Late season precipitation was low at both sites in 1998, and moisture stress may have inhibited knapweed recovery (Table 1).

A single fall mowing, when spotted knapweed was in the flowering or seed producing stage, reduced knapweed cover and adult density as much as any treatment consisting of repeated mowing at both sites in 1998 (Table 4 and 5). Although a single fall mowing each fall did not affect adult density after 2 years (1996-97), 1 fall mowing for 3 years (1996-98) decreased adult plant density. Annual mowing may have an additive effect on knapweed density. Mowing after the initiation of bolting removes the apical meristem from knapweed plants. Plants that survive this mowing initiate growth from lateral buds resulting in knapweed plants with a decumbent growth habit (Devlin and Witham 1983).

Table 3. Mean squares and degrees of freedom (df) for main and interaction effects where the response of frequency and timing of mowing on spotted knapweed and grasses was measured in 1997–98 on 2 sites in south central Montana.

Site	Source	df	Mean Squares					
			Knapweed Density (plants m ⁻²)		Cover (%)			
			Seedling	Adult	Knapweed	Grass	Litter	Bare ground
1	REP	3	231187.5* ^a	5520.8*	42.3	650.0*	4729.4*	6262.5*
	MOW ^b	15	228695.8*	10838.3*	309.7*	309.3	649.7	1145.9
	REP*MOW	45	89675.3*	1652.5	41.8	303.3*	741.7*	883.5*
	YEAR	1	59512.5	378.1	10.1	608.1	1029.4	1568.0
	REP*YEAR	3	79270.8	2444.8	218.6*	403.9*	1455.7*	368.9
	YEAR*MOW	15	102572.5	3863.1*	141.8*	223.2*	548.5	349.8
	ERROR	45	44319.7	1112.0	52.9	105.7	363.8	268.5
	2	REP	3	21628.1	1805.2	13.5	630.6*	820.4
MOW		15	29194.8*	22248.1*	583.1*	180.9	718.4	670.4*
REP*MOW		45	6665.3	4458.5*	107.8*	207.5*	552.3	302.5*
YEAR		1	363378.1*	50.0	409.7	220.5	2547.2	2072.1*
REP*YEAR		3	20103.1	3160.4	217.1*	204.1*	1812.4*	29.9
YEAR*MOW		15	22673.1*	7650.0*	165.8*	50.3	382.3	164.2
ERROR		45	9184.8	2344.9	57.0	50.6	443.3	159.7

^aMean squares followed by * are significant at the 5% level of confidence.

^bMowing treatment effect.

Plants with a prostrate growth habit are not likely to be affected because very little biomass is removed during mowing. For this reason, repeated mowing typically does not cause further reductions in adult knapweed density. The season of mowing is more important than mowing frequency in reducing adult density.

Depletion of carbohydrate reserves in response to defoliation has been shown to cause plant death in some instances (Weinmann 1948) and may explain reductions in plant density in these experiments. However, the results of a sheep grazing study indicate that growth and survival of spotted knapweed are not correlated with carbohydrate reserves (Olson and Wallander 1997). Sheep grazed grasses more intensively than knapweed in that study. Relative defoliation pressure applied to knapweed and grasses may be different in mown systems than in grazed systems because of livestock preferences. The lower growth habit of grasses may allow them to escape severe defoliation from mowing. Decreased knapweed carbohydrate reserves and light grass defoliation could interact to decrease knapweed density.

Knapweed and Grass Cover

The effect of mowing on spotted knapweed cover depended on year at both sites (Table 3). The effect of mowing on grass cover depended on year at Site 1, and grass cover was not affected by year or mowing at Site 2 (Table 3).

Only 3 treatments (SU1, F1, and SP2-F2) decreased percent cover of grass below the control at Site 1 in 1998 (Table 5). Two treatments (SP1-SU1 and SU2-

F2) consisting of repeated mowing increased grass cover above the control at Site 1 in 1997. No treatment affected cover of grass at Site 2.

While only a few treatments decreased percent cover of grass below the control, spotted knapweed cover and adult density were severely decreased by several mowing treatments. Conversely, Kennett et al. (1992) measured final foliage weight per pot and found that knapweed was less sensitive than bluebunch wheatgrass to defoliation in a greenhouse experiment. Reductions in knapweed cover and density in our experiment resulted from plant death that occurred in response to 3 years

of mowing. Kennett et al. (1992) found that 1 year of clipping reduced knapweed root, crown, and foliage at final harvest, and this weakening of plants may result in plant death if clipping treatments are continued for multiple years. Blaisdell and Pechanec (1949) found that annual clipping at the soil level affected biomass production of the indigenous forb arrowleaf balsamroot [*Balsamorhiza sagittata* (Pursh) Nutt.] less severely than bluebunch wheatgrass. In our study, mowing treatments removed much less biomass, and this may explain differences in the responses of these 2 studies.

Table 4. Response of spotted knapweed density to various mowing treatments repeated over years (1996-98) on 2 sites in south central Montana.

Mowing Treatment	Site 1				Site 2			
	Seedling ^a		Adult		Seedling		Adult	
	1997-98	1997	1998	1997	1998	1997	1998	
	(Plants m ⁻²)							
SP1	504	98	148	20	288	78	130	
SU1	135	128	93	18	90	93	175	
F1	542	43	28	95	115	173	35	
SP2	598	53	128	33	210	95	208	
SU2	152	30	45	35	100	128	148	
F2	303	20	10	98	53	115	30	
SP1-SU1	172	63	48	8	240	130	178	
SP1-F1	448	48	15	90	148	80	23	
SU1-F1	324	20	45	50	28	53	68	
SP1-SU1-F1	251	63	45	5	63	45	48	
SP2-SU2	157	70	25	0	140	35	50	
SP2-F2	119	28	10	33	173	48	8	
SU2-F2	213	23	25	25	80	83	53	
SP2-SU2-F2	108	40	18	3	70	43	33	
2WK	91	45	25	3	70	53	50	
NONMOWN	382	65	183	93	445	210	205	
Lsd _{0,05}	303		48		137		69	

^aThe year by treatment interaction was not significant at the 5% level of confidence, so treatment means were averaged across years.

Table 5. Response of spotted knapweed and grass cover to various mowing treatments repeated over years (1996–98) on 2 sites in south central Montana

Mowing Treatment	Site 1				Site 2 ^a	
	Knapweed		Grass		Knapweed	
	1997	1998	1997	1998	1997	1998
	------(%)-----					
SP1	15	32	26	25	16	25
SU1	20	16	20	6	20	21
F1	10	9	15	6	24	5
SP2	13	35	18	23	24	37
SU2	10	10	21	21	24	21
F2	9	4	25	15	15	5
SP1-SU1	16	9	44	31	29	21
SP1-F1	9	5	18	19	18	7
SU1-F1	10	9	21	16	9	7
SP1-SU1-F1	13	9	19	18	10	7
SP2-SU2	8	6	15	29	9	8
SP2-F2	6	4	21	11	6	4
SU2-F2	10	11	41	15	21	6
SP2-SU2-F2	11	4	33	16	15	7
2WK	9	4	16	22	19	9
NONMOWN	16	26	19	29	29	40
Lsd _{0,05}	10		15		11	

^aGrass cover was not affected by mowing at Site 2 at the 5% level of confidence.

Conclusions

Spotted knapweed cover was decreased more severely and consistently than grass cover by mowing. Mowing appeared to shift the competitive balance in favor of grasses, and for this reason, repeating mowing regimes for multiple years may cause a decrease in spotted knapweed and a corresponding increase in grasses.

Mowing can decrease spotted knapweed seedling density, but the response varied with site and year in this study. Several mowing regimes decreased spotted knapweed adult density below the control. After repeating mowing regimes for 3 years, a single fall mowing, when spotted knapweed was in the flowering or seed producing stage, reduced spotted knapweed cover and adult density as much as any treatment consisting of repeated mowing. Season of mowing appears more important than mowing frequency in reducing adult spotted knapweed density. We recommend a single annual mowing, applied at the flowering or seed producing stage, for the partial control of spotted knapweed.

Literature Cited

Blaisdell, J.P. and J.F. Pechanec. 1949. Effects of herbage removal at various dates on vigor of bluebunch wheatgrass and arrowleaf balsamroot. *J. Ecol.* 30:298–305.
 Bula, R.J. and K. Smith. 1954. Cold resistance and chemical composition in overwintering alfalfa, red clover and sweetclover. *Agron. J.* 46:397–401.

Chicoine, E.S., P.K. Fay, and G.A. Nielsen. 1985. Predicting weed migration from soil and climate maps. *Weed Sci.* 34:57–61.
 Davis, E.S. 1990. Spotted knapweed (*Centaurea maculosa* L.) seed longevity, chemical control and seed morphology. M.S. Thesis, Montana State Univ. Bozeman, Mont.
 Devlin, M.D. and F.H. Witham. 1983. *Plant Physiology*. Prindle, Weber and Schmidt. Boston, Mass.
 Ferrell, M.A., T.D. Whitson, D.W. Koch, and A.E. Gade. 1998. Leafy spurge (*Euphorbia esula*) control with several grass species. *Weed Technol.* 12:374–380.
 Fisher, R.A. 1960. *The Design of Experiments*, 7th ed. Hafner. New York.
 Harper, J.L., J.T. Williams, and G.R. Sagar. 1965. The behavior of seeds in soil. Part 1. The heterogeneity of soil surfaces and its role in determining the establishment of plants from seed. *J. Ecol.* 53, 273–286.
 Kennett, G.A., J.R. Lacey, C.A. Butt, K.M. Olson-Rutz, and M.R. Haferkamp. 1992. Effects of defoliation, shading and competition on spotted knapweed and bluebunch wheatgrass. *J. Range Manage.* 45:363–369.
 Lacey, J.R., C.B. Marlow, and J.R. Lane. 1989. Influence of spotted knapweed (*Centaurea maculosa*) on surface runoff and sediment yield. *Weed Technol.* 3:627–631.
 Lym, R.G. and D.A. Tober. 1997. Competitive grasses for leafy spurge (*Euphorbia esula*) reduction. *Weed Technol.* 11:787–792.
 Menke, J.W. and M.J. Trlica. 1981. Carbohydrate reserve, phenology, and growth cycles of nine Colorado range species. *J. Range Manage.* 34:269–277.
 Mueggler, W.F. and W.L. Stewart. 1980. Grassland and shrubland habitat types of western Montana. USDA Forest Service Gen. Tech. Rep. Int-66.

Olson, B.E. and R.T. Wallander. 1997. Biomass and carbohydrates of spotted knapweed and Idaho fescue after repeated grazing. *J. Range Manage.* 50:409–412.
 Olson, B.E., R.T. Wallander, and J.R. Lacey. 1997. Effects of sheep grazing on a spotted knapweed-infested Idaho fescue community. *J. Range Manage.* 50:386–390.
 Randall, J.M. 1996. Weed control for the preservation of biological diversity. *Weed Technol.* 10:370–383.
 Rees, N.E., P.C. Quimby Jr., G.L. Piper, E.M. Coombs, C.E. Turner, N.R. Spencer, and L.V. Knutson. 1996. *Biological Control of Weeds in the West*. Western Society of Weed Science, USDA-ARS. Montana State Univ., Bozeman, Mont.
 Roché, B.F., Jr. and C.J. Talbott. 1986. The collection history of *Centaureas* found in Washington State. *Agr. Res. Center Res. Bull.* XB0978. Washington State Univ., Pullman, Wash.
 Sheley, R.L. and P.M. Rice. 1995. Invasion USA: A chronicle of weed invasion. *In: Invasion exotics: A threat to the greater northwest! What is our status? Montana Weed Control Assoc. Annu. Conf. Proc.* Missoula, Mont.
 Sheley, R.L., J.S. Jacobs, and M.F. Carpinelli. 1998. Distribution, biology and management of diffuse knapweed (*Centaurea diffusa*) and spotted knapweed (*Centaurea maculosa*). *Weed Technol.* 12:353–362.
 Spoon, C.W., H.R. Bowles, and A. Kulla. 1983. Noxious weeds in the Lolo National Forest. A situation analysis staff paper. USDA Forest Service North Region. Missoula, Mont.
 Story, J.M., K.W. Boggs, W.R. Good, and R.M. Nowierski. 1989. The seed moth, *Metzneria paucipunctella*: its impact on spotted knapweed seed production and 2 seed head flies, *Urophora* spp, p. 172–174. *In: P. K. Fay and J. R. Lacey (eds.), Proc. of the Knapweed Symp.* Montana State Univ., Bozeman, Mont.
 Strang, R.M., K.M. Lindsay, and R.S. Price. 1979. Knapweeds: British Columbia's undesirable aliens. *Rangelands.* 1:141–143.
 Thompson, M. J. 1996. Winter foraging response of elk to spotted knapweed removal. *Northwest Sci.* 70:10–19.
 Tyser, R.W. and C.H. Key. 1988. Spotted knapweed in natural area fescue grasslands: and ecological assessment. *Northwest Sci.* 62:151–160.
 Watson, A.K. and A.J. Renney. 1974. The biology of Canadian weeds. *Centaurea diffusa* and *C. maculosa*. *Can. J. Plant Sci.* 54:687–701.
 Weinmann, H. 1948. Underground development and reserves of grasses. *J. Brit. Grassl. Soc.* 3:115–140.

Estimating herbage standing crop with visual obstruction in tallgrass prairie

LANCE T. VERMEIRE AND ROBERT L. GILLEN

Authors are research assistant, Department of Range, Wildlife, and Fisheries Management, Texas Tech University, Lubbock, Tex. 79409-2125, and rangeland scientist, USDA-ARS, Southern Plains Range Research Station, Woodward, Okla. 73801. At the time of research, authors were research assistant and professor, Department of Plant and Soil Sciences, Oklahoma State University, Stillwater, Okla. 74078-0507.

Abstract

We evaluated the visual obstruction method as a non-destructive means of estimating herbage standing crop in tallgrass prairie. Prediction models were developed for both plot-level and pasture-level estimates by regressing standing crop from clipped plots on visual obstruction measurements (VOM) from 48, 20-sample trials. Trials were conducted year-round on burned and non-burned sites in different seral stages and with various levels of productivity and grazing pressure. Separate models were required for burned and non-burned pastures, but both applied across all other variables and were unaffected by community heterogeneity. Coefficients of determination were 0.95 and 0.90 for burned and non-burned pastures, respectively. Use of a more precise measurement scale for visual obstruction did not improve the prediction models. Models for standing crop based on individual quadrats explained less variation than models based on transect averages. The highest correlations with visual obstruction were obtained with 20 x 50 cm quadrats placed adjacent to the measurement pole and oriented toward the observer. The visual obstruction method required little training and mean deviations of student readings from those of the trainer were less than 1 cm. Sampling efficiency is improved with the visual obstruction method because it is reasonably accurate and 6 times faster than clipping. Standing crop estimates can be calculated immediately and less field equipment is needed.

Key Words: non-destructive sampling, ocular estimation, prescribed burning, Robel pole

Measurements of herbage standing crop are often required for effective rangeland management. Standing crop can be measured directly by clipping herbage from random quadrats and extrapolating dry weight over the area of interest. The level of accuracy produced by direct measurement depends primarily on the sampling design. Although clipping is accurate, it is often dreaded by researchers and altogether avoided by many land managers because of the time and labor required to harvest the vegetation. Drying and weighing of vegetation also delay the calculation of standing crop estimates.

Numerous indirect methods have been tested to expedite the estimation of herbaceous standing crop, but accuracy is sacrificed and the applicability of individual models is typically limited

Resumen

Evaluamos el método de obstrucción visual como un medio no destructivo para estimar la cosecha de forraje en pie de praderas de zacates altos. Se desarrollaron modelos de predicción para las estimaciones a nivel de parcela y a nivel de potrero, esto se realizó mediante regresiones entre la cosecha en pie cortada de las parcelas y las mediciones obtenidas con el método de obstrucción visual en 48 ensayos de 20 muestras cada uno. Los ensayos se condujeron a lo largo del año en sitios quemados y no quemados, con diferentes etapas serales y con varios niveles de productividad y presión de apacentamiento. Se requirieron modelos separados para los potreros quemados y no quemados, pero ambos aplicaron a lo largo de otras variables y no fueron afectados por la heterogeneidad de la comunidad. Los coeficientes de determinación fueron de 0.95 y 0.90 para los potreros quemados y no quemados respectivamente. El uso de una escala de medición más precisa en el método de obstrucción visual no mejora los modelos de predicción. Los modelos para la cosecha en pie basados en cuadrantes individuales explicaron menos la variación que los modelos basados en los promedios de transectos. Las más altas correlaciones con la obstrucción visual fueron obtenidas con cuadrantes de 20 X 50 cm ubicados adyacentemente de el poste de medida y orientados hacia el observador. El método de obstrucción visual requiere poco entrenamiento y la media de desviación entre las lecturas de estudiantes y la del entrenador fue menos de 1 cm. La eficiencia de muestreo es mejorada con el método de obstrucción visual porque es razonablemente certero y 6 veces más rápido que el corte. Las estimaciones de la cosecha en pie pueden ser calculadas inmediatamente y se requiere menos equipo de campo.

(Michalk and Herbert 1977, Gonzalez et al. 1990, Catchpole and Wheeler 1992, Harms et al. 1997). However, Robel et al. (1970) detected a strong relationship between visual obstruction measurements (VOM) and standing crop in homogeneous tallgrass communities. Our overall objective was to assess the effectiveness of VOM as a non-destructive method of estimating herbaceous standing crop. Specific objectives were to: 1) determine the effects of season of year and fire management on VOM, 2) assess the effect of the precision of the measurement scale used for VOM on the resulting estimates of standing crop, 3) evaluate the effects of quadrat size and positioning, and 4) examine the time and training required to use the visual obstruction method.

Materials and Methods

Study area

The study was conducted from 1994 to 1996 on native tallgrass prairie near Stillwater, Okla. (36° 04' N, 97° 13' W). The continental climate allows a 204-day frost-free growing season from April to October. Mean annual temperature is 15° C, with an average daily minimum of -4.3° C in January and an average daily maximum of 34° C in August. Mean annual precipitation is 831 mm, with 65% falling as rain from May to October (Myers 1982). Growing-season (May to August) precipitation from 1994 to 1996 was 70, 169, and 114% of the long-term (1893 to 1980) mean, respectively.

Range sites used in the study included sandy savannah, loamy prairie, shallow prairie, and eroded prairie. Dominant grasses were big bluestem [*Andropogon gerardii* Vitman], little bluestem [*Schizachyrium scoparium* (Michx.) Nash], indiagrass [*Sorghastrum nutans* (L.) Nash], and tall dropseed [*Sporobolus asper* (Michx.) Kunth]. Western ragweed [*Ambrosia psilostachya* DC] and annual broomweed [*Amphiachyris dracunculoides* (DC) Nutt. ex Rydb.] were the dominant forbs. Grama grasses [*Bouteloua* spp. Lag.], annual threeawn [*Aristida oligantha* Michx.], and forbs were more prominent on sites in lower seral stages.

Methods

We conducted 48 trials over a wide array of standing crops and species composition. Each trial consisted of 20 plots arranged systematically along a pace transect with an approximate distance of 15 m between plots. All sites were exposed to cattle grazing at various stocking rates under short-duration, intensive-early stocking, or continuous season-long grazing systems. Trials were performed during the growing season following spring prescribed burns (n = 17), during the growing season without prescribed burning (n = 19), and during plant dormancy (n = 12). Average herbaceous standing crop among trials ranged from 570 to 3,390 kg ha⁻¹ in burned pastures and 1,680 to 6,630 kg ha⁻¹ in non-burned pastures. Herbaceous standing crop among individual plots ranged from 220 to 6,280 kg ha⁻¹ in burned pastures and 220 to 13,370 kg ha⁻¹ in non-burned pastures.

Our use of the visual obstruction method was based on the methods of Robel et al. (1970) with modifications of the measurement pole and the number of observations taken per plot. The measurement pole was

a wooden dowel (2.5 x 100 cm) with alternating red and white bands 1 dm wide and black lines at 2.5-cm intervals. A second wooden dowel (1 cm x 1 m) was attached to the measurement pole by a 4-m string to locate a consistent observation point 4 m from the measurement pole and 1 m above the ground level. The measurement pole was placed at the center of the 20-cm side of each 20 x 50 cm plot, on the side opposite the observer. A single visual obstruction reading was taken for each plot by recording the height of the lowest visible increment on the pole. The mark was considered visible if any portion of it could be seen. Visual obstruction readings were recorded in both 2.5 and 5.0-cm increments to assess whether measurement increment influenced the precision of prediction models. Vegetation in the plot was then clipped to ground level and oven-dried to a constant weight to determine standing crop. Quadrats from the first 15 trials were divided into two, 20 x 25 cm subplots to examine the effects of altering plot size and location. One subplot was the half of the plot adjacent to the measurement pole and the other subplot was the half of the plot nearer to the observer.

Sampling time was noted from the time of placing the quadrat or pole to completion of the plot measurements (visual obstruction and clipping). Two levels of training were employed to evaluate the impact of this factor on the visual obstruction method. First, 20 plots representing a range of standing crops were marked on a site. A brief (1 to 2 min.) verbal overview of VOM was given to 3 graduate students. Each student then recorded independent readings from 10 of the marked plots. The method was then described a second time in more detail, 5 visual demonstrations were made, and questions were discussed (5 to 10 min.). The students then made independent readings on the remaining 10 marked plots. Deviations of students'

readings from those of the trainer were calculated for each level of training.

Relationships between standing crop and visual obstruction were determined by regression analysis using either trial means or individual plots as observations (SAS 1985). Indicator regression was used to identify differences in models by season, burning treatment, and measurement increments (Neter et al. 1990). For trial data, residuals were regressed on coefficients of variation of standing crop to assess the effects of community heterogeneity on the prediction capabilities of VOM models. We evaluated the relationships between visual obstruction readings and standing crop from subplots and whole plots by correlation analysis (SAS 1985). All results are based on 2.5-cm visual obstruction increments except when 2.5- and 5.0-cm increments are being directly compared.

We calculated 95% prediction intervals for standing crop for the regression models based on trial means. Using the variances of standing crop estimated from clipping for each trial, we used Stein's formula (Steel and Torrie 1980) to calculate the number of clip plots required to achieve the same precision as the regression model. We compared the field time required for each method by multiplying the minutes per clip plot times the estimated number of clip plots and the minutes per visual obstruction measurement times 20 (the regression model was based on trials of 20 observations).

Results and Discussion

Prediction models did not differ between dormant and growing season trials (P = 0.85), but were affected by fire management (P < 0.01). Burned pastures had less biomass per cm of visual obstruction

Table 1. Visual obstruction regression coefficients and statistics for burned and non-burned pastures measured by 2.5 and 5.0-cm increments.

	Burned pastures		Non-burned pastures	
	Visual obstructive increment (cm)			
	2.5	5.0	2.5	5.0
Slope	129 ^a (8) ^b	130 (8)	174 (11)	175 (11)
Intercept	-21 ^c (116)	-202 (124)	398 (200)	160 (212)
Coefficient of determination (r ²)	0.95	0.95	0.90	0.90
Maximum estimate error ^d	----- (kg ha ⁻¹) -----			
Smallest	110	108	147	147
Largest	272	273	438	427
Mean	155	154	209	207

^aAll slopes are different from 0 (P < 0.05)

^bStandard error of estimate

^cAll intercepts are similar and not different from 0 (P > 0.05)

^dRange and mean of maximum estimate errors were calculated from 95% confidence intervals.

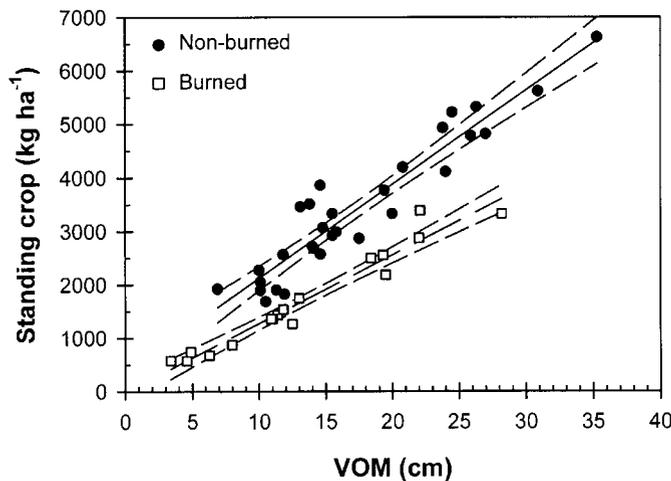


Fig. 1. Relationships between standing crop and visual obstruction measurements (VOM) with 95% confidence intervals for 17 burned and 31 non-burned pasture trials.

tion than non-burned pastures (Fig. 1). At least 90% of the variation in standing crop was explained by visual obstruction and estimate errors were low for both burned and non-burned pastures (Table 1).

Our models appear robust for heterogeneous tallgrass communities with a wide range of standing crop and species composition. Coefficients of determination were similar to the 0.95 value Robel et al. (1970) achieved using similar measurement procedures on homogeneous sites. Regression coefficients are not comparable between the 2 studies because Robel et al. (1970) did not collect the lower 5 cm of standing crop.

Although standing crop from growing- and dormant-season trials was explained with a single model, differences could occur in some areas. The ratio of standing crop to visual obstruction may be reduced as plants become weathered (Ratliff and Heady 1962, Pieper et al. 1974), or increase if heavy snow or wind compress the vegetation. Significant lodging was not encountered in this study.

Burned pastures supported less biomass per centimeter of visual obstruction because standing dead biomass from previous years' growth had largely been consumed by fire. Heavily grazed pastures might produce the same effect since limited amounts of standing dead biomass are retained between years. On the other hand, regression models from pastures rested for long periods might have greater slopes than models from our non-burned pastures because larger amounts of standing dead biomass would have been accumulated.

Residuals were not related to trial standing crop C.V. for burned ($P = 0.22$) or non-burned ($P = 0.18$) pastures, indicating

prediction capabilities were not affected by trials with greater structural heterogeneity. Coefficients of variation for standing crop were 17 to 46% for burned trials and 19 to 88% in non-burned trials.

Visual obstruction was less effective at measuring standing crop when individual plots were used as observations (Fig. 2, Fig. 3). Separate models were required for estimating the standing crop of individual plots in burned and non-burned pastures ($P < 0.01$). Coefficients of determination for models based on plots, 0.64 to 0.79, were 16 to 26 percentage units lower than those for models based on trials. Models developed for sandhills sites had coeffi-

icients of determination of only 0.31 to 0.41 (Volesky et al. 1999) but the range of standing crop sampled was smaller in the sandhills study. In contrast to our results, averaging data from 12 plots and constructing models based on pastures (or trials) did not improve the strength of the relationship between visual obstruction and standing crop (Volesky et al. 1999).

Regression models based on plots account for less variation because the true area measured by visual obstruction is unknown, 3-dimensional, and probably varies between points, but quadrat size is 2-dimensional and constant. Prediction models based on individual plots are dependent on the appropriateness of the quadrat design for any given point. Models developed at the trial level reduce this source of error by averaging both visual obstruction and standing crop over many points. At the trial level, visual obstruction is not associated with an arbitrary plot size. We recommend using models developed at the trial level because they are more relevant to measurement objectives and are also more precise.

Models developed from trial visual obstruction readings at 2.5 and 5.0-cm increments were similar for burned ($P = 0.98$) and non-burned ($P = 0.94$) pastures (Table 1). Increasing the precision of visual obstruction readings did not improve the precision of standing crop estimates. Either the method was not sensitive to small changes in visual obstruction or observers were unable to make accurate readings at 2.5-cm increments. We believe

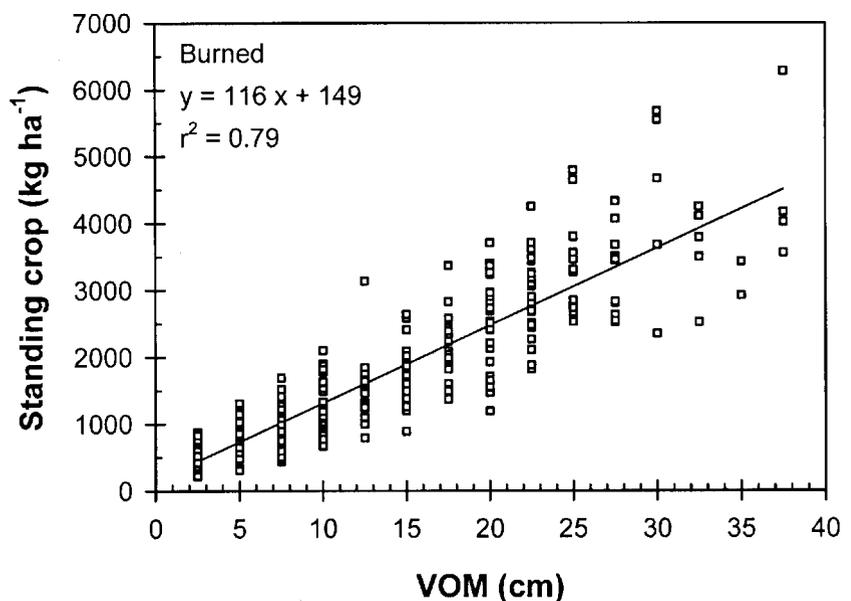


Fig. 2. Relationships between plot standing crop and visual obstruction measurements (VOM) in burned pastures ($n = 350$).

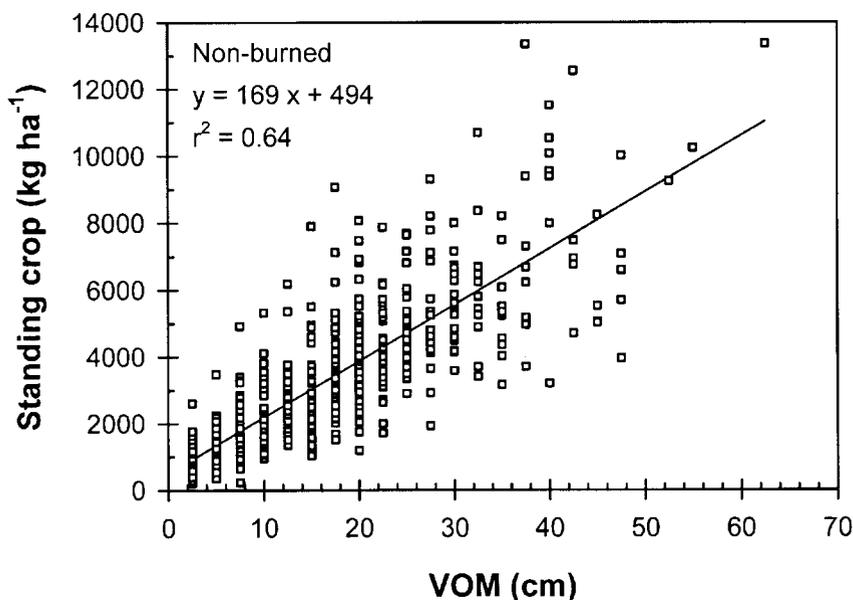


Fig. 3. Relationships between plot standing crop and visual obstruction measurements (VOM) in non-burned pastures (n = 619).

the method was not sensitive to small changes in visual obstruction increment. Harmony et al. (1997) used a 4 x 16-mm telescope to take readings and explained 63% of the variation in standing crop with individual visual obstruction readings. We obtained similar values from non-burned sites using 2.5-cm ($r^2 = 0.64$) and 5.0-cm ($r^2 = 0.63$) increments when individual readings were taken without visual aids and regressed on standing crop.

Visual obstruction measurements were correlated with standing crop estimates from all plot designs ($P < 0.01$). The strongest correlation was with 20 x 50 cm quadrats ($r = 0.78$), followed by subplots adjacent to the measurement stick ($r = 0.75$) and those nearest the observer ($r = 0.63$). We believe plant stature and morphology are the primary factors controlling the volume measured by visual obstruction. As vegetative height increases, plants farther from the measurement pole contribute to visual obstruction and longer quadrats would be required. The appropriate quadrat width should depend on whether canopies of dominant plants are horizontally compressed or diffuse. Large, widely-spreading plants adjacent to narrow plots could affect visual obstruction readings because they would cause visual obstruction but could not be accounted for by clipping since they are not rooted in the plot. In this case, all vegetation above the plot should be clipped, whether or not it is rooted in the plot. As structural homogeneity increases, plot size and shape become less important.

Mean deviations of student readings were 1.8, 1.3, and 1.0 cm from those of the trainer after a verbal description of the visual obstruction method. Visual demonstrations reduced the deviations to 0.8, 0.6, and 0.3 cm. The low variability of measurements among observers with only brief training indicates the visual obstruction method is an objective estimation technique.

To achieve equal precision between clipping and visual obstruction methods in burned pastures, an average of 44 plots must be clipped. The required number of clip plots varied with trial and ranged from 3 to 127. For unburned pastures, the number of clip plots required for equal precision averaged 346 and ranged from 36 to 1645. About 6 visual obstruction measurements could be taken in the 2 min. required to clip a 0.1-m² quadrat. On average, the time required to clip plots would require 88 min. in burned pastures and 692 min. in unburned pastures while visual obstruction would require 6.6 min. in both burned and unburned pastures. We assume that if plots were equally distributed over the sample area, total travel time between plots would be equal between methods. These comparisons do not include the time required to dry and weigh clip samples.

Conclusion

The visual obstruction method is an effective, non-destructive tool for estimating herbaceous standing crop in tallgrass prairie. Although separate VOM models

were required for non-burned pastures and those that had been burned since the previous growing season, our models predicted standing crop year-round across multiple range sites, seral stages, and stocking rates. Because the method is reasonably accurate and much faster than clipping, the amount of data obtained per unit of time can be increased greatly. Additionally, fewer materials are required in the field, the need for drying and weighing vegetation is eliminated, and standing crop estimates can be calculated immediately by entering the mean visual obstruction into the appropriate regression model. Additional tests should be conducted to evaluate the applicability of the visual obstruction method and tallgrass prairie models to other rangeland regions.

Literature Cited

- Catchpole, W.R. and C.J. Wheeler. 1992. Estimating plant biomass: a review of techniques. *Australian J. Ecol.* 17:121-131.
- Gonzalez, M.A., M.A. Hussey, and B.E. Conrad. 1990. Plant height, disk, and capacitance meters used to estimate bermudagrass herbage mass. *Agron. J.* 82:861-864.
- Harmony, K.R., K.J. Moore, J.R. George, E.C. Brummer, and J.R. Russell. 1997. Determination of pasture biomass using four indirect methods. *Agron. J.* 89:665-672.
- Michalk, D.L. and P.K. Herbert. 1977. Assessment of four techniques for estimating yield on dryland pastures. *Agron. J.* 69:864-868.
- Myers, H.R. 1982. Climatological data of Stillwater, Oklahoma, 1893-1980. Oklahoma Agr. Exp. Sta. Res. Rep. P-821.
- Neter, J., M.H. Kutner, C.J. Nachtsheim, and W. Wasserman. 1990. Applied linear regression analysis. Richard D. Irwin, Chicago, Ill.
- Pieper, R.D., C.H. Herbel, D.D. Dwyer, and R.E. Banner. 1974. Management implications of herbage weight changes on native rangeland. *J. Soil Water Conserv.* 29:227-229.
- Ratliff, R.D. and H.F. Heady. 1962. Seasonal changes in herbage weight in an annual grass community. *J. Range Manage.* 15:146-149.
- Robel, R.J., J.N. Briggs, A.D. Dayton, and L.C. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. *J. Range Manage.* 23:295-297.
- SAS Institute. 1985. SAS/STAT Guide for personal computers, Version 6 ed. Cary, N.C.
- Steel, R.G.D., and J.H. Torrie. 1980. Principles and procedures of statistics. McGraw-Hill Book Co., New York.
- Volesky, J.D., W.D. Schacht, and P.E. Reece. 1999. Leaf area, visual obstruction, and standing crop relationships on Sandhills rangeland. *J. Range Manage.* 52:494-499.

Detecting fragmentation of cover in desert grasslands using line intercept

ROBERT O. KUEHL, MITCHEL P. MCCLARAN, AND JUSTIN VAN ZEE

Authors are professor emeritus, Statistical Support; associate professor, Range Management, College of Agriculture, University of Arizona, Tucson, Ariz. 85721; and biological soils technician, USDA-ARS, Jornada Experimental Range, New Mexico State University, Las Cruces, N.M. 88003.

Abstract

Changes in the amount or spatial distribution of grass plants are thought to be indicative of the stability of desert grasslands. This study assessed, through simulation, the sensitivity of statistical properties for distance between plants (fetch length), measured with a line intercept transect, to changes in the spatial distribution and amount of plant cover. Monitoring plots, 30 X 30 m, were simulated for 1, 2.5, 5, 10 and 15% grass cover with random and fragmented spatial distribution. Fetch lengths were measured on 2 randomly placed 30 m transects. In addition to the median and interquartile range, the asymmetry of the sampling distributions was measured with a ratio $[(\text{maximum}-\text{median})/(\text{median}-\text{minimum})]$ that would identify the presence of at least 1 large open space. The accuracy of the fetch length method was confirmed by the similarity of its sampling distribution to that for the well known random point-to-plant sampling procedure. In both the fetch length and the point-to-plant measures, the median and interquartile range increased with decreasing cover for random and fragmented distribution. The asymmetry estimate increased sharply with increasing cover for the fragmented distribution but asymmetry was nearly constant with increasing cover for the random distribution. The results suggest that the evaluation of changes over time at a monitoring site could use fetch lengths measured along a line intercept transect to detect changes in both absolute and spatial arrangement of cover.

Key Words: fetch length, monitoring, simulation

In desert grasslands, changes in the amount or spatial distribution of grass plants are thought to contribute to the potential for soil erosion, the conversion from grass to shrub vegetation, and the redistribution of soil nutrients from fine-scale (centimeters), associated with grasses, to larger-scale (meters), associated with shrubs (Schlesinger et al. 1990, Weltz et al. 1998). Furthermore, these changes tend to create positive feedbacks that reinforce their trends and permanence. Until recently, detecting changes in the spatial distribution of grass cover had received very little attention for purposes of rangeland monitoring compared to efforts to detect changes in absolute amount of grass cover (Tongway and Hindley 1995, de Soyza et al. 1997, Whitford et al. 1998). These recent efforts are beginning to address the infor-

The Arizona Agricultural Experiment Station and The University of Arizona provided partial financial support for this work, and E.L. Smith and G.B. Ruyle provided helpful comments during the formative stages of this work.

Manuscript accepted: 17 Apr. 2000.

Resumen

Se piensa que los cambios en la cantidad de distribución espacial de las plantas de zacates desérticos son un indicador de la estabilidad de los pastizales desérticos. Este estudio evalúa, a través de simulación, la sensibilidad de las propiedades estadísticas de la distancia entre plantas medida con transecto de línea de intercepción a los cambios en la distribución espacial y la cantidad de cobertura vegetal. Se simularon 30 parcelas de monitoreo de 6 X 30 m con 1, 2.5, 5, 10 y 15% de cobertura de zacates con una distribución aleatoria y fragmentada. La longitud entre plantas se midió en 2 transecto de 30 m colocados aleatoriamente. Además, de la mediana y el rango intercuartil se midió la asimetría de las distribuciones de muestreo con la relación $[(\text{máximo}-\text{mediana})/(\text{mediana}-\text{mínimo})]$ que identificaría la presencia de al menos un espacio largo. La certeza del método de longitud entre plantas fue confirmada por la similitud de su distribución de muestreo con la del procedimiento de muestreo bien conocido de punto a planta. En ambos métodos (la distancia entre plantas y el punto a planta) la mediana y el rango intercuartil aumentaron al disminuir la cobertura de una distribución aleatoria y fragmentada. La estimación de la asimetría se incrementó abruptamente al incrementar la cobertura de la distribución fragmentada, pero la asimetría fue casi constante con el incremento de la cobertura de la distribución aleatoria. Estos resultados sugieren que la evaluación de los cambios a través del tiempo en un sitio de monitoreo podría utilizar la distancia entre plantas medidas a lo largo de transectos de línea de intercepción para detectar los cambios tanto en la cobertura absoluta como su arreglo espacial.

mation needed to assess changes in the spatial distribution and connectivity of vegetation patches that are called for in the next generation of soil erosion prediction models to document trends in the fragmentation of plant cover on rangelands for the purposes of assessing rangeland health (National Research Council 1994, Weltz et al. 1998).

One way that grass cover can reduce soil erosion is by creating obstructions that slow the rate of overland flow of water because shorter distances between grass plants decrease the opportunity for water to acquire the energy needed to remove soil and litter from a site (e.g. Weltz et al. 1998). If the average amount of cover is reduced, either through the reduction of average plant size, the reduction of plant density, or some combination of size and density, the probability of longer distances between plants will increase. In addition, it is important to note that the probability of finding longer distances will also increase when the spatial

arrangement of cover becomes more patchy even if absolute cover remains unchanged. Accordingly, rangeland monitoring efforts to detect changes in the potential for soil erosion should include measures of absolute as well as spatial arrangement of grass cover (National Research Council 1994, Weltz et al. 1998).

Recent attempts to include spatial distribution measures in rangeland monitoring have used the line intercept method (Canfield 1941) to record both percent cover and the distance between plants along a transect. Tongway and Hindley (1995) used the line intercept transect at a semi-arid savanna site in Queensland, Australia to measure the number of obstructions, distance between obstructions, obstruction width, and percent basal cover with the goal of documenting the potential for overland water flow and erosion. They used the term "fetch length" to describe distance between obstructions on the line intercept, and they found greater cover and shorter fetch lengths between plants on ungrazed than on grazed sites. In the desert grassland, de Soyza et al. (1997) and Whitford et al. (1998) used line intercept transects at desert grassland sites in southern New Mexico to estimate the size of bare soil patches in relation to grazing intensity along a piosphere gradient (distance from a livestock water development). They reported mean bare patch sizes that ranged from approximately 40 to 400 cm at different sites with percent cover ranging from more than 20% to less than 1%, respectively. Using line intercept transects, de Soyza et al. (1997) found the arithmetic product of the average distance between plants and the skew of log-transformed distance between plants to be positively associated with increasing grazing pressure and Whitford et al. (1998) found the arithmetic product of average distance between plants and average percent bare ground to be positively associated with increasing grazing pressure.

At this early stage in efforts to detect changes in the spatial pattern of grasses during rangeland monitoring, it is important to examine the underlying assumptions of a sample design using the line intercept method. In particular, we suggest that an examination of the statistical properties of the sample distribution for fetch lengths will provide at least part of that needed evaluation. Specifically, it is important to examine the sensitivity of the line intercept method to changes in the arrangement of plants that are independent of changes in the abundance of plant cover. The line intercept transect is an

attractive method because it traditionally has been employed to estimate percent cover and there is a considerable body of literature regarding the statistical properties of the intercept measure (see Kaiser (1983) for a comprehensive bibliography). We found no literature on the statistical properties of the line intercept measure for distance between plants or fetch length other than frequency distributions of fetch lengths measured on 4 sites in the Jornada Basin of the northern Chihuahuan Desert in southern New Mexico by de Soyza et al. (1997). They found that a logarithmic transformation of the fetch lengths led to near normal distributions, implying highly skewed distributions for fetch length. This evidence suggests some function of the mean or skew of the sample measurements of fetch length has some sensitivity to changing range conditions. However, it would be informative to have some knowledge of the general distributional properties of the fetch length measures to determine which properties of the sample distribution are most sensitive to changing spatial patterns of grass cover.

Measuring the distance to the nearest point from randomly located points is a proven and well studied method to assess the spatial arrangement of cover (Diggle 1983). The distance from the random point to the nearest point measures the size of empty spaces in a spatial point distribution. The statistical properties of these point to nearest event distances are well known and can be used to detect the degree of departure from complete spatial randomness. When points are distributed on a plane under complete spatial randomness, the probability density function for the point to nearest event distance has an exponential distribution (Diggle 1983), which has a positive (right) skew distribution, even under complete spatial randomness.

The reality of rangeland monitoring is that it is more traditional and more time efficient to use transects rather than establish numerous random sampling points. Therefore, in this study to detect changes in the spatial arrangement of cover, we used the better understood but more complicated random point to nearest event sampling technique as a benchmark to assess the sensitivity of the more easily applied fetch length distance along a line transect.

Our research objective was to assess the sensitivity of the statistical properties of distance between plants (fetch length) measured with a line intercept transect to changes in both the spatial distribution of plants and the abundance of plant cover. To reach this objective, monitoring plots

in desert grassland vegetation were simulated for 5 different amounts of grass cover, each with either random or fragmented spatial distributions of plants. The sample distributions for the distance between plants on the line intercept transect were compared with the distributions for distance between random points and plants. The sensitivity assessment used 3 simple statistical properties of distance measures (median, interquartile range, and asymmetry) and compared them across the 5 levels of cover and the random versus fragmented spatial distributions. Finally, we performed a simple validation of the simulations using the distance between plants measured along line intercept transects from 6 desert grassland locations.

Methods

Simulation of cover and spatial pattern

Programs were written in the C programming language to simulate the spatial distribution of basal cover of perennial grasses on desert grassland range sites and to simulate measurements from line intercept and random point-to-plant distance samples. The simulations were scaled to simulate sample plots of 30 X 30 m with 1, 2.5, 5, 10, and 15% basal cover. Spatial patterns simulated were (1) a random and (2) a fragmented distribution of plants. The fragmented pattern was simulated using a random distribution of plants fragmented with a random distribution of bare patch areas comprising 25% of the total area (Fig. 1a, 1b).

The random distribution of plants without bare patches was simulated in a single stage. Plant basal area was represented by a disc scaled to a 5 cm diameter. To prevent the overlap of any 2 plants, the coordinate points, representing the centers of the plant, were simulated with an algorithm designed to generate a sequential spatial inhibition (SSI) process (Matérn 1960). The SSI process sequentially lays down discs with a radius of inhibition r that do not overlap existing discs. Thus, any 2 points representing the centers of 2 plants' basal areas were at least 5 cm apart to avoid overlap. The fragmented surface was simulated in 3 stages. The first stage simulated bare patches on 25% of the total plot area as non-overlapping disks with a 300 cm diameter located randomly on the surface. Bare patch sizes of 300 cm were based on personal observation of range sites and fell within the range of fetch lengths reported by de Soyza et al. (1997) and Whitford et al. (1999). In the second

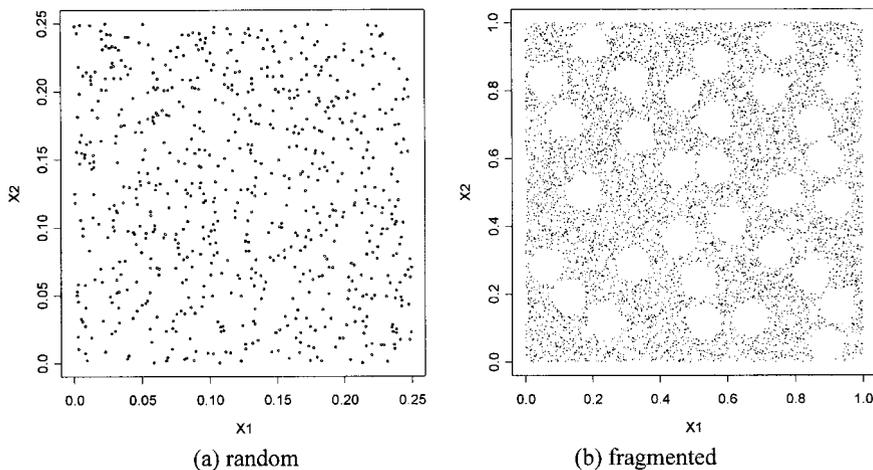


Fig. 1. Representative scenes at (a) a 10 X 10 m scale to visualize the 5 cm discs simulating basal area in the random pattern and (b) at the 30 X 30 m scale simulation to visualize the fragmented pattern.

stage, basal cover of 0.5%, represented by the randomly distributed 5 cm discs, was generated within the bare patch areas because bare patches on range sites are typically not completely devoid of plant cover. In the third stage, the remaining 75% of the simulation surface outside the bare patches was populated with the 5 cm diameter discs in a random spatial distribution and were excluded from the simulated bare patches using the SSI algorithm. The coordinate points for the random distribution of 5 cm diameter discs and the 300 cm diameter bare patches were generated on a unit square with the X1 and X2 axes coordinates independently generated with a Uniform(0,1) random number generator (ran2.c in Press et al. 1992).

Line intercept samples

Simulated line intercept transects were placed on these grassland simulations to generate the statistical distribution of distance between plants or fetch lengths. Two lines were generated to perform the line intercept measurements, each with a random starting point on the X2 axis of the unit square. The lines were scaled to a length of 30 m to span the simulated surface in the X1 axis direction. The measurement of intercept lengths on the lines were made using points at 1 cm intervals. The 1 cm distance was consistent with field methods that measure distances within 1 cm. The measurement at each point was scored as a hit (1) on a 5 cm disc or miss (0). Thus, a series of successive 1s or hits represented the length of intercept for plant basal cover and a series of successive 0s or misses represented the length of distance between plants or fetch length.

The total number of hits (1s) were used to calculate the basal cover estimate, where there were 3,000 increments of 1 cm along each 30 m transect. The number of successive misses (0s) between any two hits (1s) on a line determined the magnitude of each fetch length.

Point-to-nearest-event samples

Random points were placed on these grassland simulations to generate the statistical distribution of distance from point-to-nearest-plant measurements. The number of random points necessary to adequately characterize the distribution of distances was equal to \sqrt{N} , where N is the number of 5 cm discs generated for the simulated surface cover (Diggle 1983). The number of points generated per simulation scene to represent cover ranged from N = 4,583 for 1% cover to N = 68,754 for 15% cover.

Descriptive statistics

Descriptive statistics and their standard errors from 1,000 simulations were computed for a simple characterization of the sampling distributions for fetch lengths and random point-to-plant distances. The median was used to estimate the location of the distributions. The interquartile range between the 25th and 75th quartiles was used to estimate dispersion of the distributions. These parameters were used because they are resistant to the influence of outliers. A simple measure of sampling distribution asymmetry was constructed for these simulations so that it would be sensitive to outliers. This measure was called asymmetry and was computed as the ratio (maximum-median)/(median-minimum).

Thus, any asymmetry value greater than 1 would indicate a right skew distribution. We reasoned that this measure, especially for fetch length, would identify a condition with at least one very large open space or bare patch on a site. Furthermore, it was expected that the random point-to-plant distances and fetch lengths would produce right skewed asymmetric sampling distributions based on early trial simulations and field results given in deSoyza et al. (1997). In addition, the average basal cover with standard error estimate was computed for the simulations.

Assessment of field measures

Fetch length observations collected at 6 desert grassland sites on the Jornada Experimental Range in southern New Mexico were used to validate the characteristics of the fetch lengths from the simulations. Fetch lengths were measured on 15 different 10 m line intercept transects at 5 sites and on 14 transects at the 6th site (deSoyza et al. 1997). The 6 sites (EWC, ENC, MW1, WW3, MW3, and CW3) were selected from a larger group used by de Soyza et al. (1997) because all 15 transects on the selected sites had at least 1 fetch length measure. The absence of plants on at least 1 of the transects on each of the non-selected sites prohibited the measurement of fetch length which was necessary to calculate the descriptive statistics.

The median, IQR, and asymmetry statistics for the fetch lengths from these 6 sites were compared with the values from the simulations to assess the validity of the simulations and to assess the sensitivity of the statistics to differences in cover and non-random spatial distribution.

Results

Line intercept measures

The line intercept produced accurate measures of cover with the average of the 1,000 simulations nearly equal to the simulated cover (Table 1). The variability of the cover estimates for fragmented 5, 10 and 15% cover simulations was considerably higher than that for the random cover simulations. For example, the standard error was about 30% greater with fragmentation for the 5% cover simulations and about 60% greater for the 10% cover simulations (Table 1). The number of fetch lengths (on the 2 line intercepts combined) increased with cover and the numbers were virtually the same for random and fragmented distributions.

Table 1. Means and standard errors (in parentheses) of fetch length statistics from 1,000 random and fragmented distributions as a function of simulated cover.

Spatial Distribution	Simulated Cover (%)	Estimated Cover (%)	Number of Fetches	Fetch Length (cm)		
				Median	IQR	Asymmetry
Random	1	1.00 (.009)	32 (.25)	266 (3.2)	426 (5.5)	4.5 (.09)
Fragmented	1	1.00 (.009)	32 (.25)	272 (3.2)	428 (5.6)	4.4 (.09)
Random	2.5	2.48 (.013)	77 (.40)	107 (.80)	169 (1.3)	5.5 (.08)
Fragmented	2.5	2.52 (.015)	78 (.40)	95 (.81)	174 (1.6)	7.1 (.11)
Random	5	4.98 (.018)	153 (.50)	53 (.27)	82 (.40)	6.4 (.07)
Fragmented	5	4.97 (.023)	152 (.70)	43 (.25)	76 (.53)	10.7 (.12)
Random	10	9.98 (.024)	303 (.70)	25 (.09)	38 (.15)	7.2 (.07)
Fragmented	10	9.97 (.038)	302 (1.10)	19 (.07)	31 (.15)	19.3 (.15)
Random	15	15.00 (.027)	451 (.80)	16 (.05)	24 (.07)	7.7 (.06)
Fragmented	15	14.95 (0.57)	449 (.170)	12 (.04)	18 (.06)	29.6 (.21)

Regardless of the spatial distribution of the simulations, the median fetch length and the dispersion (IQR) of lengths decreased with increased cover while asymmetry increased with increased cover (Table 1, Fig. 2). The median fetch length for the fragmented distribution was less (between 4 and 12 cm) than the random distribution when cover exceeded 1%. The dispersion of fetch length for the fragmented distribution was less (about 6 cm) than the random distribution when cover was at least 5%.

The asymmetry measure was consistently greater than 1 regardless of amount of cover and spatial distribution, which indicates a highly right skewed sample distribution of fetch lengths (Table 1, Fig. 2). More importantly, asymmetry was the statistic that provided the most distinguishing contrasts between the random and fragmented distributions of cover. Asymmetry increased slightly with increased cover in the random distributions, from 4.5 at 1% cover to 7.7 at 15% cover. However, the asymmetry measure increased considerably with increased cover in the fragmented distribution, from 4.4 at 1% cover to 29.6 at 15% cover. Furthermore, at cover

≥ 5%, asymmetry values did not exceed 8 for random distributions, but were > 10 for the fragmented distributions.

median distances for the fragmented distribution were slightly larger than those from the random distributions. The dispersion

Table 2. Means and standard errors (in parentheses) for random point-to-plant distance statistics from 1,000 simulations of random and fragmented distributions as a function of simulated cover.

Spatial Distribution	Simulated Cover (%)	Point-to-Plant Distances (cm)		
		Median	IQR	Asymmetry
Random	1	20.8 (.06)	16.2 (.08)	1.9 (.02)
Fragmented	1	20.9 (.06)	16.7 (.08)	2.1 (.02)
Random	2.5	13.0 (.03)	10.0 (.04)	2.0 (.02)
Fragmented	2.5	13.4 (.03)	11.6 (.05)	3.6 (.03)
Random	5	8.9 (.02)	6.9 (.02)	2.0 (.01)
Fragmented	5	9.4 (.02)	9.0 (.04)	5.6 (.03)
Random	10	6.1 (.01)	4.5 (.01)	2.0 (.01)
Fragmented	10	6.4 (.01)	6.8 (.03)	9.0 (.05)
Random	15	4.9 (.01)	3.5 (.01)	2.0 (.01)
Fragmented	15	5.0 (.01)	5.6 (.04)	11.8 (.06)

Point-to-nearest-event distances

Regardless of simulation type, the median point-to-nearest-plant and the dispersion (IQR) of distances decreased with increased cover (Table 2, Fig. 3). The

of the point-to-nearest-event distances were slightly greater (from 0.5 to 2.3 cm) for the fragmented than the random distributions. Asymmetry for random distributions had a value of 2 for all of the simulations except for the 1% cover with an asymmetry value of 1.9. In contrast, asymmetry with fragmented simulations increased sharply with cover from 2.1 for 1% cover to 11.8 for 15% cover.

Field Data

The cover estimates for total vegetation measured from the line intercepts at the 6 field sites ranged from 3.4 to 8.6% with values of median, IQR, and asymmetry (Table 3) within the range of values observed for the random and fragmented spatial distribution simulations (Tables 1, 2). The median fetch length and IQR decreased with increased cover (Table 3, Fig. 4). The relationship between cover and the median for the field sites was sim-

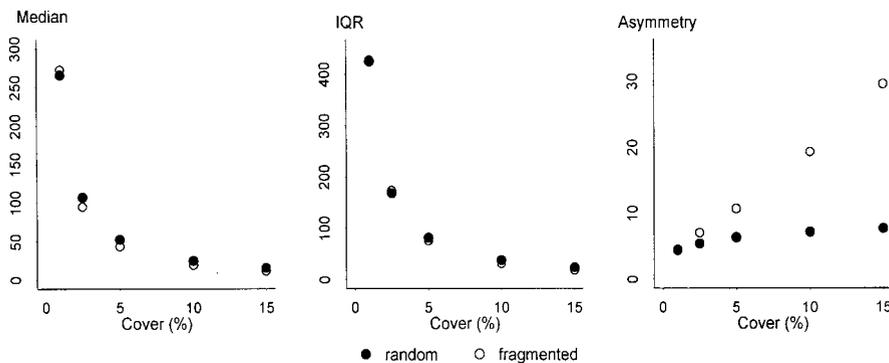


Fig. 2. Relationships between percent cover and descriptive statistics of median, interquartile range (IQR), and asymmetry for fetch lengths measured from random and fragmented spatial cover simulations.

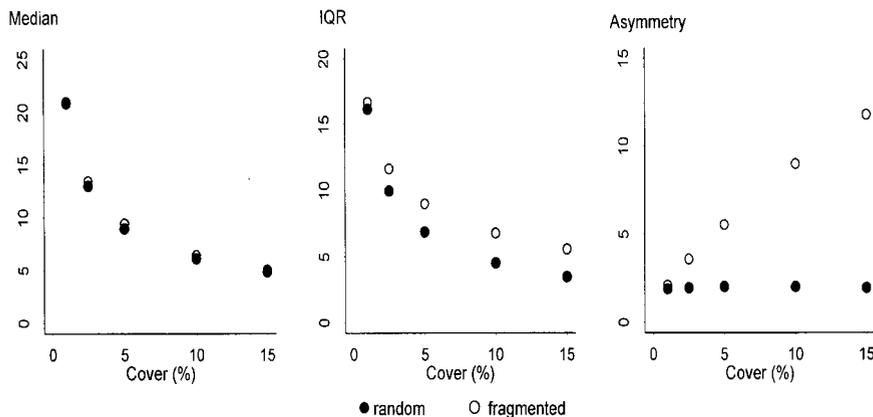


Fig. 3. Relationships between percent cover and descriptive statistics of median, interquartile range (IQR), and asymmetry for random points-to-nearest-plant distances measured from random and fragmented spatial cover simulations.

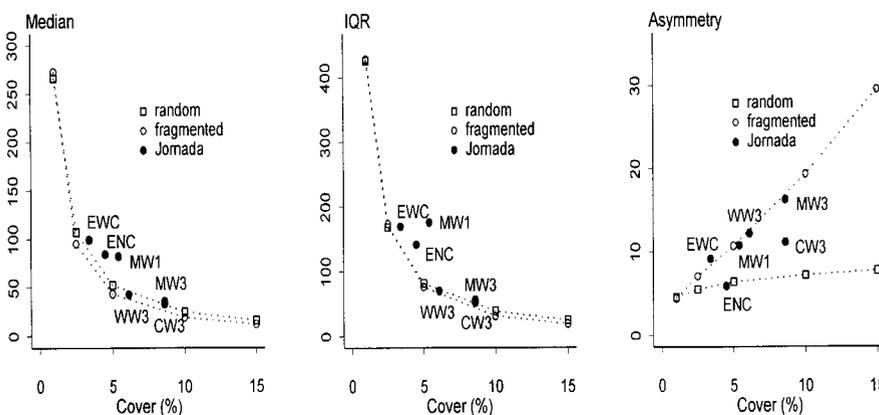


Fig. 4. Relationships between estimated cover and median, interquartile range (IQR), and asymmetry from field measured fetch lengths (Jornada) and from random and fragmented spatial cover simulations.

ilar to values from the simulations, except the MW1 site had greater median and IQR values than expected (Fig. 4).

The values for asymmetry from the field sites were within the range of values from the random and fragmented distribution simulations measured with fetch lengths on the line intercept transect (Fig. 3). A close examination of the asymmetry values from sites MW3 and CW3 illustrates how the asymmetry statistic can be used to differentiate sites with different levels of fragmentation even though the sites have equivalent cover (8.6%), median fetch length (36 and 33 cm), and IQR (56 and 52) values.

Discussion

Fetch lengths appear to provide a credible surrogate for assessing the behavior of point-to-nearest-plant distances on monitoring sites, because the behavior of fetch length statistics from the line intercept

samples corresponded to those from measurements of random point-to-nearest-plant distances. For both random and fragmented distributions of cover using both sampling methods, the median and dispersion decreased with increasing cover. Most importantly, for random spatial distributions, the asymmetry estimate for the point-to-plant distance did not increase and asymmetry for fetch length increased

only slightly with increasing cover. Conversely, for the fragmented spatial distributions, the asymmetry values increased markedly with increasing cover for both methods.

Asymmetry was the only statistic of the 3 evaluated that could be used to distinguish random from fragmented spatial distributions, and this was obvious when using either the fetch length or point-to-plant methods. The critical asymmetry value to distinguish fragmented distributions using the fetch length method was 8 for these simulations because it was never attained in the samples from the random distributions, but was exceeded in all fragmented distributions with $\geq 5\%$ cover.

The analysis of fetch lengths from line intercepts taken at 6 desert grassland locations support the validity of the simulations for plant cover and the sample distributions for fetch lengths. Furthermore, the field results support the use of the asymmetry statistic to detect deviations from random spatial distributions of plant cover.

The positive relationship between asymmetry and patchiness of plant distribution suggests that fetch lengths measured on line intercept transects can distinguish between changes in absolute cover and changes in the spatial arrangement of cover. Increased fetch distances between plants indicate a decline in absolute cover. Independent of these changes in absolute cover, a change in the asymmetry statistic indicates a change in the spatial distribution of the cover.

These simulation and field validation results support the use of fetch length measure taken along a line intercept transect as a means of estimating both absolute cover and the spatial arrangement of that cover. Therefore, we support continued research and development to incorporate fetch length measures into existing line intercept transect protocols for monitoring rangeland vegetation.

Table 3. Descriptive statistics for fetch lengths measured from six sites on the Jornada Experimental Range, New Mexico.

Site	Total Plant Cover Estimate (%)	Grass/Forb Cover Estimate (%)	Fetch Length (cm)				
			Minimum	Maximum	Median	IQR	Asymmetry
EWC	3.4	2.5	2	985	99	170	9.1
ENC	4.5	4.2	3	560	84	142	5.9
MW1	5.4	1.9	2	946	82	176	10.8
WW3	6.1	5.8	3	531	43	70	12.2
MW3	8.6	8.2	1	606	36	56	16.3
CW3	8.6	8.3	2	379	33	52	11.2

Literature Cited

- Canfield, R.H. 1941.** Application of the line intercept method in sampling range vegetation. *J. For.* 39:388–394.
- de Soyza, A.G., W.G. Whitford, and J.E. Herrick. 1997.** Sensitivity testing of indicators of ecosystem health. *Ecosystem Health* 3:44–53.
- Diggle, P.J. 1983.** *Statistical Analysis of Spatial Point Patterns.* Academic Press, London.
- Kaiser, L. 1983.** Unbiased estimation in line-intercept sampling. *Biometrics* 39:965–976.
- Matérn, B. 1960.** *Spatial Variation.* Meddelanden från Statens Skogsforskningsinstitut 49,5 1–114.
- National Research Council. 1994.** *Rangeland health: new methods to classify, inventory, and monitor rangelands.* National Academy Press, Washington, D.C.
- Press, W.H., S.A. Teukolsky, W.T. Vetterling, and B.P. Flannery. 1992.** *Numerical Recipes in C. The Art of Scientific Computing, 2nd ed.,* Cambridge University Press, New York, N.Y.
- Schlesinger, W.H., J.F. Reynolds, G.L. Cunningham, L.F. Hueneke, W.M. Jarrell, R.A. Virginia, and W.G. Whitford. 1990.** Biological feedbacks in global desertification. *Sci.* 247:1043–1048.
- Tongway, D. and N. Hindley. 1995.** *Manual for Soil Condition Assessment of Tropical Grasslands.* Division of Wildlife and Ecology, CSIRO, Canberra, Australia.
- Weltz, M.A., M. Kidwell, and H.D. Fox. 1998.** Influence of abiotic and biotic factors in measuring and modeling soil erosion on rangelands: state of knowledge. *J. Range Manage.* 51:482–495.
- Whitford, W.G., A.G. deSoyza, J.W. Van Zee, J.E. Herrick, and K.M. Havstad. 1998.** Vegetation, soil and animal indicators of rangeland health. *Environ. Monitor. and Assess.* 51:179–200.
- Whitford, W.G., J. Van Zee, M.S. Nash, W.E. Smith, and J.E. Herrick. 1999.** Ants as indicators of exposure to environmental stressors in North American desert grasslands. *Environ. Monitor. and Assess.* 54:143–171.

Statement of Ownership, Management, and Circulation

(Act. of August 12, 1970, Sec. 3685, Title 39, United States Code)

1. *Title of Publication:* Journal of Range Management
2. *Date of Filing:* September 22, 2000
3. *Frequency of Issue:* Bimonthly
4. *Location of Office of Publication:* 445 Union Blvd., Suite 230, Lakewood, Colorado 80228
5. *Location of General Business Office:* Same
6. *Name and Address of:*
Publisher: Society for Range Management, 445 Union Blvd., Suite 230, Lakewood, Colorado 80228
Editor: Gary Frasier, 7820 Stag Hollow Road, Loveland, Colo. 80538
Managing Editor: J. Craig Whitekiend, 445 Union Blvd., Suite 230, Lakewood, Colorado 80228
7. *Owner:* Society for Range Management, 445 Union Blvd., Suite 230, Lakewood, Colorado 80228
8. *Known Bondholders, Mortgages, etc.:* Membership
9. *For Completion by Nonprofit Organizations Authorized to Mail at Special Rates:* The purpose, function, and nonprofit status of this organization and the exempt status for Federal income tax purposes have not changed during preceding 12 months.
10. *Extent and Nature of Circulation*

	Avg. for 12 months	Actual for issue nearest filing date
A. <i>Total copies printed</i>	2,706	2,769
B. <i>Paid Circulation</i>		
1. <i>Dealers, counter sales</i>	0	0
2. <i>Mail subscriptions</i>	2,434	2,528
C. <i>Total paid circulation</i>	2,434	2,528
D. <i>Free distribution</i>	22	22
E. <i>Total distribution</i>	2,456	2,550
F. <i>Copies not distributed</i>	250	219
G. <i>Total</i>	2,706	2,769

I certify that the statements made by me above are correct and complete –J. Craig Whitekiend, Managing Editor.

Estimation of horizontal cover

WILLIAM B. COLLINS AND EARL F. BECKER

Authors are wildlife biologist, Alaska Department of Fish and Game, 1800 Glenn Hwy., Palmer, Alaska 99645; and biometrician, Alaska Department of Fish and Game, 333 Raspberry Rd., Anchorage, Alaska 99518.

Abstract

A method was developed to provide ecologists with an objective and efficient means for point sampling horizontal cover. This method produced estimates significantly ($p < 0.05$) more precise than cover pole and checkerboard methods, reducing variability among observers. The new method was significantly ($p < 0.05$) faster, than the other techniques. Factors affecting variability of measurements were reviewed.

Key Words: point sample, vegetation measurement, wildlife habitat

Three-dimensional distribution of vegetation significantly affects functional characteristics of plant communities such as snow accumulation, thermal transfers between animal and environment, predator/prey visibility, and the productivity and quality of understory forages. Ecologically, one of the most useful measurements of plant distribution is "cover", defined as the proportion of the ground surface occupied by a vertical projection of a plant's aerial parts (Greig-Smith 1964). Distribution of plants as viewed from a horizontal perspective is also significant, particularly as it relates to wildlife habitat values. Wildlife biologists frequently refer to the combined effects of horizontal and vertical cover in terms such as "thermal", "hiding", "screening", "escape", or "security" cover to indicate function.

The combined effects of vertical and horizontal cover may be determined through measurements of integrative variables such as wind speed, snow accumulation, light penetration, and radiant energy flux. However, actual cover in the horizontal perspective has been difficult to describe, because methods tended to be inefficient or subject to considerable observer bias. Methods available for determination of vertical cover are generally more objective and efficient than those available for estimation of horizontal cover (Bonham 1989, Higgins et al. 1994).

A personal computer program has proven useful for general assessment of hiding cover in forested stands where plant dimensional and density data are already available (Lyon and Marcum 1986). In settings where these data have not been obtained, or where integration of vegetation descriptors to estimate horizontal cover requires questionable assumptions, a more direct method is necessary.

Cover methods relying on point estimates have been considered more objective and less variable among observers than other

Resumen

Un método fué desarrollado para ofrecer ecólogos con un nudio objetivo y eficiente de se-alar cobertura horizontal. Este Método produjo un cálculo aproximado más preciso ($p < 0.05$) que polos cubiertos y métodos de tablero; reduciendo variabilidad entre los observadores. El método nuevo rápido ($p < 0.05$) que otras técnica. Los agentes que afectan la variabilidad de las mdeidas fueros revisados.

methods (Levy and Madden 1933, Bonham 1989). Dimensionless points are preferred for cover sampling, since increasing point size leads to increasing overestimation of cover (Goodall 1952). Dudley et al. (1998) used the point frame (Levy and Madden 1933) in a horizontal orientation, considering it the most accurate standard for comparison of vegetation density methods where estimates are limited to short distances.

A direct method of horizontal cover measurement based on point estimates should increase objectivity, reduce variability between observers, and produce point data compatible with corresponding point estimates of vertical cover. Such a method should allow estimates over short or long distances and at any height, depending on research objectives and vegetation characteristics. The method should be most efficient when used by 1 person.

Methods

Development of Technique

The following technique for estimating horizontal cover was developed. A dimensionless-point target, located at a selected height above ground, was observed from points systematically distributed in a circle of specific radius and height above ground surrounding the target. Each circle of observations was treated as a single observation the same as a set of dependent points from a point frame or point transect is treated as a single observation. Percent of locations around the target from which the target was obscured by vegetation indicated percent cover. Observation heights and sight distances (radii) were selected according to vegetation conditions and sampling interests. The dimensionless point target was represented by the intersection of the upper arc of a 9 cm ball and the right side of a vertical staff on which the ball was mounted.

In selecting sight distances (radii) from which to observe targets, we reasoned that relatively long distances would more fully integrate the structural variability of a stand (Shimwell 1972) than shorter distances. As with the concept of minimal area, "minimal sight distances" vary greatly depending on kind of plant

This project was funded by Federal Aid Wildlife Restoration Projects W-24-3 and W-24-4. Authors thank N. Cassara, A. Collins, L. Erie, H. Griese, M. Masteller, J. Miner, T. Miner, R. Modafferi, and S. Schmidt for their assistance.
Manuscript accepted 2 Apr. 2000.

community or stratum being sampled. Empirically determined minimal areas reported by Mueller-Dombois and Ellenberg (1974) converted to the following plot radii (sight distances):

Forests	
(including tree stratum)	8.0–12.6 m
Forest understory	4.0–8.0 m
Dry grassland	4.0–5.6 m
Dwarf-shrub heath	1.8–2.8 m
Agricultural weed communities	2.8–5.6 m
Hay meadow	1.8–2.8 m

We determined that sight distances allowing observation of target points 50% of the time produced circular plots of approximately the same areas as above. Longer sight distances resulted in cover values approaching or equaling 100%, obscuring differences in cover. Substantially more difficulty and time were required to maintain correct distance and orientation toward targets, when distances resulted in observation of about 70% or more cover.

In most applications, sight distance was determined only once for a vegetation type. When cover was determined for multiple strata, sight distance was based on the most visible stratum. If any associated strata were more than 90% obscured at the initial sight distance, a shorter sight distance was selected for those specific strata.

Once a sight distance was selected, the observer walked a complete circle around the target, stopping at systematically selected step locations to determine if the target point could be sighted with 1 eye or through 1 ocular of a pair of binoculars. To avoid biasing location of the observer's eye when reaching each succeeding observation point, a repetitious, stationary posture was assumed prior to looking toward the target. Elevation of the eye was gauged in accordance with marks on an observer-held staff that corresponded to the height(s) of target(s) being observed.

In vegetation less than 3 m tall, a chord of desired length was attached between the target and observer staffs for maintaining selected sight distances. In taller vegetation, the observer periodically checked distance from target using an optical range finder. The range finder consisted of 2 observer-specific marks on the observer's staff that triangulated from the observer's eye to a 1 m increment on the target staff, when held at arm's length and at correct distance from the target.

Total locations around the circle from which a target was observed, versus number of locations from which the target was obscured by vegetation, were recorded on

hand tally counters and used to compute percent cover. Percent cover was then divided by observation distance to produce a weighted value (%/m) for comparisons of values obtained at other distances.

Technique Test

We compared the precision (repeatability) of the staff-ball method against a tubular version (Leckenby 1984) of the profile board (Nudds 1977), a cover pole (Griffith and Youtie 1988), and a checkerboard 40 cm x 50 cm having 10-cm-wide black and white squares. We compared methods in paper birch-white spruce (*Betula papyrifera-Picea glauca*) forest, because this vegetation necessitated use of a range finder and binoculars, thereby ensuring that all possible time-consuming elements of the staff-ball method would be included in comparisons.

Eight observers estimated percent cover by each of the 4 techniques on the same 10 plots, reading each centrally located target from 22 locations uniformly spaced around a circle of 15 m radius. The methods were compared only at target and observation heights of 1.25 m, because overlapping movements of 8 observers performing 4 procedures at each plot location resulted in herbaceous ground cover becoming progressively trampled or otherwise disturbed. Observations through 2 oculars and then 1 ocular were recorded separately to document the effect of parallax.

We used a randomized block design (person) to obtain treatment means for each of the 4 cover methods. We modified Levine's test to test for differences in the

between-observer variability of the cover methods. Levine's test is recommended for testing differences in precision (Snedecor and Cochran 1980). Due to the magnitude of difference between treatment means (range: 33.46 to 71.83), we wanted a test statistic that weighted the size of the difference relative to the treatment mean. Instead of Levine's method of comparing the absolute differences of the cover measurement from the cover method mean, we compared percent absolute differences:

$$100 \left(\frac{|y - \bar{y}|}{\bar{y}} \right)$$

A priori, we tested for differences in variability between the staff ball method and each of the other 3 cover methods, using 3 contrast statements. The contrast F-statistics were converted to t-statistics (Bickel and Doksum 1977), to perform a 1-tailed hypothesis test. We were interested in determining if the staff-ball method had significantly less variability than the other 3 methods.

The efficiency of each method was measured by the time required to obtain cover estimates. Observer was treated as a blocking variable in a one-way analysis of variance of total seconds required to observe cover from 10 plots having 22 observations each. Multiple mean comparisons were made using Bonferonni method (Neter and Wasserman 1974), reducing the critical t-statistic to one associated with

$$\alpha = (0.01/3) = 0.0033.$$

All statistical tests were performed with $\alpha = 0.05$.

Table 1. Mean and modified Levine statistics for 4 cover methods used to measure cover in the 1.5 m strata of a birch-spruce forest.

Method	Mean of Cover method	Mean of modified Levine 100 (cover est - mean / mean)
Staff-ball	71.83	3.52
cover pole	37.03	12.64
profile tube	63.36	7.79
checkerboard	33.46	14.90

Table 2. Contrasts of differences in the precision of the staff-ball cover method versus each of 3 other cover methods used to measure cover in the 1.5 m strata of a birch-spruce forest.

Contrast	DF	MS	F Value	t value	Pr>t
staff-ball					
vs cover pole	1	332.888	6.007	2.451	0.0104
staff-ball					
vs profile tube	1	72.705	1.312	1.145	0.1309
staff-ball					
vs checkerboard	1	517.781	9.343	3.057	0.0025
Error	27	55.419			

Results and Discussion

There was a large range in means by cover methods as well as the modified test statistic used in Levine's test (Table 1). The staff-ball method was more precise than either the cover-pole or checkerboard method (Table 2, Fig. 1). While the staff-ball method was not significantly more precise than the profile-tube at $\alpha = 0.05$, it was significant for $\alpha > 0.131$.

The staff-ball method was significantly faster ($p < 0.05$) than any of the other methods (Table 3), presumably, because it required only simple yes/no decisions rather than subjective estimates and/or counts, and it did not require repeated repositioning of the target.

In a separate test at an observation distance of 4 m, where binoculars were not necessary to observe the target, the method averaged 5.1 times faster than the density board, 5.8 times faster than the cover pole, and 14.3 times faster than the checkerboard.

Across all observers, the 1.5-m stratum of birch-spruce forest vegetation averaged 21% less cover when both eyes were used. Similar differences were observed with the other cover methods when 1 versus both eyes was used. This reinforced the importance of sighting with 1 eye to avoid parallax problems and to obtain true point values.

In use of any horizontal cover technique, we believe it is important for sampling protocol to address the significance of observation height relative to target height, by requiring consistency between observers and across specific data collec-

tions or comparisons. Variability as a result of inconsistent observation heights is particularly significant in vegetation types where substantial differences in foliage/stem density occur with plant height (Fig 2). For example, in some birch-spruce forests an understory shrub, high bushcranberry (*Viburnum edule* (Michx.) Raf.), has a sharply defined upper boundary at about 125 cm height, below which there is an 11-fold increase in horizontal cover. Observations of cover targets positioned 25 cm below the upper boundary of that shrub stratum and 15 m from the observer varied by about 20% when observers, 172 and 187 cm tall, viewed the target from an erect stance.

If a study does not require cover measurements by stratum or strictly parallel to ground surface, targets may be observed from other heights, as long as angles of observation are consistent between observers and/or comparative uses of data. Such deviation from sampling within a stratum will enable sampling at heights exceeding that of the observer (e. g. nest sites in a tree or tall shrub canopy). In any case, consistency in heights of targets and heights of observation are necessary.

Mean horizontal cover is directly proportional to distance over which point observations are made. Therefore, sight distances may be varied from one stratum to another, if differences in vegetation

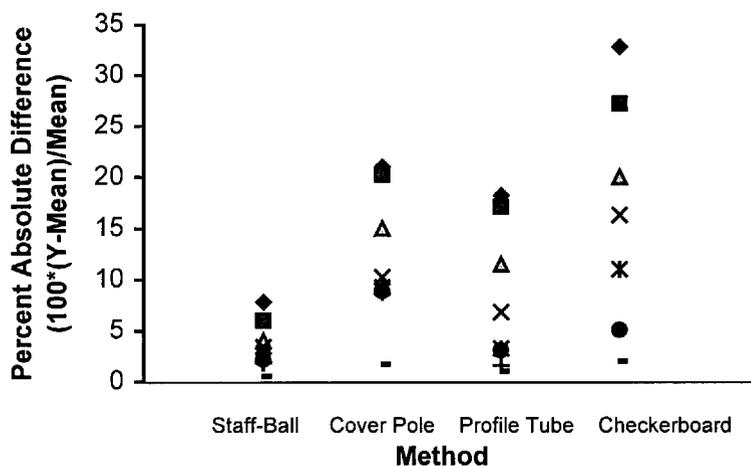


Fig. 1. Plot of modified Levine statistic by method and person. Individual observers are represented by different symbols.

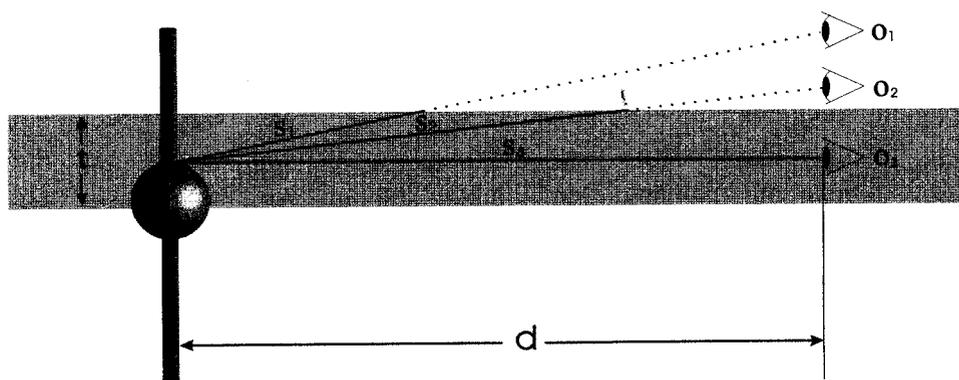


Fig. 2. Errors in cover measurements caused by differences in angles of observation. Only a truly horizontal sight (S_3) from O_3 accurately intersects all cover within a vegetation stratum (shaded area). Observations from O_1 and O_2 not only fail to measure all cover within the stratum, but differences between actual amounts of cover intersected by sight lines S_1 and S_2 contribute to significant variation between observers.

Table 3. Contrasts between staff-ball and 3 other techniques relative to time necessary to observe cover from 220 locations in the 1.5 m strata of a birch-spruce forest.

Contrast	DF	Difference	MS	F Value	t value	Pr<t
Staff-ball						
vs cover pole	1	-933	1,972,098	242.46	-15.571	0.0000
Staff-ball						
vs profile board	1	-758	1,149,128	141.28	-11,886	0.0000
Staff-ball						
vs checkerboard	1	-12,005	288,240,050	35,438.40	-188.251	0.0000
Error	9		8,133.56			

cover limit efficiency or accuracy of observation across all strata from the same sight distance. This flexibility also allows cover estimation on different scales, such as for comparison of a specific nest or bed site (e.g. distinct plant or clump of vegetation) and the overall stand.

The staff-ball method allowed more objective, more precise, and faster estimates of horizontal cover than profile boards (tubes), cover poles or checkerboards. As a method to index horizontal cover, the staff-ball will produce the most repeatable and consistent results among observers and over time. Assuming that point values are the most accurate indicators of cover, staff-ball estimates should also more closely reflect true values. The staff-ball method was versatile in application and most efficiently used by 1 person.

Literature Cited

Bickel, P.J. and K.A. Doksum. 1977. Mathematical statistics: linear basic ideas and selected topics. Holden-Day Inc. San Francisco, Calif

Bonham, C.D. 1989. Measurements for terrestrial vegetation. John Wiley and Sons. New York, N. Y.

Dudley, S.J., C.D. Bonham, S.R. Abt, and J.C. Fischenich. 1998. Comparison of methods for measuring woody riparian vegetation density. *J. Arid Environ.* 38:77-86.

Goodall, D.W. 1952. Some considerations in the use of point quadrats for the analysis of vegetation. *Aust. J. Sci. Res. Ser. B.* 5:1-41.

Greig-Smith, P. 1964. Quantitative plant ecology, Second ed. Butterworths. London.

Griffith, B. and B.A. Youtie. 1988. Two devices for estimating foliage density and deer hiding cover. *Wildl. Soc. Bull.* 16:206-210.

Higgins, K.F., J.L. Oldemeyer, K.J. Jenkins, G.K. Clambey, and R.F. Harlow. 1994. Vegetation sampling and measurement. p. 567-591. *In:* T. A. Bookhout, ed. Research and management techniques for wildlife and habitats. Fifth ed. The Wildl. Soc., Bethesda, Md.

Leckny, D.A. 1984. Elk use and availability of cover and forage habitat components in the Blue Mountains, northeast Oregon 1976-1982. Oregon Dept. of Fish and Wildl., Wildl. Res. Rep. No. 14.

Levy, E.B. and E.A. Madden. 1933. The point method of pasture analysis. *N. Z. J. Agr.* 46:267-279.

Lyon, L.J. and C.L. Marcum. 1986. Field test of a PC program to evaluate hiding cover for elk. p. 271-274. *In:* Western States and Provinces Elk Workshop Proc. Oregon Dept. Fish and Wildlife.

Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York, New York.

Neter, J. and W. Wasserman. 1974. Applied linear statistical models. Richard D. Irwin, Inc., Homewood, Ill.

Nudds, T.D. 1977. Quantifying the vegetative structure of wildlife cover. *Wildl. Soc. Bull.* 5:113-117.

Shimwell, D.W. 1972. The description and classification of vegetation. Univ. of Washington Press. Seattle, Washington.

Snedecor, G.W. and W.G. Cochran. 1980. Statistical methods. Iowa State University Press. Ames, Iowa

Dry-weight-rank method assessment in heterogeneous communities

STEVEN L. DOWHOWER, W. RICHARD TEAGUE, R. JAMES ANSLEY, AND WILLIAM E. PINCHAK

Authors are research associate, range ecologist, range ecologist, and range nutritionist, Texas Agricultural Experiment Station, P.O. Box 1658, Vernon, Tex. 76384.

Abstract

Assessment of herbaceous standing crop in heterogeneous range plant communities requires large numbers of samples to account for inherent variability. The dry-weight-rank method (DWR) was developed to eliminate the need for clipping and sorting of herbage to determine relative proportions on a dry weight basis. The technique was assessed for applicability and accuracy in the mixed prairie of the Texas Rolling Plains. Much of the herbage within the communities investigated occurred in monospecific patches that resulted in only 15% of quadrats having 3 species ranked for which DWR was designed. Non-harvest methods of determining grass proportion by species were compared to harvested proportions in mesquite (*Prosopis glandulosa* Torr.) and redberry juniper (*Juniperus pinchotii* Sudw.) communities. Estimation methods evaluated were 1) harvest by species, 2) weight estimation by species, 3) DWR with quadrat weighting, 4) unweighted estimated proportion by species, and 5) unweighted DWR.

Correlations of non-harvest to harvest proportions were improved with quadrat weighting. Weighting improved values more in the juniper than in the mesquite communities. Although cumulative ranking of DWR multipliers was necessary in 85% of sample quadrats, there was a high correlation ($r^2 > 0.995$) between weight estimation and weighted DWR and between estimated proportion and unweighted DWR. This indicates that cumulative ranking with the original DWR multipliers was virtually the same as evaluator estimation.

Analysis of variance indicated significant differences in non-harvest methods compared to harvesting. Quadrat weighting with DWR was necessary to draw the same statistical conclusions between means that harvest data provided. Ranks are easier to apply and more likely to be applied similarly by individual evaluators than estimated proportions. For sites with high standing crop variation and patchiness of species that require considerable use of cumulative ranking, DWR with quadrat weighting provides adequate determination of species proportions of biomass.

Key Words: botanical composition, estimation, landscape, standing crop proportion

We gratefully acknowledge the facilities made available to us on the Y Experimental Ranch by C.C. Burgess and the financial support of the E. Paul and Helen Buck Waggoner Foundation, Inc. We would also like to thank Jay Hunt, Doug Tolleson and Jan Worrall for technical support. Jerry Cox, Darrell Ueckert and Steve Whisenant kindly reviewed this manuscript.

Manuscript accepted 12 Mar. 2000.

Resumen

La evaluación de la cosecha en pie de la vegetación herbácea de comunidades de pastizal heterogéneas requiere de un gran número de muestras para contabilizar la variabilidad inherente de estas comunidades. El método de clasificación de peso seco (DWR) se desarrolló para eliminar la necesidad de cortar y ordenar el forraje herbáceo para determinar las proporciones relativas en base a peso seco. La técnica se evaluó para valorar su aplicabilidad y certeza en las praderas mixtas de las planicies onduladas de Texas. Mucho del forraje herbáceo dentro de las comunidades investigadas ocurrió en manchones de una sola especie, resultando en que solo el 15% de los cuadrantes tuvieran 3 de las especies clasificadas para lo que se diseñó el DWR. Se compararon métodos no destructivos para determinar la proporción de zacate por especie y se compararon con las proporciones cosechadas en comunidades de "Mezquite" (*Prosopis glandulosa* Torr.) y "Redberry juniper" (*Juniperus pinchotii* Sudw.) Los métodos de estimación evaluados fueron: 1) cosecha por especie, 2) estimación de peso por especie, 3) DWR pesando cuadrantes, 4) la estimación sin pesar de la proporción por especie y 5) DWR si pesar.

Las correlaciones entre las proporciones obtenidas con métodos no destructivos y por cosecha se mejoraron con el peso de cuadrantes. El pesar mejoró más los valores en las comunidades de "Juniper" que en las de "Mezquite". Aunque la clasificación acumulativa de los multiplicadores del DWR fue necesaria en 85% de los cuadrantes de la muestra, hubo una alta correlación ($r^2 > 0.995$) entre la estimación de peso y la del DWR pesad cuadrantes y entre la proporción estimada y el DWR sin pesar cuadrantes. Esto indica que la clasificación acumulativa con los multiplicadores originales del DWR fue virtualmente la misma que la estimación del evaluador.

El análisis de varianza indicó diferencias significativas entre los métodos de cosecha y no cosecha. El peso de cuadrantes en el DWR fue necesario para inferir las mismas conclusiones estadísticas entre las medias que proveyeron los de datos de cosecha. La clasificación es fácil usar y más probable de ser aplicada en forma similar por evaluadores individuales que las proporciones estimadas. Para sitios con variación alta de cosecha en pie y con especies en manchones que requieren el uso considerable de la clasificación acumulativa, el DWR con peso de cuadrantes provee una determinación adecuada de la proporción de biomasa por especie.

Assessment of standing crop by species in heterogeneous range plant communities requires numerous samples to account for inherent variability. Often, at the landscape scale, it is logistically

untenable to harvest and sort enough samples to adequately account for such variability. The dry-weight-rank (DWR) method was developed (t'Mannetje and Haydock 1963) to eliminate the need for clipping and sorting to assess species proportions of standing crop on a dry weight basis, therefore, saving time and allowing for greater sample sizes. When using DWR, which species occupy first, second and third place in order of their dry weight is judged within a quadrat. Rankings are converted to dry weight species composition by multiplying the proportion of occurrences of each rank for a species by multipliers of 0.70, 0.21, and 0.09 for the first, second, and third ranked species, respectively (t'Mannetje and Haydock 1963). The DWR method aims to eliminate the need to develop predictive models for individual species by using multipliers that apply to a large range of pasture types and species. The DWR multipliers were derived by multiple regression of actual dry weight proportion by species to number of occurrences of that species for rank 1, rank 2, and rank 3. Jones and Hargreaves (1979) derived similar multipliers to t'Mannetje and Haydock (1963) from a broader range of pasture types and climates, but obtained only minor improvements in species proportions by dry weight. Jones and Hargreaves (1979) recommend using rank multipliers derived from larger data sets, because rank multipliers developed from smaller data sets were often illogical (ie. rank 1 < rank 2 or rank 3) or were inconsistent between dates.

The DWR method works best when the number of species per quadrat is low and variation of their proportions is high (Sandland et al. 1982). For pastures that are homogeneous at the quadrat level DWR is less suited, because the same species would receive the same rank and its dry weight proportions would always equal the rank values. Species forming monospecific patches tend to be underestimated. Modifications by Jones and Hargreaves (1979) reduced this problem by assigning first and second rank to the dominant species when it is judged to be 85% or greater of quadrat dry matter, an adjustment referred to as 'cumulative ranking'. A second potential problem with DWR is that a consistent relationship between quadrat standing crop and the order that a species is ranked can result in over- or under-estimation of that species. If a species was always associated with low standing crop patches, its proportion at a site would be overestimated. Jones and Hargreaves (1979) reduced this prob-

lem by applying a weighting factor to the DWR multipliers, based on standing crop in each quadrat. A weighting factor or actual quadrat weights can be applied to estimated proportions of species to provide an index or estimate of standing crop by species.

Applicability of DWR has been studied in a variety of rangelands (Jones and Hargreaves 1979). In both tallgrass prairie (Gillen and Smith 1986) and arid rangeland (Friedel et al. 1988), there was no improvement in estimation of standing crop composition using quadrat weighting with DWR. Both t'Mannetje and Haydock (1963) and Jones and Hargreaves (1979) doubt whether DWR is applicable where quadrat size or pasture conditions result in a high incidence of cumulative ranking.

Our region of northwest Texas is semi-arid, consisting of plant communities that have a very patchy distribution of species and standing crop with large monospecific patches. As a result, the use of DWR requires the frequent use of cumulative ranking. In this paper, we test the applicability and accuracy of DWR under these conditions. We also assess the effects of applying quadrat weighting and DWR multipliers for improving the estimate of species proportion of standing crop.

Methods

Site Description

The study was conducted on the Y Experimental Ranch, located 25 km southeast of Crowell (33° 52' N, 100° 00' W) in north central Texas. Much of the vegetation is comprised of communities distinguished by dominant shrubs redberry juniper (*Juniperus pinchotii* Sudw.) or mesquite (*Prosopis glandulosa* Torr.). The juniper community occurred on shallow clay-loam soils (Vernon-Weymouth clay-loam complex) which have exposed rock or gypsum areas with sparse herbaceous vegetation as well as deeper soils with much greater herbaceous biomass. The mesquite community occurred on deeper, clay-loam soils (Tillman clay-loam) with a greater spatial continuity of herbaceous vegetation. Both communities had similar herbaceous standing crops with a patchy distribution of species. Patches of single species ranged from 1 m to 10 m in diameter. The herbaceous vegetation in both communities was dominated by tobosa grass [*Hilaria mutica* (Buckl.)Benth.], buffalo grass [*Buchloe dactyloides* (Nutt.)Engelm.], and sideoats grama [*Bouteloua curtipendula* (Michx.)Torr.].

Mesquite communities had a greater annual grass component [primarily *Bromus japonicus* Thunb., *Hordeum pusillum* Nutt., and *Bromus unioloides* (Wild.)H.B.K.] while juniper communities had relatively greater amounts of slim tridens [*Tridens muticus* (Torr.)Nash.]. Texas wintergrass [*Stipa leucotricha* Trin.&Rupr.] was common on sites in both communities. Other short grasses and other midgrasses were recorded individually but grouped for analysis. Forbs were important within these habitats, but were a minor component of cattle diets. Therefore, they were analyzed separately from grasses and were not used in these analyses. A more detailed description of the vegetation can be found in Donges (1994).

Sampling

Each method was evaluated at 3 juniper and 3 mesquite replicate sites (2.5 ha each) sampled on 4 dates (October 1993, January, April, and June 1994) by a single experienced evaluator. Sites were chosen from 3 pastures to represent the variation in forage observed within juniper and mesquite communities that were temporarily fenced (about 1 week in duration, seasonally) for another study. For each site, grasses within 40 quadrats (0.05 m²) were placed at 15 m intervals along 7 randomly selected line transects. Species were visually weight estimated, dry-weight-ranked (DWR), and harvested by species group. Species were collectively bagged by site, dried and weighed. The 3 most abundant grasses in a quadrat were ranked and ascribed the proportional values of 0.70, 0.21, and 0.09, respectively. If a species contributed 85% or more of standing crop in a quadrat it received ranks 1 and 2 (cumulative ranking). If a species was very minor (<1–2%) the prior ranked species additionally received rank 3. The visually estimated standing crop of each quadrat was used as the weighting factor as recommended by Jones and Hargreaves (1979). Cumulative ranking as well as quadrat weighting was potentially important because numerous samples were dominated by a single species, particularly where tobosa grass was encountered.

Assessment time

Evaluation and harvest of 40 quadrats at each site by species groups were accomplished by 3 people (1 evaluator and 2 harvesters) in about 2 hours. Evaluation and harvest (collectively by site) of 40 quadrats by grass or forb were accomplished by 1 person in about 2 hours. Ranking and weight estimation without

harvesting would require a single evaluator and be 2–3 times faster (about 40–60 quadrats hr⁻¹). This compares to 35 quadrats hr⁻¹ evaluated in tall-grass prairie (Gillen and Smith 1986) and 45 quadrats hr⁻¹ evaluated in arid rangeland (Friedel et al. 1988).

Calculations

The proportion of each species in the total standing crop was determined using the following equations:

$$\text{Harvest} = \sum Sw / \sum Qw$$

$$\text{ESTw} = \sum Se / \sum Qe$$

$$\text{DWRw} = \sum [(.70)Sf1 + (.21)Sf2 + (.09)Sf3] Qe / \sum Qe$$

$$\text{NRw} = \sum [Sf / Qf] Qe / \sum Qe$$

$$\text{ESTu} = \sum [Se / Qe] / n$$

$$\text{DWRu} = \sum [(.70)Sf1 + (.21)Sf2 + (.09)Sf3] / n$$

$$\text{NRu} = \sum Sf / \sum Qf$$

Where:

n = number of quadrats

∑ = sum for quadrats 1–n

Sw = dry weight of Species

Qw = dry weight of Quadrat

Se = estimated dry weight of Species

Qe = estimated dry weight of Quadrat

Sf1, Sf2, Sf3 = frequency of rank 1, 2, or 3 for Species, Sf1, Sf2, Sf3 = 1 or 0

Sf = frequency of ranked Species, Sf = 1 or 0

Qf = frequency of species within a Quadrat, Qf = 0, 1, 2, or 3

Harvest was the proportion of species standing crop based on total standing crop and was the check for the study. The ESTw, DWRw, and NRw were non-harvest methods using quadrat weight estimates to determine proportions based on total estimated standing crop. ESTu, DWRu, and NRu were non-harvest methods that give equal weighting to each quadrat. The ESTu and DWRu were averages of proportions of species. The NRu was based on relative number of ranked occurrences of a species. Because of the high degree of cumulative ranking within these sites and biomass differences associated with species, unranked proportions (NRw and NRu) were calculated to assess the relative importance of dry-weight-rank multipliers and quadrat weighting in improving values.

Statistical Analysis

Precision of non-harvest methods were evaluated with no-intercept regressions because intercepts were not significantly different from 0. Arcsine transformations of squareroot of proportions were per-

formed to reduce the non-linear affect of dominant to minor species on goodness of fit determination (after t'Mannetje and Haydock 1963). Regression coefficients and coefficient of determination were squared to account for the effect of transformation. Multiple regression was used to derive rank multipliers for comparison to established DWR values. For all regressions probability of slope = 0 was < 0.0001.

Because the same quadrats were evaluated for Harvest as for non-harvest methods, regressions did not include sampling

Clipped, sorted, and weighed

Estimated weight

Weighted Dry-Weight-Rank

Weighted, but Not Ranked

Unweighted Estimated Species

Proportion

Unweighted Dry-Weight-Rank

Unweighted and Not Ranked

(relative frequency of ranked species)

Results and Discussion

Dry-weight-rank (DWR) with cumulative ranking was necessary within quadrats because of the frequent presence of large monospecific patches of a grass species with high standing crop (in particular, tobosa grass) and monospecific patches of other species with low standing crop. Areas devoid of herbaceous vegetation were encountered in sub-canopy positions or because of geological features (ie. rocks, gypsum soils), particularly in juniper sites. About 7% of quadrats had no herbaceous vegetation in the juniper community compared to 1% in the mesquite community. Other vegetation sampling within these communities with 0.25 m² quadrats (Parajulee et al. 1997) resulted in a high incidence of cumulative ranking 69% vs. 85% with 0.05 m² quadrat used in this study. Standard error of means (n = 40) for standing crop in juniper communities was 9–21% with 0.25 m² quadrats and 9–15% with 0.05 m² quadrats. Standard error of means for standing crop in mesquite communities were 5–11% with 0.25 m² quadrats and 8–12% with 0.05 m² quadrats.

Proportions determined by estimate methods

Individual sites within juniper and mesquite communities varied considerably in species proportions of standing crop (Fig. 1). Harvest and non-harvest methods were similar and highly correlated within a site. Analysis of variance by species indicated that proportions of standing crop were similar between weighted methods (ESTw and DWRw) or between unweighted methods (DWRu and ESTu). The weighted methods were more accurate than unweighted methods. All non-harvest methods overestimated buffalo grass (P < 0.01) and under-estimated tobosa grass (P < 0.05 for weighted methods and P < 0.01 for unweighted methods). This indicated a bias towards aerial cover in visual estimation, because for a given cover or volume, tobosa grass was more dense while buffalo grass was less dense than expected. Additionally, for unweighted methods (ESTu and DWRu) annual grasses and Texas wintergrass were statistically different from Harvest proportions (P < 0.01 and P < 0.05, respectively). Annual grass was the dominant species within a quadrat only when quadrat standing crop was low, thus causing annual grass to be overestimated with unweighted methods. Additional differences between non-harvest methods and Harvest proportions

Table 1. No-intercept regression coefficient of determinations (r^2) of species composition between estimate methods of arcsine of square root transformed proportions.

COMMUNITY	METHOD	ESTw	DWRw	NRw	ESTu	DWRu	NRu
Juniper	Harvest	.956	.952	.936	.884	.880	.869
	ESTw		.998	.984	.962	.958	.940
Mesquite	Harvest	.979	.975	.909	.932	.929	.831
	ESTw		.999	.945	.967	.966	.878

were detected using regression but were not considered as important because no sampling error due to quadrat placement was incorporated.

Relationships between methods and communities

All non-harvest methods were highly correlated to Harvest standing crop proportions (Table 1). Harvest proportions were more correlated to weighted methods (ESTw and DWRw) than unweighted methods (ESTu and DWRu). Weighting improved values particularly for the juniper community as indicated by the greater difference between r^2 of weighted and unweighted methods. Similarly, Jones and Hargreaves (1979) found that where a consistent relation between quadrat yield and species rank occurs, quadrat weighting can improve DWR composition estimation.

The unweighted, unranked method (NRu) represents the least improved estimates of Harvest proportions. Harvest to NRu r^2 s were similar for juniper and mesquite communities. Ranking alone (DWRu) improved values slightly in juniper communities and substantially in mesquite communities. Weighting without ranking (NRw) improved values for both communities. Estimation or ranking with quadrat weighting (ESTw and DWRw) were more highly correlated with Harvest proportions than other methods tested for either community. All non-harvest methods were more highly correlated to ESTw than to Harvest proportion. This may indicate non-harvest methods are sensitive to the degree of evaluator training and that frequently recurring minor species are more likely to be overestimated. Initial training to identify the relative differences in plant dry weight is considered important (t'Mannetje and Haydock 1963, Gillen and Smith. 1986, Friedel et al. 1988).

The lower importance of ranking in the juniper community when compared to the mesquite community was due to all species at juniper sites having equal distribution of the three ranks (t'Mannetje and Haydock 1963, Jones and Hargreaves

1979, Sandland et al. 1982). In mesquite communities the greater importance of ranking was in part because tobosa grass, when present within a quadrat, was almost always the dominant species and annual grass was almost always the minor species.

Multiple regression analysis to provide rank multiplier values (Table 2) for ESTw based on species ranks and quadrat weights, produced similar rank multipliers to those of t'Mannetje and Haydock (1960). However, other multiple regressions resulted in poorer model fit and some illogical negative multipliers. These data indicate that the original multipliers that are derived from a broad range of pasture types were satisfactory for our community types.

Table 2. Values for species rank multipliers derived with multiple regression and coefficient of determination (r^2). The dependent variable was species proportion with independent variables of frequency of that species with rank 1, 2, and 3; or the dependent variable was species weight with dependent variable of the sum of quadrat estimated weight for that species of rank 1, 2, and 3.

	Rank 1	Rank 2	Rank	r^2
DWR proportion*	0.70	0.21	0.09	.894
Harvest proportion	0.68	0.65	-0.33	.894
Estimated proportion	0.71	0.45	-0.16	.960
Harvest weight	0.67	0.34	-0.01	.962
Estimated weight*	0.68	0.22	0.10	.998

*DWR multipliers derived by t'Mannetje and Haydock (1963).

Differences between methods, communities, sites and dates

Regression analyses are limited to describing paired data which reflects little sampling error. Of more importance is how error associated with a method compares to inherent sampling error. Analysis of variance provides a tool to discern the effects of methods within communities and sites on species proportions (Table 3). Method pair source of variation was for a complete model with r^2 totaling 100%. Significant species differences were expected because dominant species were compared with other species. Other main effects have equal proportions and do not account for more variation. Species interactions and

species x method interactions are of interest as indices to account for variation ascribed to methods. Without including variation associated with methods, residual error (species x community x site x date) would be 7–8% with 120 degrees of freedom. This indicates powerful tests of the hypothesis are possible. Both the magnitude of effect variation (r^2) and significance of hypothesis test are important in evaluating method differences.

Estimation and DWR produced virtually the same species proportions. Unweighted methods ESTw vs. DWRw were very similar, as were ESTu vs. DWRu, with total method interaction variation of only 0.2% of model r^2 . Therefore, Harvest to ESTw and Harvest to ESTu comparisons are not presented. Compared to Harvest, DWRw sum of method interaction r^2 was 2.29% while DWRu was 6.14%. DWRw residual error r^2 (species x community x site x date) was 8.13% while DWRu was 6.88%. For DWRu compared to Harvest, the sum of method variation was approaching that of residual error. Individual sites (species x community x site) and residual error (species x community x site x date) accounted for more variation than non-harvest method (sum of method interaction).

Species proportions for non-harvest methods were significantly different from Harvest proportions (method x species) (Table 3 and Fig.1). The magnitude of species differences from harvest was greater for DWRu than DWRw. All methods calculated consistent differences in species proportions within sites and communities (species x community x site). This indicated that individual sites were adequately sampled, but likelihood of finding differences at the community level was decreased because this was used as the error term to test for community differences. Unweighted methods (Harvest vs. DWRu and ESTu vs. DWRu) resulted in exaggerated differences in species propor-

Table 3. Sources of variation within analysis of variance comparing method pairs of calculated species proportions. Values are the ratio of effect sum of squares to total sum of squares which are equivalent to effect portions of model r^2 expressed as percent.

	df	Harvest vs DWRw	Harvest vs DWRu	DWRw vs DWRu	ESTw vs DWRw	ESTu vs DWRu
Sp	7	48.92**	44.06**	44.24**	47.39**	41.40
Sp*C	7	10.81	13.98*	16.63*	12.81	21.14*
Sp*C*S	28	28.02**	26.90**	28.71**	29.66**	29.26**
Sp*D	21	1.83	1.62	1.47	1.73	1.33
Sp*C*S*D	120	8.13	6.88	6.72	8.32	6.80
M*Sp	7	1.18**	3.10**	.62*	.01	.01
M*Sp*C	7	.07	.46	.24	.01	.01
M*Sp*C*S	28	.34	1.18	.62	.01	.01
M*Sp*D	21	.23	.28	.08	.02	.01
M*Sp*C*S*D	120	.47	1.12	.68	.15	.14
Sum of M	183	2.29	6.14	2.24	.20	.18

Sp = species Significance of effect F-value: * = $P < 0.05$; ** = $P < 0.01$
M = method
C = community Sp and Sp*C tested with Sp*C*S
S = site Sp*C*S and Sp*D tested with Sp*C*S*D
D = date Method interactions tested with Sp*C*S*D + M*Sp*C*S*D

tions between juniper and mesquite communities. This was indicated by higher r^2 for species x community relative to fairly constant variation of r^2 across methods pairs for species x community x site resulting in significant F-values. Although DWRw species proportions were significantly different from Harvest, these differences were smaller than DWRu and did not exaggerate differences between communities as much as DWRu.

Conclusions

Unlike studies which present dry-weight-rank (DWR) results derived from ideally ranked and weighted data from harvest studies, these calculations are based on visual estimation made in the field prior to clipping, sorting, and weighing. These data are also from sites with high variability in standing crop and high spatial heterogeneity of species resulting in most quadrats being cumulatively ranked. The DWR method was preferred to visual quadrat composition estimates because ranking was easier, quicker, and less-likely to be biased between evaluators. Species proportions using DWR derived by trained evaluators were highly correlated (t'Mannetje and Haydock 1963, Walker 1970, Gillen and Smith 1986, Everson and Clarke 1987, Friedel et al. 1988).

The ability of the published DWR multiplier values of 0.70, 0.21, and 0.09 (t'Mannetje and Haydock 1963) with cumulative ranking to predict dry-weight species proportions was supported in 3 instances. Firstly, correlation of DWRw to ESTw or DWRu to ESTu was high ($r^2 > 0.996$). Secondly, analysis of variance

indicated that variation between DWRw and ESTw or between DWRu and ESTu was small, about 0.2% of model r^2 . Thirdly, multiple regression analysis to solve for rank multipliers for ESTw based on species ranks and quadrat weights produced similar rank multipliers to those of t'Mannetje and Haydock (1960). The DWR method very nearly predicted species proportions the evaluator estimated to be present.

Deficiencies in DWR with quadrat weighting were relatively minor and were due to misapplication of ranks to certain species because of evaluator error. Although the evaluator was experienced in harvest techniques, tobosa grass and buffalo grass were consistently under- and over-estimated, respectively. A combination of more perfect ranking and quadrat

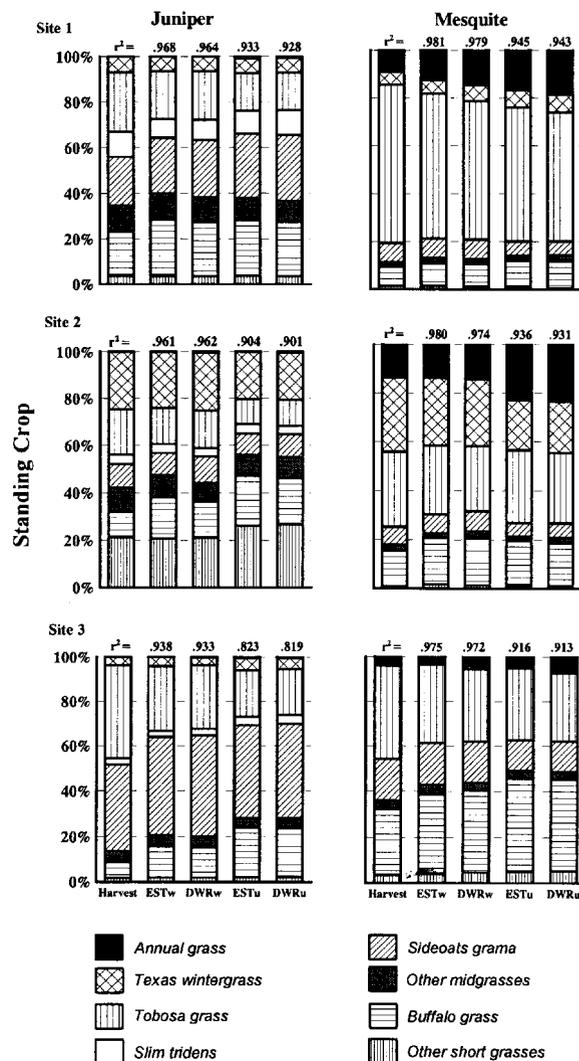


Fig. 1. Standing crop proportions by species at different sites within juniper and mesquite communities as determined by Harvest vs. non-harvest methods. Coefficient of determinations (r^2) were of non-harvest to Harvest method based on no-intercept regression of arcsine of squareroot of proportions over 4 dates.

weighting would potentially improve values particularly for tobosa grass and buffalo grass. Quadrat weighting improved values and, additionally, can be used with species proportions to estimate standing crop by species.

Quadrat weighting of DWR improved species proportions in this study and the studies of Jones and Hargreaves (1979) and Sandland et al. (1982). However, quadrat weighted and unweighted DWR proportions were similar in studies by Gillen and Smith (1986) and Friedel et al. (1988). The effect of ranking and quadrat weighting on estimates of species proportions was also different for mesquite and juniper communities. For mesquite communities, ranking and weighting resulted in similar improvement of values towards harvest proportions. For juniper communities weighting was necessary to improve values. When making comparisons between communities using analysis of variance, DWR with quadrat weighting was necessary to draw similar statistical conclusions between means that harvest data provided.

When initially using DWR within a community, we recommend quadrat weighting so that comparisons can be made to insure unweighted values are similar to weighted values. Acceptable estimates of species proportions were obtained with weighted DWR for communities with high spatial variability of species and standing crop. The time taken to estimate standing crop proportions by species using quadrat weight estimates and DWR compared well with use of DWR in other studies. Ranking and weight estimation was considerably faster than any harvest method.

Literature Cited

Donges, R.D. 1994. An internship on two experimental ranches. Master of Agriculture Thesis, Texas A&M Univ., College Station, Tex.

Everson, C.S. and P.Y. Clarke. 1987. A comparison of six methods of botanical analysis in the montane grasslands of Natal. *Vegetatio*. 73:47-51.

Friedel, M.H., V.H. Chewings, and Bastin. 1988. The use of comparative and dry-weight-rank techniques for monitoring arid rangeland. *J. Range Manage.* 40:430-435.

Gillen, R.L. and E.L. Smith. 1986. Evaluation of the dry-weight-rank method for determining species composition in tallgrass prairie. *Range Manage.* 39:283-285.

Jones, R.M. and Hargreaves, J.N.G. 1979. Improvements to the dry-weight-rank method for measuring botanical composition. *Range and Forage Sci.* 34:181-189.

t'Mannetje, L. 'T and Haydock, K.P. 1982. The dry-weight rank method for botanical analysis of pasture. *J. Brit. Grassl. Soc.* 18:268-275.

Parajulee, M.N., Slosser, J.E., Montado, Dowhower, S.L., and Pinchak, W.E. 1982. Rangeland grasshoppers (Orthoptera: Acrididae) associated with mesquite and juniper habitats in the Texas Rolling Plains. *Environ. Ent.* 26(3):528-536.

Sandland, R.L., Alexander, J.C., Haydock, K.P. 1982. A statistical assessment of the dry-weight-rank method of pasture sampling. *Grass and Forage Sci.* 37:263-268.

Statistical Analysis System (SAS). 1985. *Statistical Analysis System (SAS) User's Guide.* SAS Institute Inc., Cary, NC.

Walker, B.H. 1970. An evaluation of methods of botanical analysis of grasslands in Rhodesia. *J. Applied Ecol.* 7:403-411.



granite
SEED

Your one-stop supplier for:

- Pasture and range grasses
- Alfalfa, shrubs, & wildflowers
- Custom seed blends
- Erosion control materials
- Environmental consulting services

Ask for our catalog featuring over 600 native species and named varieties.

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

Animal age and sex effects on diets of grazing cattle

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

Authors are research animal scientist, research physiologist, rangeland scientist, and supervisory rangeland scientist, USDA, Agricultural Research Service, Fort Keogh Livestock and Range Research Laboratory, Miles City, Mont. 59301.

Abstract

The effects of animal age and sex on chemical and botanical composition of diets of cattle grazing native rangelands were evaluated in a 2-year study. Samples were collected monthly from June through October using esophageally cannulated suckling calves, yearling heifers, mature cows, and mature steers. Dietary crude protein and digestibility differed among animal classes, but these differences varied over time. These 2 diet quality indicators did not vary in the same manner over time for all animal classes. Dietary crude protein varied from a low of 7.2% for steers in August 1994 to a high of 14.3% for heifers in June 1993. In vitro digestibility varied from a low of 50.7% for cows in October 1993 to a high of 74.3% for calves in June 1993. Botanical composition of diets varied with animal class and sampling date with interactions among these. Cool-season grasses accounted for an average of 70% of the diet with a range of 33 to 90%. Shrubs varied from 1 to 61% of the diet. Differences in chemical composition among age and sex classes of cattle grazing native rangeland during the growing season may be partially related to differences in botanical composition of diets. Animals used to obtain diet samples should, therefore, be of similar physiological state and age as animals being monitored for performance.

Resumen

En un estudio de dos años se evaluó el efecto de la edad y sexo del animal en la composición botánica y química de la dieta del ganado apacentando pastizales nativos. Las muestras se colectaron mensualmente de Junio a Octubre utilizando becerros sin destetar, vaquillas, vacas maduras y novillos con cánulas esofágicas. La proteína cruda dietaria y la digestibilidad difirieron entre las clases de animal y estas diferencias variaron a través del tiempo. Estos dos indicadores de la calidad de la dieta no cambiaron de la misma manera a través del tiempo para todas las clases de animal. La variación de la proteína cruda dietaria fue de 7.2% en la dieta de los novillos en agosto de 1994 a 14.3% en la dieta de las vaquillas en Junio de 1993. La digestibilidad in vitro vario de de 50.7% en la dieta de las vacas en Octubre de 1993 a 74.3% en la dieta de los becerros en Junio de 1993. La composición botánica de la dieta vario con la clase de animal y la fecha de muestreo con interacciones entre estos factores. Los zacates de estación fría aportaron aproximadamente el 70% de la dieta y el rango de ellos fue del 33 al 90%, los arbustos variaron del 1 al 6% de la dieta. Las diferencias en la composición química de la dieta entre edad y sexo del animal del ganado apacentando pastizales nativos durante la estación de crecimiento puede estar parcialmente relacionada a las diferencias en la composición botánica de las dietas. Los animales utilizados para obtener las muestras de las dietas deben estar en el mismo estado fisiológico y edad que los animales que están siendo monitoreados para determinar su comportamiento productivo.

Key Words: diet selection, beef cattle, calf, steer, heifer

Esophageal diet sampling is one technique used to obtain diet quality information needed to estimate digestibility and intake of grazing cattle. Researchers often use a single class of animals to determine diet quality for all animals. For example, some researchers have used mature steers for sampling because of their ease of handling. These steers may differ in physical stature, body composition, intake as a proportion of body weight, and nutrient requirements compared with the cattle being monitored for performance. A number of researchers have observed differ-

ences in diet selection between young, suckling ruminants and older animals (Horn et al. 1979, Ferrar Cazcarra and Petit 1995, Grings et al. 1995). Langlands (1969) found differences in diet selection due to animal age, but not sex. Mohammad et al. (1996) found limited diet compositional differences between mature cows and 2-year-old steers on semidesert range. The greatest differences occurred during fall and these authors suggested differences in diet selection between sexes may be more apparent during periods of limited forage availability. The effects of animal class (age or sex) on diet selection may be dependent on the quality as well as quantity of available herbage. Wallace et al. (1972) suggested the lack of difference between quality of available forage and selected diets of cattle on eastern Colorado rangeland during winter was due to the uniform chemical composition of forages available. The objective of this study was to evaluate the influence of animal age and sex on botanical and chemical composition of diets obtained by cattle grazing Northern Great Plains rangeland.

The authors express appreciation to Byron Hould, Richard Bonine, and Brooke Shipp for assistance in sample collection, Susan Reil for sample collection and laboratory analysis, Mary Ellen French for assistance with graphics, and Dr. Michael MacNeil for assistance with statistical analysis.

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.

Mention of a proprietary product does not constitute a guarantee or warranty of the product by USDA, Montana Agri. Exp. Sta., or the authors and does not imply its approval to the exclusion of other products that may also be suitable.

Manuscript accepted 25 Apr. 2000.

Material and Methods

The study was conducted at the Fort Keogh Livestock and Range Research Laboratory near Miles City, Montana (46° 22' N 105° 5' W). Climate is continental and semi-arid with vegetation 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 (Fig. 1)

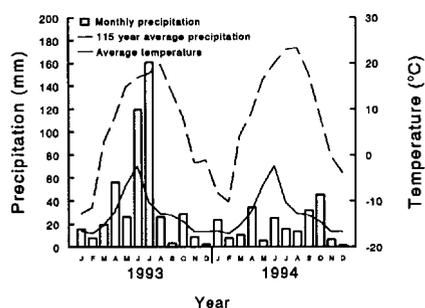


Fig. 1. Average precipitation (bars) during the study years of 1993 and 1994 compared to a 115-year average (solid line) and average monthly temperature (dashed line) during the study years.

The study utilized esophageally cannulated suckling heifer calves, yearling heifers, mature cows, and mature steers. Six mature steers (5- to 6-years old) and 6 lactating cows (2- to 5-years old) were used. All but 1 cow were used both years. Weight, body condition, and physical stature of cows was different than steers. Calves were 4 months old at the first sample collection period after having been cannulated at 2 months of age. During 1993, 6 yearling heifers and 6 heifer calves were used, while during 1994, 4 yearling heifers and 8 heifer calves were used. Yearling heifers used during 1994 were the calves used during 1993. Steers and cows had considerable experience in the pastures during earlier winters and were familiar with the vegetation and topography. Heifers had previously grazed pastures with similar range sites and were experienced with the forage species available. Calves had grazing experience but not with all forage species available.

Samples were collected each month from June through October of 1993 and 1994 in 2 vegetatively similar native rangeland pastures of 85 and 90 ha. These pastures were grazed with yearling steers at a density of 4.4 ha steer⁻¹ from mid-May to mid-September 1993 and from mid-May to late August 1994.

Cattle used for diet sampling were brought to the site the day before sampling and were held overnight without feed but with water available. Collection bags were placed on cattle at 0700 hours and they were allowed to graze the first pasture for 30 to 45 min. These procedures were repeated a second day in the second pasture. Due to problems with sample collections, not all animals collected a sample for each month. Except for yearling heifers, samples from the 2 days were composited by weight, frozen, lyophilized, and ground to pass a 1-mm mesh screen in a Wiley mill. Samples for yearling heifers for all months except October were being used to evaluate diet quality for a concurrent study that required analysis by individual pasture. Therefore, analyses were conducted on individual samples and averaged over 2 days.

Samples were divided with one-half used for analysis of crude protein (Hach 1987) and in vitro organic matter digestibility (Tilley and Terry 1963) without supplemental nitrogen and the other half used for microhistological analysis for botanical composition (Sparks and Malechek 1968). One slide of each sample was read (20 fields) for microhistological analysis at a commercial laboratory (Composition Analysis Laboratory, Fort Collins, Colo).

Forage availability on 2 representative range sites was determined during the same week that diet samples were collected. The sites were clay pan and silty-shallow and represented 15 and 49%, respectively, of the pasture area. Standing crops were visually estimated by giving a score of 1 (high) to 4 (low) in 20 randomly placed 0.25 m² quadrats within each of 2 range sites. Every fifth plot was clipped to ground level, dried, and weighed. Linear regression was used to estimate standing crops from vegetation abundance scores. Separate regressions were used for each range site and month. Additional pastures were evaluated at the same time so that 16 clipped plots were used for each regression. Botanical composition of each plot was estimated by the dry weight rank method (t'Mannetje and Haydock 1963). Forage samples were composited by range site, ground to pass a 1 mm mesh screen in a Wiley mill and ana-

lyzed for crude protein and in vitro organic matter digestibility.

Data were analyzed using the General Linear Models Procedures of SAS (1989). Error mean squares were generated from a model containing animal class, month, year, and all associated interactions, and individual animal within animal class. This last component was used to test the effect of animal class on diet selection. Because animal class changed between years (i.e., 1993 calves became 1994 yearling heifers), the term for individual animal within animal class was deleted and the model rerun to produce estimable least squares means. Standard errors of the least square means were then corrected using the error mean square from the initial model. Mean separation was by least significant difference if a significant F-test was observed.

Results and Discussion

Botanical composition of the pastures was dominated by cool-season grasses with some warm-season grasses, annual grasses, sedges, and forbs present (Table 1). Shrub biomass was not estimated.

Table 1. Average botanical composition of available herbage on 2 representative range sites within the pastures sampled for diet quality. Shrubs were not included in the estimates.

	1993	1994
	---(% of biomass)---	
Cool-season grasses	54	61
Warm-season grasses	17	21
Annual grasses	3	1
<i>Carex</i> spp.	6	5
Forbs	20	12

Forage availability ranged from 1,129 to 2,047 kg ha⁻¹ on 2 sites within the pastures (Table 2). Precipitation between the 2 years differed (Fig. 1) with resulting differences in available forage and herbage quality (Table 3 and 4).

Seasonal diet quality trends were observed for all animal classes, but dietary crude protein exhibited various interactions among animal class, month, and year ($P < 0.10$; Table 3). The only animal class-month combinations not differing in dietary crude protein between years were diets of calves, heifers, and cows in June and heifers in July.

Diets of calves and heifers generally had greater crude protein concentrations than

Table 2. Herbage mass of 2 range sites within pastures sampled by esophageally cannulated cattle on 5 dates in 2 years. Standard error of the mean = 26.8, n = 20.

	June	July	Aug	Sep	Oct
1993	------(kg ha ⁻¹)-----				
Clay pan	2047	1762	1799	1754	1737
Silty-shallow	1426	1555	1590	1344	1363
1994					
Clay pan	1957	1967	1879	1803	1129
Silty-shallow	1507	2008	1490	1275	1393

Table 3. Least square means of dietary crude protein and during 2 growing seasons for 4 classes of cattle. Pooled standard error of the mean for diet crude protein = 0.08.

	June	July	Aug	Sep	Oct
1993	------(% of organic matter)-----				
Calves	14.2 ^{a1}	12.6 ^a	10.9 ^a	10.8 ^a	8.9
Heifers	13.5 ^a	11.7 ^{ab}	10.8 ^a	9.1 ^b	8.9
Cows	11.8 ^b	11.2 ^b	9.9 ^a	8.8 ^b	8.7
Steers	9.8 ^c	9.8 ^c	8.3 ^b	7.8 ^c	8.5
Herbage	9.2	11.5	10.0	9.0	8.6
1994					
Calves	14.2 ^a	10.9 ^a	8.5 ^a	7.7 ^a	12.7 ^a
Heifers	14.3 ^a	11.0 ^a	9.0 ^a	7.6 ^a	12.3 ^{ab}
Cows	11.7 ^b	8.2 ^b	7.3 ^b	7.5 ^a	13.2 ^{bc}
Steers	11.1 ^b	8.2 ^b	7.2 ^b	9.6 ^b	13.6 ^c
Herbage	8.5	9.0	6.3	8.3	8.4

¹Means within month by year with different superscripts differ by animal class (P < 0.05). Significant effects in the model were animal class, P < 0.01; month, P < 0.01; animal class x month, P < 0.01; animal class x year, P < 0.01; month x year, P < 0.01, individual animal within animal class, P < 0.01, animal class x month x year, P < 0.10.

other animal classes, but differences decreased as the season progressed. During 1993, steer diets contained less crude protein than diets of other animal classes except at the October sampling, when there were no differences due to animal class. During 1994, crude protein concentrations of steer diets did not differ from those of cows except in September, when diets of steers had greater crude protein concentrations than any other animal class.

There were fewer differences among animal classes for in vitro organic matter digestibility (Table 4) than for crude protein. Digestibility did not differ (P > 0.10) among animal classes for the August 1993, July 1994, and October 1994 samples. Heifer diets were often lower in digestibility than calf diets, even when they did not differ in crude protein.

While general trends in diet quality throughout a growing season may be similar among animal classes, absolute values may be different. Animal class by month interactions for both crude protein and in vitro organic matter digestibility indicate that prediction of the diet quality of one class from another is not advised.

The differences in dietary selection between steers and cows may be related to more than gender. Physiological states and

physical stature of these animal classes were quite different. They differed in energy needs as well as muzzle size. It is not apparent from this study what caused differences between cow and steer diet selection.

Several researchers have reported that diets of calves may differ in nutritive quality compared to older animals, but that this difference varies with forage conditions (Hodgson and Jamieson 1981, Le Du and

Table 4. Least square means of in vitro organic matter digestibility during 2 growing seasons for 4 classes of cattle. Pooled standard error of the mean for diet in vitro organic matter digestibility = 0.18.

	June	July	Aug	Sep	Oct
1993	------(% of organic matter)-----				
Calves	74.3 ^{a1}	68.3 ^a	62.5	61.9 ^a	54.7 ^a
Heifers	66.5 ^b	62.5 ^b	59.8	58.6 ^b	56.6 ^{ab}
Cows	72.7 ^a	65.0 ^{bc}	62.4	58.6 ^b	50.7 ^c
Steers	69.3 ^b	67.9 ^{ac}	60.9	58.5 ^b	58.6 ^b
Herbage	52.4	52.6	49.3	49.5	46.9
1994					
Calves	68.5 ^a	61.2	58.7 ^a	60.6 ^a	62.1
Heifers	65.9 ^a	57.8	55.3 ^b	56.2 ^b	62.4
Cows	67.1 ^a	59.7	57.7 ^{ab}	58.7 ^{ab}	63.6
Steers	64.4 ^a	61.1	56.4 ^{ab}	58.1 ^{ab}	63.9
Herbage	52.5	51.4	47.5	51.3	50.2

¹Means within month by year with different superscripts differ by animal class (P < 0.05). Significant effects in the model were animal class, P < 0.01; month, P < 0.01; animal class x month, P < 0.01; animal class x year, P < 0.10; month x year, P < 0.01; animal class x month x year, P < 0.05; individual animal within animal class, P < 0.01.

Baker 1981). Ferrar Cazcarra and Petit (1995) reported that 7-month-old calves had higher fecal nitrogen than both 18-month-old heifers and adult cows. This occurred irrespective of sward height in pastures of orchardgrass (*Dactylis glomerata* L.). These researchers suggested that calves ate smaller, shallower bites resulting in a diet consisting of more leaf with higher protein content than heifers or cows.

The choice of animal class to use for studies intended to rank varieties or forage treatments may be of limited concern, but it is critical to use the appropriate animal class when nutrient intake and digestion are being considered. For example, if mature steers had been used to estimate diet quality for yearlings during June 1993, crude protein would have been underestimated by 4 percentage units (9.8 vs 13.5%, Table 3) compared to using yearlings to collect diet samples. The subsequent error in nutrient intake and digestibility would be quite large. The heifers in this study were being used to estimate diet quality for steers grazing these pastures during this time period. Using heifer diet quality values resulted in crude protein intakes of 737 g day⁻¹ for yearling steers. If we had used diet quality as collected by mature steers, our crude protein intake estimates would have been only 521 g day⁻¹. We might have suggested differing management strategies for these cattle based upon our erroneous results.

Crude protein levels of available forage were below that of all selected diets during June and October of 1994, indicating strong diet selection at these times (Table 3). Relationship of diet crude protein to forage crude protein during other months differed. In vitro organic matter digestibility of available forage was always well below that of diets (Table 4).

Table 5. Least squares means of botanical composition of diets of cattle of 4 animal classes and total standing crop, June– October, 1993 and 1994.

	1993					1994					Mean	SEM
	June	July	Aug	Sep	Oct	June	July	Aug	Sep	Oct		
Number of samples in mean	------(n)-----											
Calves	5	6	6	6	6	2	7	8	8	8		
Heifers	5	5	5	5	5	4	4	4	4	3		
Cows	6	6	6	6	6	6	6	6	6	6		
Steers	6	5	6	6	5	6	6	6	6	6		
Cool-season grasses (abcd) ¹	------(%)-----											
Calves	45	74	96	73	61	69	70	67	78	86	72	1.1
Heifers	67	43	74	69	60	76	56	76	79	88	69	
Cows	50	70	90	84	58	67	62	82	68	88	72	
Steers	44	79	90	91	33	69	56	83	35	79	66	
Warm-season grasses (cde)												
Calves	0	2	1	2	6	3	3	6	4	1	3	.2
Heifers	2	8	11	10	6	4	4	3	5	2	5	
Cows	0	1	1	5	1	3	1	4	1	1	2	
Steers	1	0	5	3	2	5	2	7	0	1	2	
Annual grasses (ace)												
Calves	2	1	0	2	6	0	1	1	1	3	1	.1
Heifers	2	1	0	10	6	3	2	3	3	4	2	
Cows	2	2	1	5	1	4	1	0	0	5	2	
Steers	2	1	0	3	2	0	1	0	0	2	1	
Sedges (acef)												
Calves	5	6	1	2	17	5	6	6	1	3	5	0.4
Heifers	7	9	11	18	19	7	9	15	1	4	10	
Cows	2	8	4	7	19	2	8	4	1	4	6	
Steers	4	8	3	4	12	4	8	2	0	0	5	
Forbs (ab)												
Calves	3	1	1	1	0	6	2	0	0	1	1	0.1
Heifers	1	1	0	1	1	2	1	0	1	0	1	
Cows	2	1	0	1	0	1	0	1	0	1	1	
Steers	0	2	0	1	0	3	0	0	4	0	1	
Shrubs (abcde)												
Calves	44	16	1	22	14	22	20	20	15	6	18	1.1
Heifers	22	38	4	3	13	13	24	2	12	2	13	
Cows	44	19	4	2	1	21	32	8	29	21	18	
Steers	49	11	2	1	50	22	31	14	61	18	26	

¹Within botanical species there were significant effects of a month, b animal type x month, c month x year, d animal type x month x year, e animal type, and f year.

During mid-summer, diet quality did not always differ from available forage quality. This may have been influenced by the relative contributions of warm-season grasses. Warm-season grasses comprised about 18% of the standing crop on 2 common range sites within the study area. Diets of cattle contained only 1.8 (steers) to 6.8% (heifers) warm-season grasses during the months of July to September. Cattle were not selecting warm-season grasses even though they had the potential to increase dietary protein concentrations by doing so. In contrast, digestibility of diets was greater than the digestibility of available forage. Warm-season grasses may have lower digestibility than cool-season grasses (Haferkamp et al. 2001) and this may indicate why warm-season grasses were not highly preferred species.

Cool-season grasses accounted for an average of 70% of all diets (Table 5). Shrubs, averaging 19%, were the next greatest component of the diet. Shrubs in

the diet included winterfat (*Ceratoides lanata* (Pursh.) J.T. Howell), greasewood (*Sarcobatus vermiculatus* [Hook.] Emory.), shadscale (*Atriplex confertifolia* (Torr. and Frem.) Wats.), western snowberry (*Symphoricarpos occidentalis* Hook.), Wyoming big sagebrush (*Artemisia tridentata* Pursh. subsp. *wyomingensis* Beetle and Young), and fringed sagewort (*Artemisia frigida* Willd.). Forbs were a minor component of the standing crop and were, therefore, a minor component of the diet of this vegetation type.

Steer diets collected during September 1994 contained a large proportion of shrubs (61%). This resulted in a crude protein concentration that was 2 percentage units above other animal classes. We observed some instances of either steers or older cows leading the herd to what appeared to be preferred sites within the pasture, often with a component of winterfat in the community. Winterfat accounted for 18 to 86% of the 6 steer diet samples

collected during September 1994. Possibly, this degree of shrub consumption would not be maintained throughout an entire day of grazing. However, increased shrub consumption through even a portion of the day could have a significant influence on the chemical composition of the diet, such that diets of other animal classes would not be well represented by the diet collected from these steers.

Mohammed et al. (1996) found dietary overlap between cows and steers to vary with season with a range from 70 to 90%. During spring and winter, cows consumed more grass and less forbs than steers. Although differences in shrub content in cow and steer diets differed at times, this difference was never greater than 4%, much less than that observed during our study. Diet composition in the study of Mohammed et al. (1996) was determined from fecal samples and would represent a longer gazing period than our samples.

We collected diet samples during a 30 to 45 min grazing bout on each of 2 mornings. Diurnal variation in diet selection may occur (Obioha et al. 1970, Van Dyne and Heady 1965), with potential compensation throughout the day for differences observed within the sampling period. However, it is common for researchers to use short-term grazing bouts to determine diet quality. Researchers utilizing fecal sampling to evaluate animal class comparisons (Langlands 1969, Mohammad et al. 1996) have also observed variation of diets among animal classes.

Conclusions

Alterations in botanical composition of diets of differing age and physiological classes of cattle can result in variations in chemical composition of those diets. Other factors are also involved in the variation in diet quality. Therefore, animals used to obtain diet samples on rangelands with diverse botanical composition should be of similar class as the animals being monitored for performance. This caution should be exhibited especially when forage availability is low, botanical diversity is high, and/or results are being used to estimate nutrient intakes.

Literature Cited

- Ferrar Cazcarra, R. and M. Petit. 1995.** The influence of animal age and sward height on the herbage intake and grazing behavior of Charolais cattle. *Anim. Sci. (Pencaitland)* 61:497–506.
- Grings, E.E., D.C. Adams, and R.E. Short. 1995.** Diet quality of suckling calves and mature steers on Northern Great Plains rangelands. *J. Range Manage.* 48:438–441.
- Hach. 1987.** Feed analysis manual. Hach Co., Ames, Iowa.
- Haferkamp, M.R., R.K. Heitschmidt, E.E. Grings, M.D. MacNeil, and M.G. Karl. 2001.** Suppression of annual bromes impacts rangeland: vegetation responses. *J. Range Manage.* 53 (In press).
- Hodgson, J. and W.S. Jamieson. 1981.** Variations in herbage mass and digestibility, and the grazing behaviour and herbage intake of adult cattle and weaned calves. *Grass and Forage Sci.* 36:39–48.
- Horn, F.P., J.P. Telford, J.E. McCroskey, D.F. Stephans, J.V. Whiteman, and R. Totusek. 1979.** Relationship of animal performance and dry matter intake to chemical constituents of grazed forage. *J. Anim. Sci.* 49:1051–1058.
- Langlands, J.P. 1969.** Studies on the nutritive value of the diet selected by grazing sheep. IV. Variation in the diet selected by sheep differing in age, breed, sex, strain and previous history. *Anim. Prod.* 11:369–378.
- Le Du, Y.L.P. and R.D. Baker. 1981.** The digestibility of herbage selected by oesophageally fistulated cows, steer calves, and wether sheep when strip-grazing together. *Grass and Forage Sci.* 36:237–239.
- Mohammad, A.G., C.A. Ferrando, L.W. Murray, R.D. Pieper, and J.D. Wallace. 1996.** Season and sex influences on botanical composition of cattle diets in southern New Mexico. *J. Range Manage.* 49:204–208.
- Obioha, F.C., D.C. Clanton, L.R. Rittenhouse, and C.L. Streeter. 1970.** Source of variation in chemical composition of forage ingested by esophageal fistulated cattle. *J. Range Manage.* 23:133–136.
- SAS. 1989.** SAS user's guide. Statistical Analysis System Institute, Inc., Cary, N.C.
- Sparks, D.R. and J.C. Malechek. 1968.** Estimating percentage dry weight in diets using a microscopic technique. *J. Range Manage.* 21:264–265.
- 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. Brit. Grassl. Soc.* 18:268–275.
- Van Dyne, G.M. and H.F. Heady. 1965.** Dietary chemical composition of cattle and sheep grazing in common on a dry annual range. *J. Range Manage.* 18:78–85.
- Wallace, J.D., J.C. Free, and A.H. Denham. 1972.** Seasonal changes in herbage and cattle diets on sandhills grassland. *J. Range Manage.* 25:100–104.

Nutritive value and aversion of honey mesquite leaves to sheep

R. BAPTISTA AND K.L. LAUNCHBAUGH

At the time of research, authors were graduate research assistant and assistant professor in the Range, Wildlife and Fisheries Management Department, Texas Tech University, Lubbock, Tex 79409-2125. Currently, authors are Altiplano Regional Coordinator for the Programa Campesino Alternativo de Desarrollo (Alternative Development Peasant Program), La Paz, Bolivia and assistant professor of Rangeland Ecology and Management Department, University of Idaho, Moscow, Ida 83844-1135, respectively.

Abstract

Honey mesquite (*Prosopis glandulosa* Torr.) is an invasive native plant that is abundant in Mexico and the Southwestern United States. We initiated 2 studies to determine if: 1) mesquite could provide valuable forage for domestic herbivores; and 2) if mesquite causes conditioned flavor aversions in ruminants. An in vivo digestion trial was completed with 15 lambs assigned to diets of 0, 5, 10, 15, or 20% dried mesquite leaves mixed with alfalfa hay to measure effects of mesquite on intake and digestion. Proportions of mesquite leaves > 5% of the diet negatively affected dry matter (DM) intake, nitrogen (N) balance, energy balance and weight gain. Mesquite intake was highest at the 5% level averaging 1.81 g kg⁻¹ body weight (BW), mesquite intake of the other mesquite-containing diets averaged 0.78 g kg⁻¹ BW. Apparent digestibility was not affected by the level of mesquite in the diet. An in situ digestion trial did however, reveal that pure alfalfa was more digestible than mesquite leaves. A conditioned flavor aversion (CFA) trial tested the effect of post-ingestive feedback from mesquite on the intake of a novel food (rye). Lambs were offered rye and then ground mesquite was infused into their rumens by esophageal tube. Twenty one lambs were assigned to 3 dosing treatments: 0 (control), 3.0 (low), or 4.5 (high) g of mesquite per kg BW. Two days after dosing, lambs that received mesquite infusions ate less rye than controls indicating the formation of a CFA. The aversion to rye persisted for at least 2 days. The high dose of mesquite also decreased intake of the alfalfa basal ration for at least 3 days and resulted in persistent diarrhea in lambs. Chemical analysis of mesquite leaves revealed similar nutritive quality (crude protein, gross energy, and fiber) as mature alfalfa. However, to exploit the forage value of mesquite, the allelochemicals that cause flavor aversions and other negative digestive consequences need to be identified and overcome.

Key Words: browse, conditioned aversion, digestion trial, forage value, *Prosopis glandulosa*, secondary compounds

Mesquite species (*Prosopis* spp.) cover approximately 34 million hectares of rangeland in the southwestern United States (Dahl 1982), and are among the most predominant invasive

Resumen

El mesquite dulce (*Prosopis glandulosa* Torr.) es una planta invasora nativa, abundante en Mexico y en el suroeste de los Estados Unidos. Se realizaron 2 estudios para determinar si el mesquite: 1) puede proveer valor forrajero para herbívoros domésticos; y 2) si provoca aversiones condicionadas en rumiantes. Se realizó un ensayo de digestión in vivo con quince corderos alimentados con dietas conteniendo 0, 5, 10, o 20% de hojas secas de mesquite mezcladas con heno de alfalfa para medir los efectos del mesquite sobre algunos parámetros digestivos. Proporciones de hoja de mesquite en la dieta superiores al 5% afectaron negativamente el consumo de materia seca, el balance de nitrógeno, el balance de energía y las ganancias de peso. El consumo de mesquite fué más alto al nivel del 5%, promediando 1.81 g kg⁻¹ de peso vivo. El consumo de mesquite en las otras dietas promedio 0.78 g kg⁻¹ de peso vivo. La digestibilidad aparente de la materia seca no se vio afectada por el nivel de mesquite en la dieta. Sin embargo, un ensayo de digestión in situ reveló que la alfalfa fué mas digestible que las hojas de mesquite. El experimento de aversión condicionada (AC) determinó el efecto de las consecuencias post-ingestivas del mesquite sobre el consumo de un alimento no familiar (centeno). Los corderos recibieron una oferta de centeno y a continuación infusiones de mesquite molido en sus rumenes mediante el uso de un tubo esofágico. Veintiún corderos fueron asignados a las siguientes dosis de mesquite: 0 (control), 3.0 (dosis baja), y 4.5 (dosis alta) g de mesquite por kg de peso vivo. Dos días después de aplicar las dosis, los corderos que recibieron infusiones de mesquite consumieron menos centeno que los controles, indicando la formación de una AC. La aversión al centeno persistió por al menos 2 días. La dosis alta de mesquite también disminuyó el consumo de la dieta basal de alfalfa por al menos 3 días y provocó diarrea persistente en los corderos. Los análisis químicos de las hojas de mesquite revelaron una calidad nutricional (proteína cruda, energía bruta, y fibra) similar a la de la alfalfa. Sin embargo, para aprovechar el valor forrajero de mesquite, es necesario identificar y anular los compuestos químicos que causan aversiones y otras consecuencias digestivas negativas.

plants of this region. Mesquite competes for water, light, and nutrients with desirable forage species (Meyer et al. 1971). Honey mesquite (*Prosopis glandulosa* Torr.) is the most common species of mesquite in Texas, infesting about 23 million hectares (Fisher 1977). Fifty years of efforts to control mesquite by mechanical, chemical, and pyric means have not significantly

Research was funded by College of Agricultural Sciences and Natural Resources at Texas Tech University and the World Bank Bolivia Project.

Authors wish to thank Drs. Emilio Laca and Rodney Preston for invaluable advice on design of the digestion and aversion experiments.

Manuscript accepted 24 Apr. 2000.

slowed expansion nor reduced density of mesquite except in small intensively managed areas (Dahl and Sosebee 1984). As mesquite control becomes increasingly expensive (Holechek and Hess 1994), it is important to consider potential uses and benefits of mesquite.

As a forage, mesquite beans have long been recognized as an important energy source for humans and animals (Meyer et al. 1971, Zolfaghari et al. 1982). Mesquite leaves, however, are considered unpalatable and of low forage value (Lyon et al. 1988). The reason for this low forage value is unclear because mesquite leaves contain levels of crude protein and fiber similar to mature alfalfa (Unpublished data, Launchbaugh and Laca). Mesquite leaves do, however, contain flavanoids (Solbrig et al. 1977), alkaloids and non-protein amino acids (Cates and Rhoades 1977) that may act as feeding deterrents or toxicants. The forage value of mesquite leaves could be improved if reasons for low palatability and toxicity could be identified and overcome. Mesquite stems have thorns that may also limit browsing. However, it is apparent that they are not the primary limiting factor because spines do not prevent the consumption of mesquite beans.

To understand why herbivores do not readily eat mesquite leaves and to assess their nutritional value for ruminants, we measured the voluntary intake and digestibility of mesquite leaves by sheep. Our initial objective for this research was to determine the effect of mesquite leaves in mixed alfalfa diets on dry matter intake, apparent digestibility, nitrogen retention, and energy digestibility by sheep. Our first set of experiments revealed a profound effect of mesquite content on the intake of mesquite-containing diets. To determine why mesquite influences voluntary intake we conducted a feeding trial to see if mesquite ingestion causes aversive feedback resulting in conditioned aversions. Conditioned aversions have been observed for many plants and have been hypothesized as the major mechanism by which herbivores learn to avoid plants that contain allelochemicals (Provenza et al. 1992).

Materials and Methods¹

Research was conducted with domestic sheep at the Texas Tech University agricultural research facility near New Deal,

¹Research protocol was approved by the Texas Tech University Animal Care and Use Committee (Protocol# 95463).

Tex. (33° 43' N, 101° 50' W). All experiments were conducted with honey mesquite leaves collected at the Texas Tech Experimental Ranch near Justiceburg, Tex. (33° 02' N, 101° 12' W). Sheep were selected for this research because the research was designed to improve livestock grazing practices on Texas rangeland. We studied sheep, instead of cattle, because they eat much less, making the research more feasible, and digestion parameters elucidated with sheep are generally applicable to cattle (Van Dyne and Weir 1964, Harris et al. 1967)

In Vivo Digestion Trial

In vivo digestibility was determined for mixed diets of alfalfa hay and mesquite leaves. Five diets were prepared with 0, 5, 10, 15, and 20% mesquite mixed with alfalfa hay on an as-fed basis. The highest level was set at 20% because a preliminary experiment showed very limited intake of diets containing more than 20% mesquite. A low quality alfalfa hay was selected for this study because it has similar nitrogen (N) and fiber content as mesquite leaves (Unpublished data, Launchbaugh and Laca). Diets were prepared with dried mesquite leaves, rather than fresh, because results of a preliminary experiment showed no difference in intake between fresh and dried leaves, indicating allelochemicals in mesquite are not volatilized when dried. In preliminary experiments, 18 lambs were fed diets of either fresh or dried chopped mesquite leaves at 10, 30, or 50% of an alfalfa hay ration for 10 days. A summary of the last 5 days of the trial revealed that intake of diets containing 10% mesquite was more than intake of diets with 50% mesquite leaves (12.3 and 4.4 g kg⁻¹ body weight, respectively). Overall, intake of diets containing dry mesquite leaves was similar to diets with fresh mesquite leaves (8.1 and 9.1 g kg⁻¹, respectively). Dried leaves allowed for easier storage and handling.

Mesquite leaves were collected by hand plucked during 2 weeks in September and October of 1995 and oven dried at 45°-50° C for 5-7 days then stored in a dry unheated building. Leaves were dried at < 50° C to maintain moderate levels of fermentable carbohydrates without reducing digestibility through the Malliard or other complexing reaction (Wolf and Carson 1973, Deinum and Maassen 1994). Both mesquite and alfalfa hay were ground with a hammer mill (12.7 mm screen) to reduce sorting of mixed diets when fed.

Digestion Trial. Fifteen fine-wool

wether lambs (8-9 months old) were used in a digestion trial consisting of a 5-day pre-trial feeding period, 5-day acclimation period, and 7-day collection period. Animals were weighed (after fasting 12 hours) before the acclimation period and after the collection period. The average initial weight of lambs was 28.1 kg ± 2.6 SE. Lambs were randomly assigned to 1 of 5 diets (3 lambs per diet): 0, 5, 10, 15, or 20% dried mesquite leaves mixed with alfalfa hay, as fed. In the pre-trial feeding period, each lamb was placed in an individual 1.5 x 2 m wire pen and given ad libitum access to food twice daily (0800 and 1800 hours). Uneaten food, generally less than 200 g, was removed and replaced with a freshly prepared ration at each feeding. We did not estimate the proportion of mesquite in orts to determine the extent of sorting by lambs. Orts were of similar crude protein and gross energy content as the diet, and visual inspection revealed little evidence of sorting. Lambs were placed in metabolism crates (0.75 x 1.5 m) 5 days before the experimental collection period to allow acclimation to the crates. Metabolism crates had wire mesh floors through which dung fell onto a screen collection tray. Urine passed through the dung screen tray and was deposited in a metal pan that was angled so that urine was collected in 2-gallon plastic buckets. Feeding during the acclimation period was as pre-trial feeding. During the 7-day collection period, treatment diets were offered twice daily (0800 and 1800 hours) and dung and urine were collected each day (1700 hours).

Dung was weighed by individual and a 20% aliquot was pooled with other daily samples of that individual and frozen. At the end of the trial, the total dung sample from each animal was thawed and mixed thoroughly and a 400 g subsample was taken. Subsamples were dried at 55°C and ground to pass through a 1 mm screen for subsequent chemical analysis. Dung was analyzed for nitrogen (N) and gross energy (GE) content using macro Kjeldahl (AOAC 1984) and bomb calorimetry procedures (Harris 1970), respectively.

Total urine output was measured for each animal and a 10% aliquot (by volume) was collected daily, composited, and refrigerated. To each urine collection container, 200 ml of 0.1N HCL was added to prevent volatilization of ammonia (Schneider and Flatt 1975). At the end of the collection period, a subsample (400 ml) of each pooled urine sample was collected and frozen for chemical analysis. Analysis of urine included N by macro

Kjeldahl (AOAC 1984) and GE by bomb calorimetry (Harris 1970). For bomb calorimetry, urine samples (100 ml) were filtered into glass beakers, frozen, then freeze dried; the residue was weighed and made into pellets. Urine pellets, weighing 0.3 to 0.5 g, were stored in a freezer to ensure dryness for bomb calorimetry (Paladines et al. 1963). Urine samples were weighed before and after freeze drying to determine dry matter content.

Composition of Experimental Diets. Diets were analyzed for N by Kjeldahl techniques (AOAC 1984) and GE by bomb calorimetry (Harris 1970). Neutral detergent fiber (NDF) and acid detergent fiber (ADF) were determined following the filter bag technique (Komarek et al. 1994), which is a modification of the conventional Van Soest fiber analysis (Van Soest et al. 1991).

Four rumen cannulated fine-wool wethers (1 year old) were used to determine in situ dry matter (DM) digestibility of experimental diets (Harris 1970). Wethers were fed an alfalfa hay basal ration containing 5% mesquite for 15 days before the experiment. Six levels of mesquite (0, 5, 10, 15, 20, and 100%) were mixed with alfalfa hay. Mesquite and alfalfa samples were ground separately in a Wiley mill to pass a 2-mm screen. Twelve dacron bags (50 cm², 60 μ mesh) were prepared for each sheep (2 bags/treatment). Alfalfa-mesquite samples were weighed to 1 g and placed in bags. Two glass marbles were also placed in each bag to ensure bag immersion into rumen fluid. Each bag was closed by tightly tying with nylon fishing line and then dried overnight at 60° C to obtain the initial weight. The in situ bags were soaked in cool tap water for about 15 minutes and then inserted in the rumen-fistulated sheep for 48 hours. After rumen fermentation, the bags were removed and rinsed with tap water until water ran clear, then oven dried at 60° C for 24 hours and weighed to obtain final undigested DM. In situ DM digestibility was defined as the weight of sample lost during fermentation expressed as a percentage of initial sample weight.

Data Summary and Experimental Design. Based on chemical analysis of feed, orts, dung and urine, we calculated the DM digestibility, N balance (consisting of N intake, N output, and retained N), GE intake, GE output, and Digestible Energy (DE) for lambs on various alfalfa-mesquite diets by equations presented by Pritz et al. (1997). The in vivo digestion trial was analyzed as a completely randomized analysis of variance (ANOVA)

with DM intake as a covariate. SYSTAT for Windows (1992) and SAS (1996) statistical packages were used for analysis. Logarithmic or fractal transformations were conducted on data that did not follow a normal distribution or did not have homogenous variances (Steel and Torrie 1980). Mean separation was performed using Fisher protected LSD procedure with a 0.05 α-level. Orthogonal comparisons were conducted to examine linear, quadratic, and cubic relationships between intake variables and proportion of mesquite in the diet (Steel and Torrie 1980).

Conditioned Flavor Aversion Trial

When an animal eats a new food and experiences gastro-intestinal malaise it forms a dislike for the food known as a conditioned flavor aversion (CFA). To determine if the low palatability of mesquite was due, at least in part, to a CFA we offered lambs a novel food and then infused mesquite into their rumens. We later examined consumption of the novel food for evidence of a CFA.

Adjustment Period. Twenty-one cross-bred fine-wool lambs (1 year old) were each placed in an individual pen (1.5 x 2 m) and fed a basal ration of ground alfalfa hay; 2% BW fed daily at 1100 hours. Lambs for this trial were those used in the digestion trial and 6 from related experiments with mesquite. Water and trace mineral salt were offered ad libitum. Novel foods were offered before the trial to familiarize the lambs with the frequent presentation of new foods. Novel foods (300 g) were offered for 15 min per day at 0900 hours. Novel foods were soybean meal, crimped barley, and oregano-flavored rice (1% oregano) offered for 3, 2, and 1 day(s), respectively.

Experimental Period. Seven days after animals were penned and offered novel foods daily, lambs were offered 300 g of rye grain, a novel food, at 0900 hours.

After 30 min, rye intake was recorded. Lambs were randomly assigned to 1 of 3 treatments and dosed with 0, 3, or 4.5 g of mesquite per kg BW. Mesquite had been ground to pass a 0.5 mm screen and mixed with 1.5 liters of distilled water. Control animals were dosed with water only. Water and ground mesquite were infused through a flexible tube into the lamb's esophagus within 30 minutes of rye consumption. This day of mesquite dosing was designated as Day 0 of the trial.

The day after dosing (Day 1), lambs were fed a familiar feed, barley (300 g at 0900 hours), and the alfalfa basal ration (2% BW at 1100) to allow recovery. Two and 3 days after dosing (Days 2 and 3), lambs were offered rye again (300 g for 30 min at 0900 hours) to test for a CFA induced by mesquite. A familiar feed, rice (200 g), was offered after rye for 30 min. to assess effects of dosing on appetite. Intake of the alfalfa basal ration was also measured before and after dosing to examine potential negative effects of mesquite on appetite and gastro-intestinal function.

Experimental Design. Intake of novel and familiar foods was analyzed as a completely randomized design. Intake of rye and the alfalfa ration were examined on Days 2 and 3 as repeated measures (SAS 1996). Differences between means were determined using Fisher's protected LSD.

Results and Discussion

In vivo Digestion Trial

Quality of Treatment Diets. Crude protein (CP = N x 6.25; Van Soest 1994) of treatment diets was not affected by increasing levels of mesquite (Table 1). A high proportion of the N in mesquite may consist of non-protein nitrogenated compounds, such as non-protein amino acids, alkaloids, and other allelochemicals

Table 1. Crude protein (CP), in situ digestibility, neutral detergent fiber (NDF), acid detergent fiber (ADF), and gross energy (GE) for diets consisting of various proportions of mesquite leaves and alfalfa.

Parameter	Levels of mesquite (%)					
	0(Control)	5	10	15	20	100 ¹
CP (%)	11.5 ^a ± 1.7	12.9 ^a ± 0.7	12.2 ^a ± 1.7	13.5 ^a ± 1.7	12.9 ^a ± 0.7	12.2 ^a ± <.1
Digestibility						
In Situ (%)	68.6 ^a ± 1.4	67.6 ^a ± 2.5	67.3 ^a ± 2.1	68.4 ^a ± 2.3	66.8 ^a ± 1.7	59.6 ^b ± 1.0
NDF (%)	40.6 ^a ± 0.2	33.4 ^a ± 0.2	36.4 ^a ± 0.3	35.4 ^a ± 0.7	36.3 ^a ± 0.4	40.2 ^a ± 0.1
ADF (%)	30.6 ^a ± 0.6	23.9 ^a ± 0.4	27.4 ^a ± 0.4	25.7 ^a ± 0.1	26.7 ^a ± 0.3	28.4 ^a ± 0.3
GE (cal g ⁻¹)	4085 ^a ± 36	4082 ^a ± 20	4094 ^a ± 15	4148 ^a ± 13	4264 ^a ± 79	4385 ^b ± 10

¹ = 100% mesquite was a control determination and it was not offered to lambs.

Means ± Standard Error of lab duplicate and triplicate samples therefore not representing true replicates. Values in rows followed by the same superscript are not different (P > 0.05)

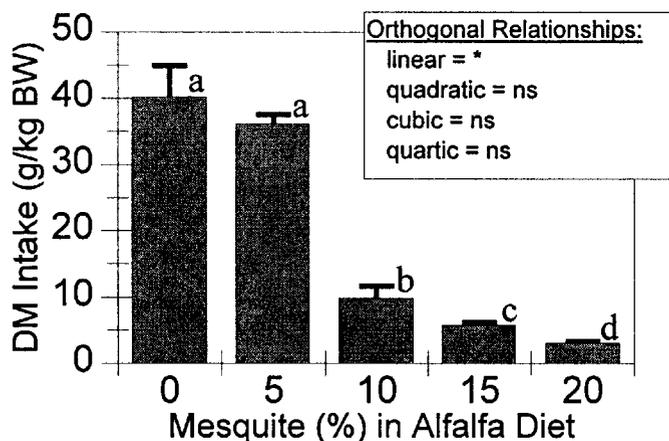


Fig. 1. Average daily dry matter (DM) intake of 4 levels of mesquite mixed with alfalfa hay by lambs. Vertical lines above bars illustrate standard errors, and bars with the same letter indicate no difference between treatments ($P > 0.05$). Orthogonal effects are designated as significant (*; $P < 0.05$) or not significant (ns; $P > 0.05$).

(Solbrig et al. 1977). Thus, "protein" may be a misleading term in this case. The proportion of mesquite in the treatment diets (0 to 20%) did not affect in situ digestibility. However, a t-test comparing DM digestibility of alfalfa hay (0% mesquite) and mesquite leaves (100% mesquite) revealed a higher digestibility of alfalfa hay. Fiber analysis revealed no clear trend or effect of increasing proportions of dietary mesquite on NDF or ADF. The variability in these parameters indicates high heterogeneity in the diet samples or imprecise application of lab protocols for measuring NDF and ADF. Gross energy was positively related to increasing amounts of mesquite in treatment diets. The 100% mesquite sample had clearly more energy (cal g^{-1}) than the alfalfa con-

trol (Table 1).

Voluntary Intake. Mesquite leaves added to an alfalfa diet had a marked negative effect on DM intake (Fig. 1). Lambs offered a 5% mesquite diet had the same intake as lambs eating pure alfalfa. However, animals that were offered diets with 10% mesquite or more showed markedly lower intake than controls (Fig. 1). We attributed the low intake of diets containing more than 5% mesquite to the effect of plant allelochemicals. The voluntary intake of chemically defended plants by herbivorous mammals is hypothetically dependent on their detoxification capacity (Freeland 1991, Foley et al. 1995), thus the level of mesquite in the diet may have set an upper limit to total daily intake. If the intake of mesquite-containing diets

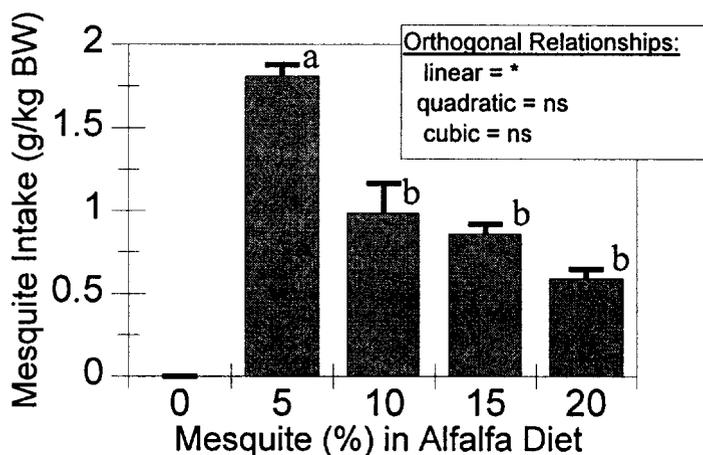


Fig. 2. Average daily dry matter (DM) intake of mesquite in diets with 4 levels of mesquite mixed with alfalfa hay by lambs. Vertical lines above bars illustrate standard errors, and bars with the same letter indicate no difference between treatments ($P > 0.05$). Orthogonal effects are designated as significant (*; $P < 0.05$) or not significant (ns; $P > 0.05$).

was set by the maximum amount of mesquite a lamb could detoxify in a day, then the total daily intake of mesquite should be the same for all sheep, regardless of the proportion of mesquite in their diets. This was not the case. Lambs offered diets of 10, 15, and 20% mesquite ate an average of $0.78 \text{ g kg}^{-1} \text{ BW}$ of mesquite daily. Lambs offered diets with 5% mesquite, ate more mesquite averaging $1.81 \text{ g kg}^{-1} \text{ BW}$ (Fig. 2). Lambs may have been more able to detoxify and digest the dietary mesquite at the 5% level because they had greater energy and nutrient intake from the greater proportion of alfalfa in their diets. This is speculative, however, abundant nutrient and energy resources can enhance an animal's ability to detoxify allelochemicals in plants (Foley et al. 1995, Launchbaugh 1996).

Changes in Live Weight. Low intake of diets with more than 5% mesquite resulted in weight loss for lambs assigned to those treatments. Lambs offered diets with 10, 15, and 20% mesquite lost 4.5, 5.0, and 6.2 kg, respectively, during the trial with no difference between treatments. Weight loss in this short 17-day trial may be primarily attributed to loss of digestive tract fill. Diets with 0% and 5% mesquite resulted in 0.1 and 0.8 kg weight gain, respectively, during the trial with no difference between levels.

Apparent Digestibility. The proportion of mesquite in the diet did not affect DM digestibility (Fig. 3). The major effect of adding mesquite to the diet was depression of intake (Fig. 1). Although decreased intake often results in higher digestibility of foods (Van Soest 1994), no differences in digestibility were found when DM intake was accounted for as a covariate in this analysis. Similarly, no effect of mesquite on digestibility was observed in the assessment of in situ DM digestibility (Table 1). The in situ technique did yield comparatively higher digestibility than the in vivo method (Fig. 3 and Table 1). This difference may have resulted from differences in fermentation time. In vitro studies were conducted with 48 hours of fermentation whereas, in vivo digestion trials yielded an undetermined rumen residence time which may have been shorter than 48 hours.

Nitrogen Balance. Nitrogen retention was greatly reduced for animals offered diets with $> 5\%$ mesquite (Table 2). Retained N for lambs eating diets of 0% and 5% mesquite was very low but similar, indicating dietary protein levels close to maintenance requirements. When retained N was expressed as a percent of N intake, lambs eating diets with 0 or 5%

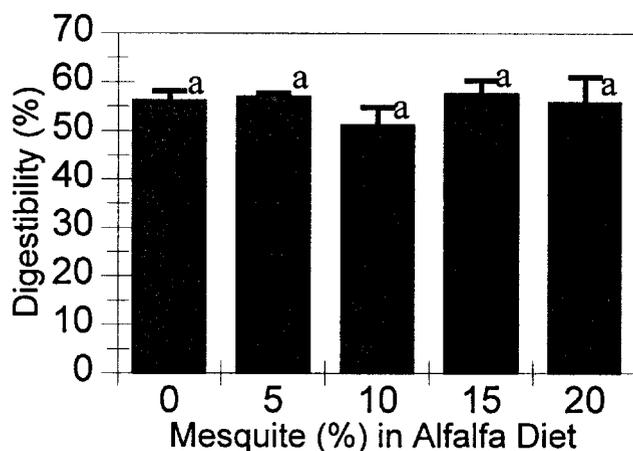


Fig. 3. Average coefficients of digestibility of 4 levels of mesquite added to alfalfa hay diets and eaten by lambs in a digestion trial. Vertical lines above bars illustrate standard errors.

mesquite had similar and positive retained N whereas lambs eating diets with > 5% mesquite were in a negative N balance. Total N output was similar for lambs eating diets of 0% and 5% mesquite, but markedly higher than for lambs offered diets with more than 5% mesquite. Nitrogen output in urine, as a percentage of total N output, was highest for levels of dietary mesquite > 5% (Table 2) suggesting catabolism of body protein to obtain energy for basal metabolism (Maynard et al. 1979).

Digestible Energy. Total intake of GE was negatively related to the mesquite level in the diet (Table 3). GE intake was similar for lambs eating diets with 0% and 5% mesquite, but began to decrease sharply when 10% or more mesquite was added to the diet. Mesquite in treatment diets also strongly affected digestible energy intake per day. However, when DE was expressed as a % of intake, there was no difference between treatments. This indicates that GE was equally digestible in all diets. Total output of GE was also affected

by dietary mesquite levels. Although, lambs assigned to 0% and 5% dietary mesquite showed no significant differences in GE output. Gross energy output of animals assigned to levels of mesquite greater than 5% differed from one another with animals eating diets with 20% mesquite having the lowest GE output (Table 3).

Conditioned Flavor Aversion (CFA) Trial

On the day animals were dosed with mesquite (Day 0), all lambs ingested similar amounts of the novel feed, rye (Table 4). The animals were then dosed with mesquite within 30 minutes of rye consumption. The following day (Day 1), the consumption of the familiar food, barley, was not affected by the dose of infused mesquite. Therefore, if mesquite dosing caused gastro-intestinal malaise, it was not apparent 24 hours after dosing.

Mesquite dosing after rye consumption created a strong CFA to rye. On Day 2, lambs receiving either levels of mesquite infusion ate less rye than the control group (Table 4). There were no differences in the amount of rye eaten between lambs dosed with 3.0 or 4.5 g of mesquite kg⁻¹ BW. On the same day, intake of a familiar feed, rice, immediately after consumption of rye, was similar among the 3 groups of

Table 2. Daily nitrogen balance of lambs fed diets with 5 levels of mesquite leaves in an alfalfa hay diet. Values were adjusted to the weight of an average lamb (28.1 kg) in this trial.

Treatments	Intake ¹ (g)	Retained		Total Output		Fecal		Urinary	
		(g)	(% Intake)	(g)	(% Intake)	(g)	(% Output)	(g)	(% Output)
Control	21.0 ± 3.1 ^a	1.3 ± 1.6 ^a	6.2 ^a	19.7 ± 2.6 ^a	93.8	6.9 ± 1.6	35.0 ^a	12.9 ± 1.6	65.5 ^a
5	21.2 ± 1.0 ^a	2.0 ± 0.5 ^a	9.4 ^a	19.2 ± 0.8 ^a	90.6	6.2 ± 0.4	32.3 ^{ab}	13.0 ± 0.5	67.7 ^{ab}
10	5.5 ± 1.2 ^b	-2.5 ± 0.7 ^{ab}	-45.5 ^b	8.0 ± 1.2 ^b	145.5	2.1 ± 0.3	26.2 ^{bc}	5.9 ± 0.8	73.8 ^{bc}
15	3.5 ± 0.3 ^b	-1.6 ± 0.1 ^b	-45.7 ^b	5.1 ± 0.4 ^{bc}	145.7	1.0 ± 0.1	19.6 ^c	4.1 ± 0.2	80.4 ^c
20	1.7 ± 0.2 ^c	-0.8 ± 0.2 ^c	-47.1 ^b	2.5 ± 0.4 ^c	147.1	0.6 ± 0.0	24.0 ^{bc}	1.9 ± 0.3	76.0 ^{bc}

Means ± Standard Errors

Values in columns followed by the same superscript are not different (P>0.05)

¹ = Natural log (x) transformed for homoscedasticity

² = 1/x values transformed for homoscedasticity

Table 3. Effects of 5 levels of mesquite leaves in alfalfa hay diets on gross energy (GE) intake, digestible energy, and energy output. Data from in vivo digestion trial with lambs. Values were adjusted for an average animal (28.1 kg) in this trial.

Treatments	GE Intake		Digestible Energy		Total GE Output		Fecal GE Output		Urinary GE Output	
	(Kcal)	(% Intake)	(Kcal)	(%)	(Kcal)	(% Intake)	(Kcal)	(% Output)	(Kcal)	(% Output)
Control	4662 ± 679 ^a	51.4	2431 ± 216 ^a	52.1 ^a	2396 ^a ± 426	51.4	2231 ± 418	93.1 ^a	165 ± 21	6.9 ^a
5	4191 ± 194 ^a	50.6	2229 ± 113 ^a	53.2 ^a	2122 ^a ± 68	50.6	1963 ± 56	92.5 ^a	59 ± 12	7.5 ^a
10	1146 ± 25 ^b	58.1	542 ± 130 ^b	47.3 ^a	666 ^b ± 108	58.1	603 ± 102	90.5 ^a	63 ± 6	9.5 ^a
15	676 ± 58 ^c	53.0	362 ± 4 ^b	53.6 ^a	358 ^c ± 56	53.0	314 ± 55	87.7 ^b	44 ± 3	12.3 ^b
20	359 ± 42 ^d	56.5	169 ± 25 ^c	52.8 ^a	203 ^d ± 28	56.5	169 ± 25	83.3 ^c	33 ± 4	16.7 ^c

Means ± standard errors

Values in columns followed by the same superscript are not different (P > 0.05)

Table 4. Mean intake of novel food (rye), and familiar food (rice) by lambs before and after intraruminal dosing with ground mesquite.

Mesquite Dose g/kg BW	Before dosing		After dosing					
	Day 0		Day 2		Day 2		Day 3	
	Rye	% ¹	Rye	% ²	Rice	% ²	Rye	% ¹
	----- (g ± SE) -----							
0	259.9 ± 25.1 ^a	87	211.1 ± 22.5 ^a	84	200.0 ± 0.0 ^a	100	293.3 ± 4.0 ^a	98
3	260.3 ± 19.8 ^a	87	22.4 ± 21.4 ^b	9	171.7 ± 28.3 ^a	86	52.7 ± 49.1 ^b	18
4.5	277.6 ± 14.5 ^a	93	52.1 ± 35.3 ^b	21	135.9 ± 33.8 ^a	68	109.2 ± 60.6 ^b	36

¹% of total offered (300 g) before dosing and on third day after dosing

²% of total offered rye (250 g) and rice (200 g) after dosing

Means in columns followed by the same letter are not different

lambs. Thus, the low rye intake by lambs dosed with mesquite was not because of a general loss of appetite for all grains; but rather, a specific aversion to rye. On Day 3, intake of rye by lambs receiving either the low or high mesquite dose was higher than on Day 2 increasing by 52.7 and 109.2 g, respectively. This increased intake probably indicates initial extinction of the aversion to rye.

Alfalfa Intake. Intake of the alfalfa basal ration before and for 3 days after dosing showed a variable pattern with some animals apparently less affected by the mesquite dosing than others. After dosing, lambs receiving the highest dose of mesquite ate less alfalfa than lambs receiving the control or low mesquite dose (Table 5). After 2 days, lambs receiving the high dose of mesquite increased their average intake of alfalfa slightly (from 8.6 to 12.1 kg⁻¹ BW; Table 5), but still ate less than other lambs. This may be explained by an aversion to the familiar alfalfa ration (Burritt and Provenza 1991). Alfalfa was fed 90 min after dosing and the negative post-ingestive feedback caused by mesquite may have created an aversion to chopped alfalfa. Alternatively, the lower consumption of the chopped alfalfa hay may reflect a general loss of appetite. Lambs infused with the highest mesquite dose showed symptoms of gastro-intestinal distress. Only 2 lambs receiving the low dose showed symptoms of diarrhea and they recovered completely by the last day of the trial, while, 4 (out of 6) lambs receiving the highest mesquite dose, showed symptoms of diarrhea that lasted until the last day of the trial. Allelochemicals in mesquite may have caused diarrhea through effects on gastro-intestinal motility, fore-stomach disorders, or osmotic overload (Smith 1990).

Conclusions and Management Implications

Mesquite leaves added at increasing proportions to alfalfa hay did not change basic composition (CP, GE, in situ digestibility, ADF or NDF) of the diet as measured by laboratory methods. Likewise, no differences in the in vivo DM digestibility of mesquite containing diets were found. The main effect of increasing levels of mesquite in experimental diets was reduced intake. In the digestion trial, lambs offered diets with 5% mesquite had similar intake and weight gain as lambs offered 100% alfalfa diets. This observed maximum consumption around 5% of the diet agrees with studies of wild and domestic animals in range conditions that seldom report more than 5% dietary mesquite (Warren et al. 1984, Krausman et al. 1997).

The strong negative effect of mesquite on intake in this study indicates that one or several allelochemicals in mesquite act as powerful feeding deterrents. The formation of a CFA to a novel food after ruminal infusion of mesquite in our second trial was evidence of negative post-ingestive feedback from mesquite leaves. The palatability of mesquite is certainly influenced by post-ingestive feedback although an inherently aversive taste may also play a role (Provenza et al. 1990, Launchbaugh 1996). Intake of the alfalfa basal ration was also affected by mesquite dosing.

Animals that received the highest mesquite dose reduced their intake of the familiar alfalfa diet and showed symptoms of diarrhea for at least three days.

Allelochemicals are known to limit the nutritive value of many plants and can have various biological effects, such as interfering with metabolism or inhibiting digestion (Provenza 1995, Launchbaugh 1996). The main groups of allelochemicals identified in honey mesquite leaves are flavonoids and non-protein amino acids which may have antitoxicity properties (Solbrig et al. 1977). Allelochemicals identified in other mesquite species include phenolics (Lyon et al. 1988) and alkaloids (Cates and Rhoades 1977). The animal response in our experiments agrees with a general feeding strategy of herbivores to minimize the ingestion of defensive compounds (Freeland 1991).

This research suggests that grazing management practices could be designed to rely on mesquite leaves for about 5% of the grazing animal's dry matter requirements. It is unlikely that mesquite could constitute a large (>10%) proportion of forage allowance on rangeland. However, mesquite may be an important source of nitrogen and vitamin A in late summer because it continues active growth after herbaceous forage becomes senescent.

Increased consumption of mesquite as part of mesquite management plans could be accomplished by selecting animals with enhanced detoxification or tolerance for mesquite. In our trials and in other studies (Warren et al. 1984), there was considerable variation between individuals with respect to voluntary mesquite consumption. Assembling herds or flocks of animals with enhanced detoxification or tolerance abilities could constitute a management strategy to increase the use of mesquite as forage on rangeland. Breeding animals for high mesquite consumption could also be used as a management tool if the metabolic basis for mesquite tolerance or detoxification is inherited. Finally, research is needed to identify the specific chemicals that make mesquite unpalatable and the mechanisms by which these chem-

Table 5. Mean intake (± standard error) of alfalfa hay ration by lambs before and after intraruminal dosing with ground mesquite leaves.

Mesquite Dose g/kg BW	Before	After		
	Day 0	Day 1	Day 2	Day 3
	----- (g kg ⁻¹ of body weight) -----			
0	20.1 ± 1.0 ^a	20.1 ± 1.0 ^a	20.1 ± 1.0 ^a	20.1 ± 1.0 ^a
3	20.4 ± 0.4 ^a	20.2 ± 0.5 ^a	17.4 ± 1.5 ^a	20.4 ± 0.4 ^a
4.5	17.9 ± 3.1 ^a	15.2 ± 2.8 ^a	8.6 ± 1.8 ^b	12.1 ± 2.8 ^b

Means followed by the same superscripts in columns are not different (P > 0.05)

icals affect herbivores. Understanding these chemical effects could lead to pharmaceutical or nutritional products that aid in detoxification or tolerance. These elements may one day become part of viable grazing management strategies for mesquite-dominated rangelands.

Literature Cited

- AOAC. 1984.** Official methods of analysis. (14th Ed). Assoc. of Official Analytical Chem., Washington, D.C.
- Burrit, E.A. and F.D. Provenza. 1991.** Ability of lambs to learn with a delay between food ingestion and consequences given meals containing novel and familiar foods. *Appl. Anim. Behav. Sci.* 32:179-189.
- Cates, R.G. and D.F. Rhoades. 1977.** *Prosopis* leaves as a resource for insects, p. 61-83. *In: B.B. Simpson (ed.), Mesquite: Its biology in two desert ecosystems.* Dowden, Hutchinson & Ross, Inc., Stroudsburg, Penn.
- Dahl, B.E. 1982.** Mesquite as a rangeland plant. p. A1-A20. *In: H.W. Parker (ed.) Mesquite utilization. Symposium on Mesquite Utilization.* Texas Tech Univ. Press, Lubbock, Tex.
- Dahl, B.E. and R.E. Sosebee. 1984.** Timing - the key to herbicidal control of mesquite. *Texas Tech. Univ. Manage. Note.* N 2.
- Deinum, B. and A. Maassen. 1994.** Effects of drying temperature on chemical composition and in vitro digestibility of forages. *Animal Feed Sci. and Tech.* 46:74-86.
- Fisher, C.E. 1977.** Mesquite and modern man in southwestern North America. p. 177-188. *In: B.B. Simpson (ed.) Mesquite: Its biology in two desert ecosystems.* Dowden, Hutchinson & Ross, Inc., Stroudsburg, Penn.
- Foley, W.J., S. McLean and S.J. Cork. 1995.** Consequences of biotransformation of plant secondary metabolites on acid-base metabolism in mammals: A final common pathway? *J. Chem. Ecol.* 21:721-743.
- Freeland, W.J. 1991.** Plant secondary metabolites. Biochemical coevolution with herbivores. p. 61-81. *In: R.T. Palo, and C.T. Robbins (eds.), Plant defenses against mammalian herbivory.* CRC Press, Inc., Boca Raton, Fla.
- Harris, L.E. 1970.** Nutrition research techniques for domestic and wild animals. Vol.1. Utah State Univ. Logan, Ut.
- Harris L.E., G.P. Lofgreen, C.J. Kercher, R.J. Raleigh and V.R. Bohman. 1967.** Techniques of research in range livestock nutrition. *Utah Agr. Exp. Sta. Bull.* 471. Logan, Ut.
- Holechek, J.L. and K. Hess. 1994.** Brush control considerations: A financial perspective. *Rangelands* 14:279-284.
- Komarek, A.R., J.B. Robertson, and P.J. Van Soest. 1994.** A comparison of methods for determining ADF using the filter bag technique versus conventional filtration. *J. Dairy Sc.* 77: Suppl. 1.
- Krausman, P.R., A.J. Kuenzi, R.C. Etchberger, K.R. Rautenstrauch, L.L. Ordway, and J.J. Herbert. 1997.** Diets of desert mule deer. *J. Range Manage.* 50:513-522.
- Launchbaugh, K.L. 1996.** Biochemical aspects of grazing behavior. p. 159-184. *In: J. Hodgson, and A.W. Illius (eds.), The ecology and management of grazing systems.* CAB International, Wallingford, U.K.
- Lyon, C.K., M.R. Gumbmann, and R. Becker. 1988.** Value of mesquite leaves as forage. *J. Sci. Food. Agr.* 44:111-117.
- Maynard, L.A., J.K. Loosli, H.F. Hintz, R.G. Warner. 1979.** *Animal Nutrition.* 7th Ed. McGraw-Hill Book Co.
- Meyer, R.E., H.L. Morton, R.H. Haas, E.D. Robison, and T.E. Riley. 1971.** Morphology and anatomy of honey mesquite. *Agr. Res. Serv. USDA. Tech. Bull.* 1423.
- Paladines, O.L., J.T. Reid, B.D.H. Van Niekerk, and A. Bensadoun. 1963.** Relationship between the nitrogen content and the heat of combustion value of sheep urine. *J. Anim. Sci.* 23:528-532.
- Pritz, R.K., K.L. Launchbaugh, and C.A. Taylor, Jr. 1997.** Effects of breed and dietary experience on juniper consumption by goats. *J. Range Manage.* 50:600-606.
- Provenza, F.D. 1995.** Postingestive feedback as an elementary determinant of food preference and intake in ruminants. *J. Range Manage.* 48:2-17.
- Provenza, F.D., J.A. Pfister, and C.D. Cheney. 1992.** Mechanisms of learning in diet selection with reference to phytotoxicosis in herbivores. *J. Range Manage.* 45:36-45.
- Provenza, F.D., E.A. Burrit, T.P. Clausen, J.P. Bryant, P.B. Reichardt, and R.A. Distel. 1990.** Conditioned flavor aversion: a mechanism for goats to void condensed tannins in blackbrush. *Amer. Nat.,* 136:810-828.
- SAS. 1996.** Statistical analysis system. Ver. 6.09. SAS Institute Inc. Cary, N.C.
- Schneider, B.H. and W.P. Flatt. 1975.** The evaluation of feeds through digestibility experiments. Univ. of Georgia Press, Athens, Ga.
- Smith, B.P. 1990.** Alternations in alimentary and hepatic function. P. 117-124. *In: B.P. Smith (ed.) Large Animal Intestinal Medicine.* CV Mosby Comp. St. Louis, Mo.
- Solbrig, O.T., K. Bawa, N.J. Carman, J.H. Hunziker, C.A. Naranjo, R.A. Palacios, L. Poggio, and B.B. Simpson. 1977.** p. 44-60. Patterns of variation. *In: B.B. Simpson (ed.) Mesquite: Its biology in two desert ecosystems.* Dowden, Hutchinson & Ross, Inc. Stroudsburg, Penn.
- Steel, R.G.D. and J.H. Torrie. 1980.** Principles and procedures of statistics. 2nd Ed. McGraw-Hill Book Company, Inc., N.Y.
- SYSTAT. 1992.** Systat for windows: Statistics. Version 5 Ed. Evanston, Ill.
- Van Dyne, G.M. and W.C. Weir. 1964.** Variation among cattle and sheep in digestive power measured by microdigestion techniques. *J. Animal. Sci.* 23:1116-1123.
- Van Soest, P.J. 1994.** Nutritional ecology of the ruminant. Cornell University Press, Ithaca, N.Y.
- Van Soest, P.J., J.B. Robertson, and B.A. Lewis. 1991.** Methods for dietary fiber, neutral detergent fiber and non-starch polysaccharides in relation to animal nutrition. *J. Dairy Sci.* 74:3583-3597.
- Warren, L.E., D.N. Ueckert, and J.M. Shelton. 1984.** Comparative diets of Rambouillet, Barbado, and Karrakul sheep and Spanish and Angora goats. *J. Range Manage.* 37:172-180.
- Wolf, D.D. and E.W. Carson. 1973.** Respiration during drying of alfalfa herbage. *Crop. Sci.* 13:660-662.
- Zolfaghari, R., M. Harden and L. Hopkins. 1982.** Nutritional value of mesquite beans (*P. glandulosa*). p. K1-K12. *In: H.W. Parker (ed.) Mesquite utilization. Symposium on mesquite utilization.* Texas Tech Univ. Press, Lubbock, Tex.

Effects of biosolids on tobosagrass growth in the Chihuahuan desert

PEDRO JURADO AND DAVID B. WESTER

Authors are graduate research assistant and professor, Department of Range, Wildlife and Fisheries Management, Texas Tech University, Lubbock, Tex. 79409.

Abstract

Little information is available about seasonal application and carry-over effects of biosolids application to semi-arid grasslands. Biosolids rates of 0 (control), 7, 18, or 34 Mg ha⁻¹ were topically applied to tobosagrass (*Hilaria mutica* (Buckl.) Benth.) experimental plots in a Chihuahuan desert grassland in western Texas. Biosolids were applied twice in 1994, for one-year-only, either in winter-and-summer (WS), or spring-and-summer (SS) seasons. Half of the plots were irrigated every summer for 4 years (1994-1997). Tobosagrass standing crop (herbage yield) and total Kjeldahl nitrogen concentration (plant %TKN) were measured every year during the 4 years of the study (1994-1997). An increase in biosolids rate increased tobosagrass herbage yield linearly during the 4 growing seasons. Linear and quadratic responses to biosolids rates were observed in %TKN during the experiment. Irrigation increased tobosagrass herbage yield. Irrigation decreased %TKN in 1995 and 1996 and had no influence during the other years. Winter-and-summer applications increased herbage yield more than spring and summer applications in 3 out of 4 years. Spring-and-summer applications increased %TKN more than winter and summer applications only in 1996. Carry-over effects on tobosagrass herbage yield and %TKN were observed in the second, third, and fourth growing seasons after biosolids application. Twice-a-year application of biosolids for 1-year-only offers an excellent means to improve tobosagrass productivity and forage quality.

Key Words: *Hilaria mutica*, Chihuahuan desert grassland, biosolids surface-application, biosolids land-application, irrigation, standing crop, forage quality, carry-over effects

Application of inorganic fertilizers to arid and semiarid rangelands is beneficial (Freeman and Humphrey 1956, Holt and Wilson 1961, Herbel 1963, Stroehlein et al. 1968, Dwyer 1971, Pieper et al. 1974, Stephens and Whitford 1993) but not practical because of high costs and lack of carry-over effects (Herbel 1963). Use of organic materials is promising since they can improve long-term physical, chemical, and biological processes in arid and semiarid soils (Khaleel et al. 1981, Fuller 1991, Day and Ludeke 1993), thereby improving plant growing conditions.

Research was funded partially by MERCO Joint Venture, CONACYT (MEXICO), and INIFAP (MEXICO). Authors wish to thank R. Sosebee, E. Fish, R. Zartman, C. Moffet, R. Gatewood, M. Benton, P. Cooley, C. Brenton, C. Shanks, C. Villalobos, and R. Mata for their assistance. This is manuscript no. T-9-854, College of Agricultural Sciences and Natural Resources, Texas Tech Univ.

Manuscript accepted 24 Apr. 2000.

Resumen

Escasa informacion existe acerca de los efectos de aplicaciones de biosolidos en diferentes epocas del año y sus efectos residuales en pastizales semiaridos. Cuatro niveles de biosolidos fueron superficialmente aplicados en dosis de 0 (control), 7, 18, o 34 Mg ha⁻¹ en parcelas experimentales de zacate toboso (*Hilaria mutica* (Buckl.) Benth.) en un pastizal desertico del oeste de Texas. Los biosolidos fueron aplicados dos veces por año en 1994, por un año solamente, en invierno-y-verano (IV) o primavera-y-verano (PV). La mitad de las parcelas fueron irrigadas a traves de cada verano durante cuatro años (1994-1997). La produccion de forraje y la concentracion total de nitrogeno (CTN) del toboso fueron estimados durante los cuatro años del estudio (1994-1997). El incremento en los niveles de biosolidos aumento la produccion de toboso linealmente a traves de los cuatro años de estudio. Se observaron respuestas lineales y cuadraticas de CTN con las dosis de biosolidos a traves del experimento. Las parcelas irrigadas incrementaron la produccion de forraje. La irrigacion disminuyo CTN en 1995 y 1996, aunque no influyo en los demas años. Las aplicaciones de IV incrementaron la produccion de forraje sobre las aplicaciones de PV en tres de los cuatro años. Las aplicaciones de PV incrementaron CTN sobre las aplicaciones de IV solo en 1996. Se observaron efectos residuales de la aplicacion de biosolidos en produccion de forraje y CTN a traves de la segunda, tercera, y cuarta estaciones de crecimiento. La aplicacion de biosolidos dos veces al año en ambas estaciones (IV y PV) ofrece una excelente herramienta para el mejoramiento de la produccion y la calidad de forraje del zacate toboso.

Anaerobically digested biosolids is a by-product of wastewater treatment. Efficient biosolids disposal is needed since municipalities generate approximately 6.2 million dry Mg yr⁻¹ of biosolids. Biosolids generation is expected to reach over 12.4 million dry Mg yr⁻¹ by the end of the year 2000 (USEPA 1989).

Experimental results with biosolids topically applied once-a-year for 1-year-only at rates of 4 to 90 Mg ha⁻¹ benefit soil physical, chemical, and biological properties and plant growth in arid and semi-arid grasslands (Fresquez et al. 1990, Harris-Pierce et al. 1993, 1995, Aguilar et al. 1994, Brenton 1995, Moffet 1997, Benton and Wester 1998, Pierce et al. 1998, Rostagno 1998). Current regulations for application of biosolids to cropland in Texas allow once-a-year application of 18 dry Mg ha⁻¹ (Gass and Sweeten 1992). The Environmental Protection Agency (EPA) recommends an annual application rate (AAR) for domestic sewage application to land, forest, or reclamation site of AAR=1.121N/0.0026, where N=amount of nitrogen (kg/ha/yr)

needed by vegetation grown on land (USEPA 1996).

Tobosagrass (*Hilaria mutica* (Buckl.) Benth.) is one of the dominant grasses in the northern Chihuahuan desert. It is a perennial, native, warm season grass, with good to fair forage value for livestock (Stubbenieck et al. 1992). Although tobosagrass forage productivity (Herbel 1963, Britton and Steuter 1983) and quality (Nelson and Johnson 1987, Brown and Houston 1993) are poor, they can be improved with increased soil fertility and moisture (Herbel 1963, Wright 1969, Britton and Steuter 1983).

There is no information on the forage yield and quality from twice-a-year, for 1-year-only, land application of biosolids to desert grasslands. Furthermore, there is little information on seasonal applications of biosolids and their carry-over effects on forage yield and quality of tobosagrass. This study was initiated to determine the effects of twice-a-year, for 1-year-only, application of biosolids on tobosagrass forage yield and nitrogen concentration.

Materials and Methods

Study Area

The study was conducted on the Sierra Blanca Ranch located 10 km north of Sierra Blanca, Texas (Hudspeth Co.) (Latitude 31° 16'N, Longitude 105° 22'W). Soils on the study site occur on planar slopes of the lower parts of an alluvial fan. Soils are deep, well drained, and are tentatively classified as Stellar taxadjunct very fine sandy loam, 1 to 3% slope, fine, mixed, thermic Vertic Paleargids (Casby-Horton 1997). The study site is on a Loamy (variant) Range Site. The vegetation is a Chihuahuan desert grassland, with tobosagrass, alkali sacaton (*Sporobolus airoides* (Torr.) Torr.), burrograss (*Scleropogon brevifolius* Phil.), and blue grama (*Bouteloua gracilis* (H.B.K.) Lag. ex Steud.) as common grasses. Honey mesquite (*Prosopis glandulosa* var. *glandulosa* Torr.) and lotebush (*Ziziphus obtusifolia* (T.&G.) Gray) are the most common shrubs. Domestic livestock, which grazed the site for at least 9 years prior to this research, were excluded since 1992.

Climate is a southwestern type (Holecheck et al. 1989), characterized by cool winters, dry hot springs, wet hot summers, and cool dry falls. Annual long-term precipitation averages 310 mm with 65% occurring between July and September (N.O.A.A. 1993, Fig. 1). Annual precipitation data from 1994 to 1997 were recorded by a weather station near the study site.

Treatments

Ninety-six experimental units (1m x 1m) were established in tobosagrass-dominated vegetation. Prior to biosolids application, biomass was harvested by hand-clipping all herbage at a 5-cm height in late December 1993. Plots were protected with poultry netting (60 cm tall, 5-cm mesh) to reduce lagomorph herbivory. A square plywood frame (70.71 x 70.71 x 10-cm) located in the center of each plot was used to retain biosolids on the plot area, and to define a vegetation sampling area of 0.5 m² within the frame.

Anaerobically digested municipal biosolids from New York City were provided by a commercial applicator on site for this study. Biosolids were applied twice in 1994, for 1-year-only, either in winter (11 January) and summer (8 July) seasons (WS), or in spring (16 April) and summer (8 July) seasons (SS), at rates of 0, 7, 18, or 34 dry Mg ha⁻¹ per application. Therefore, a total of 0 (control), 14, 36, or 68 Mg ha⁻¹yr⁻¹ of biosolids were applied (on a dry weight basis) to the experimental units. For each biosolids application, 5 samples of fresh biosolids were randomly collected and frozen prior to shipment to New Mexico State University, Soil, Water, and Air Testing Laboratory for chemical analysis. Samples were oven dried for 24 hours at 60° C to determine biosolids moisture content. Biosolids were weighed in the field, applied topically, and hand-distributed uniformly throughout each plot according to season and rate of application.

Supplemental irrigation of 15 mm of water was provided manually with a sprinkler bucket early in the morning to half of the plots every 2 weeks during the growing season for each year of the study. A total of 75 mm of supplemental water was applied throughout the growing season each year. Nonirrigated plots were exposed to only natural rainfall conditions.

Aboveground tobosagrass standing crop (hereafter referred to as herbage yield) was harvested by hand-clipping all herbage at 5 cm above the soil surface at the end of each growing season. Herbage samples were oven-dried at 60°C for 48 hours and weighed to the nearest 0.01 g to estimate herbage yield. Herbage samples were ground and passed through a 40 mesh screen in preparation for chemical analysis. Total Kjeldahl nitrogen concentration (%TKN) of each sample was determined (AOAC 1990) each year. A Tecator digestion system 40 (1016 Digester), along with a Tecator Kjeltec system 1026 distilling unit and a Mettler DL40RC titrator, were used for %TKN analysis.

Experimental Design and Data Analyses

A split plot arrangement of a completely randomized design was used for this study, with seasons of application (2 levels) as the main plot factor. Within each season of application, a factorial combination of 4 biosolids rates and 2 levels of irrigation were randomly assigned to individual 1-m² plots (subplots). There were 6 replications of each treatment for standing crop data, and 5 replications for plant nitrogen data. Years-after-application (4 levels) were analyzed as repeated measurements (sub-subplots).

Analysis of variance was used to test hypotheses of interest. The Shapiro-Wilk (1965) test was used to assess normality of main plot, subplot, and sub-subplot experimental errors. Levene's (1960) test was used to test for homogeneous variances in the main plot; Mauchly's (1940) test was used to test for sphericity in the subplot and sub-subplot portions of the analysis of variance. Herbage yield and %TKN data more closely satisfied assumptions for F tests when analyzed on a natural log-scale (Goodall 1970, Benton and Wester 1998). Although natural log-transformed data were analyzed, treatment means were back-transformed for data presentation; back transformed means are estimates of medians on the observed scale (Jager and Looman 1987). Adjusted F tests were used when sphericity was violated. Covariance analysis was performed in the first year for herbage yield data using initial biomass as a covariate to provide unbiased estimates of treatment effects.

Treatment mean separation was performed with the Fisher's Least Significant Difference (LSD) test for significant effects (Steel and Torrie 1980). Separate error terms were used for mean separation because of sphericity violation in the sub-subplot (Kirk 1995). Regression analysis was used to describe the response of tobosagrass herbage yield and %TKN to biosolids rate.

Results and Discussion

Biosolids Chemical Constituents

Biosolids moisture average was 71%. Although element concentrations varied among applications, concentrations for WS and SS averages were similar for most of the constituents analyzed (Table 1).

Precipitation

Precipitation amount and distribution varied greatly among the years of the

Table 1. Chemical composition of biosolids applied during winter, spring, or summer, 1994, Sierra Blanca, Texas.

Constituent	Winter 94 (n=2)	Spring 94 (n=5)	Summer 94 (n=5)	WS ¹ Avg.	SS ¹ Avg.
TKN(%)	3.36	2.92	3.62	3.49	3.27
P(%)	1.47	1.93	1.41	1.44	1.67
K(%)	0.68	0.09	0.04	0.36	0.06
Ca(%)	1.29	2.55	1.90	1.59	2.22
Mg(%)	0.44	0.91	0.38	0.41	0.65
Mn(mg kg ⁻¹)	544	1019	651	597	835
Zn(mg kg ⁻¹)	812	1147	1100	956	1123
Fe(mg kg ⁻¹)	23360	23092	19798	21579	21445
Cu(mg kg ⁻¹)	562	420	1033	797	726
B(mg kg ⁻¹)	34	33	33	33	33
Al(mg kg ⁻¹)	7531	7197	8279	7905	7738
Ni(mg kg ⁻¹)	26	43	22	24	32
Cd(mg kg ⁻¹)	8	9	8	8	8.5
Pb(mg kg ⁻¹)	212	321	187	199	254
EC ² (dS m ⁻¹)	14.0	-	11.6	12.8	11.6

¹WS = Average of winter and summer; SS = Average of spring and summer.

²EC = Electrical conductivity.

study (Fig. 1). These differences influenced tobosagrass herbage yield and plant %TKN. Precipitation was about 30, 27, and 54% below the long-term average in 1994, 1995, and 1997, respectively, and approximately average in 1996.

Tobosagrass Herbage Yield

The response of tobosagrass herbage yield to biosolids depended on application rate ($P < 0.0001$, Fig. 2). However, rate of biosolids did not interact with years ($P > 0.6135$) or with irrigation ($P > 0.6577$). A linear regression explained 93% ($P < 0.0001$) of the variation in the rate response. Herbage yield was similar

between control and 7 Mg ha⁻¹ rate. Herbage yield increased at 18 Mg ha⁻¹ and 34 Mg ha⁻¹ rates compared to the control rate (60 and 83%, respectively) and the 7 Mg ha⁻¹ rate. Herbage yield was similar between 18 and 34 Mg ha⁻¹ rates.

The beneficial response of tobosagrass herbage yield to twice-a-year, for 1-year-only, biosolids surface application indicates that biosolids improved plant growing conditions, including improved nutrient status. This agrees with research by Khaleel et al. (1981), Whitford et al. (1989), and Fuller (1991) where organic materials improved soil properties. The linear response of tobosagrass herbage yield to biosolids rate also suggests that

desert grasslands are nutrient-limited environments (West and Klemmedson 1978). Some studies indicate that biosolids application can increase soil water availability by increasing water infiltration and reducing water runoff (Whitford et al. 1989, Aguilar et al. 1994, Harris-Pierce et al. 1995, Moffet 1997, Rostagno 1998).

In addition to their hydrological effects, biosolids may have supplied soil nutrients and organic matter that may improve soil chemical and physical properties (Seaker and Sopper 1988, USEPA 1989, Fresquez et al. 1990, Harris-Pierce et al. 1993, Aguilar et al. 1994, Brenton 1995, Moffet 1997, Rostagno 1998). Furthermore, biosolids could have increased soil microbial populations (Dennis and Fresquez 1989, Whitford et al. 1989, Fresquez and Dennis 1990, Strait 1996) because of their organic content, thus enhancing nutrient availability to plants. Hence, by improving hydrological, physical, chemical, and biological soil properties, biosolids may have acted both as fertilizer and soil conditioner in arid grasslands (Fresquez et al. 1990, Gass and Sweeten 1992).

Similar beneficial results in herbage yield of warm-season perennial grasses in semi-arid grasslands during the first growing season have been observed in field studies with 1-time surface-applied biosolids. For example, Fresquez et al. (1990) showed positive yield responses of blue grama and galleta (*Hilaria jamesii* (Torr.) Benth.) biosolids applied in the autumn at 22.5 to 90 Mg ha⁻¹ on a degraded rangeland in New Mexico. Also, Harris-Pierce et al. (1993) found increased blue grama yield after summer application of biosolids from 4 to 34 Mg ha⁻¹ in the short-grass plains in Colorado. Benton and Wester (1998) also indicate increasing forage production in both tobosagrass and alkali sacaton with winter or summer application of biosolids from 7 to 90 Mg ha⁻¹ in a desert grassland in western Texas. In contrast, Pierce et al. (1998) did not observe beneficial herbage yield effects of summer biosolids application from 5 to 40 Mg ha⁻¹ on cool season perennial grasses such as western wheatgrass (*Agropyron smithii* Rydb.), bluebunch wheatgrass (*A. spicatum* (Pursh.) Scribn. & Smith), or Indian ricegrass (*Oryzopsis hymenoides* (R.& S.) Ricker.) in mountain sagebrush vegetation in Colorado during the first growing.

Tobosagrass herbage yield was greater ($P < 0.0001$) in irrigated plots (430 kg ha⁻¹) than in nonirrigated plots (262 kg ha⁻¹). This was expected since water is one of the most important limiting plant growth factors in arid and semiarid environments

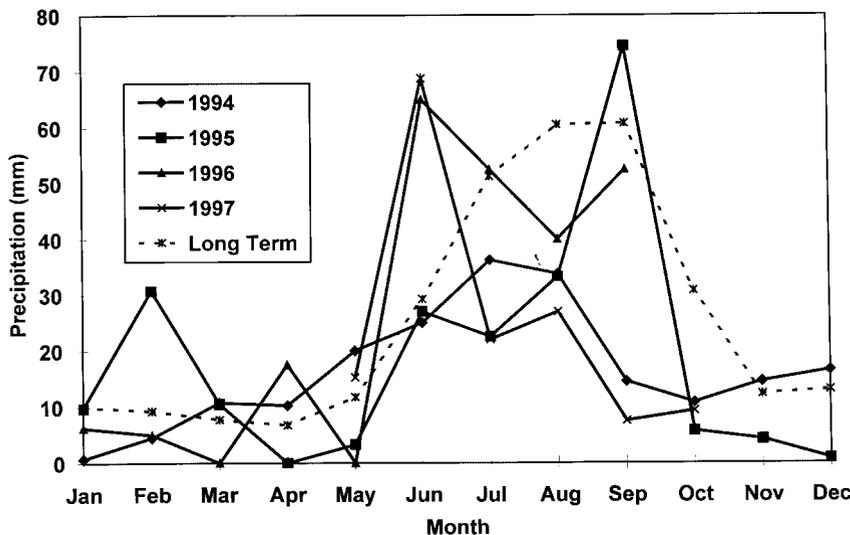


Fig. 1. Monthly precipitation throughout the 4 years of the study (recorded at the study site) and the long-term average precipitation (from N.O.A.A.) at Sierra Blanca, Texas. Missing data for early 1996, and early and late 1997.

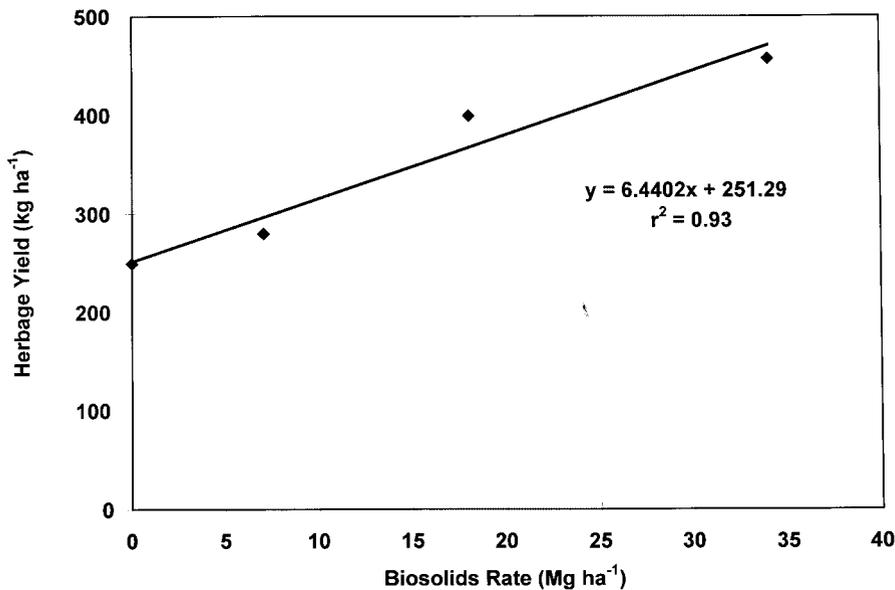


Fig. 2. Tobosagrass herbage yield response to biosolids application during the 4 years of the study (1994-1997). For rate comparisons, $LSD_{0.05} = 0.2314$ (log scale) ($n = 96$).

(Noy-Meir 1973, Day and Ludeke 1993, Brown 1995), and summer rainfall was below normal during most of the years of the study. These results agree with other studies on the effects of irrigation on tobosagrass and alkali sacaton (Benton and Wester 1998), tobosagrass and blue grama (Cooley 1998), black grama (*Bouteloua eriopoda* (Torr.) Torr.) (Stephens and Whitford 1993), and fluffgrass (*Erioneuron pulchellum* (H.B.K.) Tateoka) (Ettershank et al. 1978) in Chihuahuan desert grasslands.

The significant main effects of biosolids rate and irrigation on herbage yield, together with the absence of an interaction between these 2 factors, do not support the "water limited-nutrient regulated" hypothesis of Ludwig et al. (1989) offered to explain the effects of water and nutrients on plant growth in Chihuahuan desert ecosystems. Instead, these results support a "water and nutrient limited" hypothesis (Benton and Wester 1998): although growth is limited by each of these resources, their effects evidently are not synergistic.

Also, tobosagrass herbage yield was affected by seasons of biosolids application, a factor that interacted with years-after-application ($P < 0.02$, Fig. 3). Winter and summer applications increased herbage yield more than spring and summer applications during the first, third, and fourth growing seasons after biosolids application in this study.

The greater response to winter and summer applications on tobosagrass herbage yield during the first growing season may

be attributed to the improvement of plant growing conditions such as higher soil water availability and/or nutrient supply to the plants: these effects may have been initiated by the winter application in this treatment, providing a "headstart" effect for plants relative to later seasonal applications. The lower response to spring and summer applications can be attributed to below normal rainfall conditions after application (see Cooley 1998).

Furthermore, spring and summer applications may have supplied less nitrogen to the soil because of potential ammonia volatilization losses from biosolids applied under warm conditions (Beauchamp et al. 1978, Harmel et al. 1997). Similar seasonal effects of biosolids applications on forage production were first reported by Benton and Wester (1998) under once-a-year topical application of biosolids at 7 to 90 Mg ha⁻¹ in both tobosagrass and alkali sacaton herbage yield during the first growing season in desert grasslands. This effect was extended into the second growing season for alkali sacaton in their study.

The absence of seasonal effects on herbage yield in the second year (Fig. 3) of this study may be attributed to atypical growing conditions and to plant growth stage at the time of clipping. After a very dry early summer, a significant rainfall event (75 mm) in the middle of September stimulated late-season plant growth. Plots were clipped 1 month afterward when plants were still in the early stage of vegetative growth. Under these growing conditions, it is likely that effects of seasonal biosolids applications were similar.

The beneficial effect of winter and summer applications on herbage yield during the third growing season (Fig. 3) may be attributed to the initial effect of winter and summer applications that improved plant growth conditions. The same effect was also observed in the fourth growing season (1997) even under dry conditions. This may be related to previous favorable

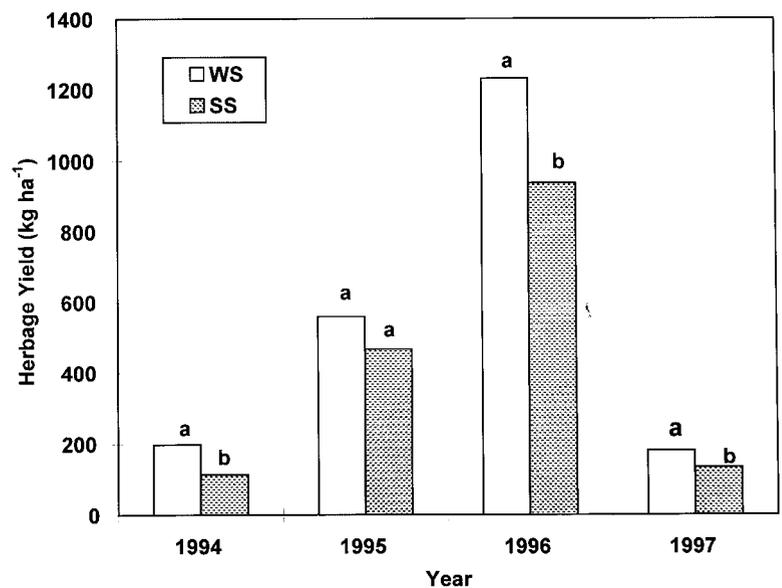


Fig. 3. Tobosagrass herbage yield response to seasons of biosolids application and years-after-application of biosolids. Treatments were applied in winter-and-summer (WS) or spring-and-summer (SS), 1994. Treatments with different letters within a year are significantly different ($P < 0.05$).

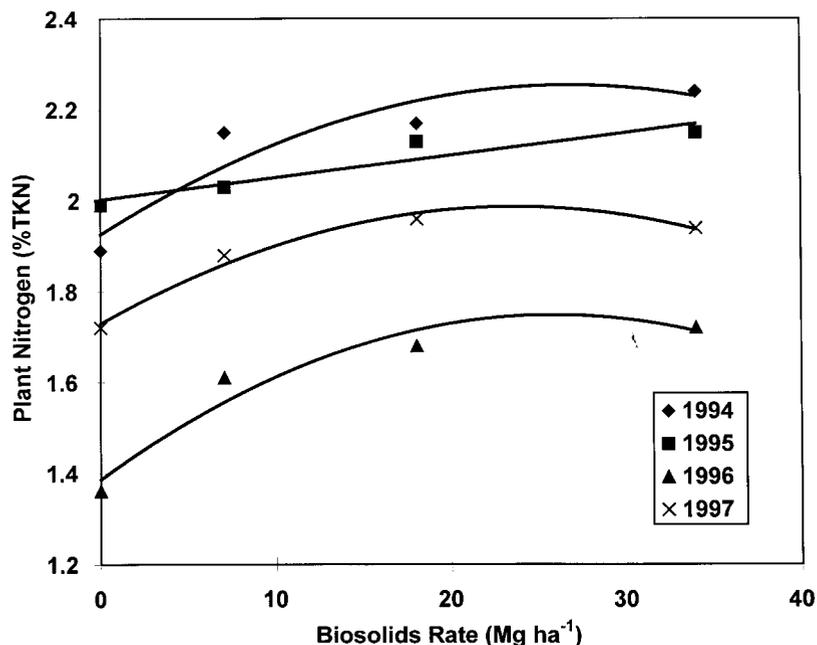


Fig. 4. Tobosagrass total nitrogen concentration (%TKN) response to biosolids rates and years-after-application of biosolids. In 1994: $Y = 1.9262 + 0.0245X - 0.0005X^2$, $R^2 = 0.86$. In 1995: $Y = 2.0028 + 0.0049X$, $R^2 = 0.85$. In 1996: $Y = 1.3862 + 0.0281X - 0.0005X^2$, $R^2 = 0.92$. In 1997: $Y = 1.7297 + 0.0219X - 0.0005X^2$, $R^2 = 0.97$. For rate comparisons, $LSD_{0.05} = 0.068, 0.056, 0.055, \text{ and } 0.064$ on a log scale from 1994 to 1997, respectively. Plant N was measured at the end of each growing season.

growing conditions in 1996. However, mechanisms by which winter and summer applications increased herbage yield more than spring and summer applications are unknown.

Tobosagrass Total Nitrogen Concentration

Although the response of plant %TKN to biosolids application depended on biosolids rate, this effect interacted with years-after-application ($P < 0.0093$, Fig. 4). In general, %TKN increased with biosolids rate. In 1994, a quadratic regression explained 86% of the rate response. All biosolids rates increased %TKN compared to the control treatments. In 1995, %TKN increased with biosolids in a linear fashion ($r^2 = 0.85$). Tobosagrass total nitrogen concentration increased at 34 $Mg\ ha^{-1}$ compared to 7 $Mg\ ha^{-1}$ and control rates. Total nitrogen concentration was similar between 18 and 34 $Mg\ ha^{-1}$ and between 7 $Mg\ ha^{-1}$ and control rate. In 1996, a quadratic equation explained 92% of the variation in %TKN. Tobosagrass total nitrogen concentration increased at 18 and 34 $Mg\ ha^{-1}$ rates compared to the control rate. Total nitrogen concentration increased at 7 and 18 $Mg\ ha^{-1}$ rates compared to the control rate. Tobosagrass total nitrogen concentration was similar

between 7 and 18 $Mg\ ha^{-1}$ rates, and between 18 and 34 $Mg\ ha^{-1}$ rates. In 1997, %TKN increased with biosolids rate with a quadratic response with an $r^2 = 0.97$. Total nitrogen concentration increased at

all biosolids rates compared to the control rate.

The increase in plant %TKN suggests an increase in plant available nitrogen in the soil. These beneficial effects on plant quality with biosolids application have also been observed by Harris-Pierce et al. (1993) in blue grama nitrogen throughout 1 growing season after biosolids application; by Aguilar et al. (1994) in blue grama nitrogen after 2 growing seasons of biosolids application; and by Wester et al. (unpublished data) in tobosagrass throughout 2 growing seasons after application. Western wheatgrass, a cool-season grass, also showed an increase in plant tissue nitrogen concentration after 1 year of biosolids application in Colorado (Pierce et al. 1998).

The response of plant %TKN to biosolids also depended on irrigation. However, irrigation interacted with years-after-application ($P < 0.0001$, Fig. 5). Total nitrogen concentration was similar between non-irrigated and irrigated treatments in dry years (1994 and 1997), and decreased with irrigation in closer to normal precipitation years (1995 and 1996). This could be attributed to plant physiological mechanisms of tobosagrass in response to growing conditions, or the so called "dilution" effect of Black and Wight (1979).

The response of plant %TKN to biosolids also depended on seasons of application. However, seasons interacted

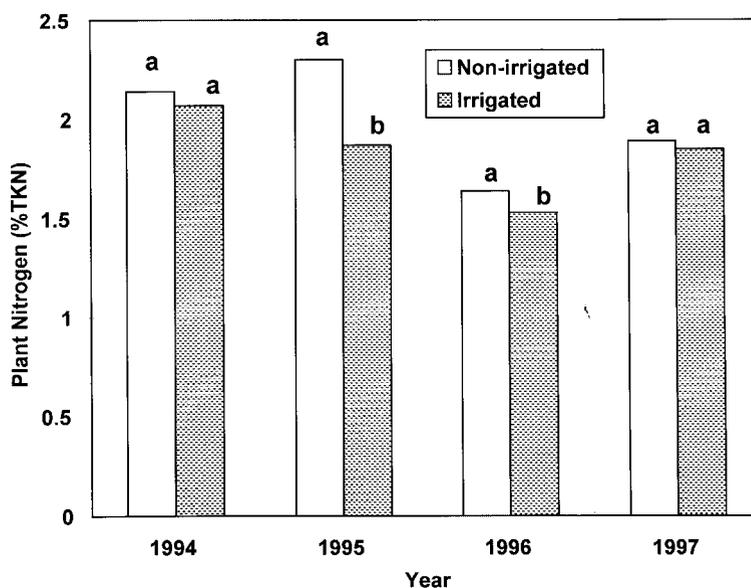


Fig. 5. Tobosagrass total nitrogen concentration (%TKN) response to irrigation and years-after-application of biosolids. Treatments with different letters within a year are significantly different ($P < 0.05$).

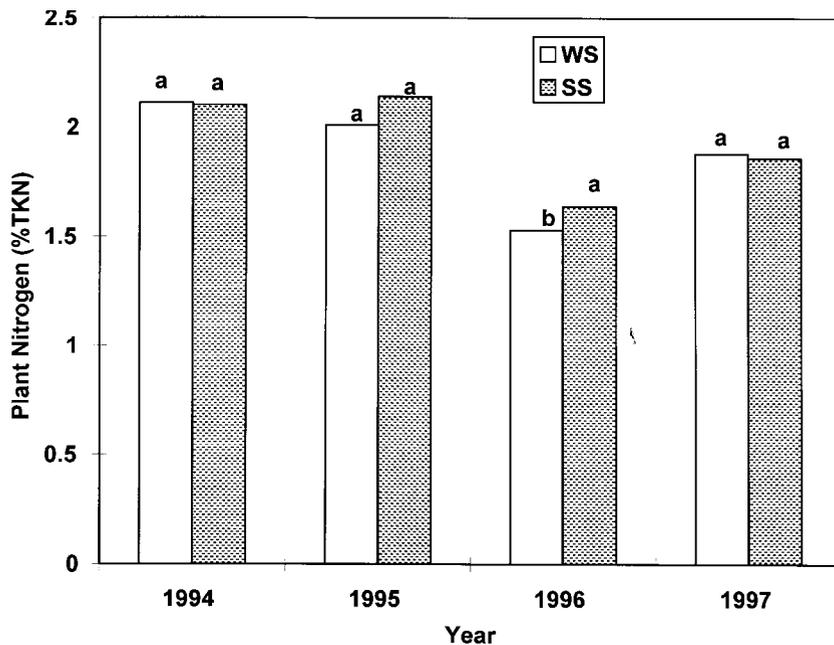


Fig. 6. Tobosagrass total nitrogen concentration (%TKN) response to seasons of biosolids application and years-after-application of biosolids. Treatments were applied in winter-and-summer (WS) or spring and summer (SS), 1994. Treatments with different letters within a year are significantly different ($P < 0.05$).

with years-after-application ($P < 0.01$, Fig. 6). Total nitrogen concentration was similar between winter and summer and spring and summer applications in most years (1994, 1995, and 1997). Tobosagrass total nitrogen concentration decreased with winter-summer applications compared to spring-summer treatments in 1996. These results could be related to the "dilution" effect (Black and Wight 1979) since higher herbage yield under winter and summer applications produced lower %TKN, and spring-summer applications had lower herbage yield and higher %TKN. However, the mechanisms of the seasonal effects of biosolids application on %TKN are unknown. These mechanisms could also be related to physical and/or chemical effects of biosolids on soil properties and to plant physiological factors.

Biosolids Carry-Over Effects

The absence of a rate by years-after-application interaction suggests a strong carry-over effect in herbage yield into the second, third, and fourth growing seasons in this study. Biosolids applied at 18 and 34 Mg ha⁻¹ provided similar beneficial effects in both dry and normal years for four growing seasons after application in this study. This indicates a long-term and consistent beneficial effect of biosolids on tobosagrass herbage yield. Similar results

were observed by Fresquez et al. (1990) on the response of blue grama herbage yield to a single summer biosolids application of 22.5 and 45 Mg ha⁻¹ throughout four growing seasons and by Benton and Wester (1998) with once-a-year winter or summer biosolids rates at 18 or 34 Mg ha⁻¹ throughout a 4-year study in alkali sacaton herbage yield.

Carry-over effects on herbage yield after biosolids application have also been observed into the third growing season by Cooley (1998) under once-a-year biosolids rates at 34 Mg ha⁻¹ on blue grama attributed to a normal precipitation growing season. Benton and Wester (1998) also showed carry-over effects on tobosagrass production at 7, 18, and 34 Mg ha⁻¹ in a desert grassland in western Texas and Pierce et al. (1998) documented carry-over effects with 1-time biosolids topically-applied up to 40 Mg ha⁻¹ to cool-season perennial grasses in Colorado. In contrast, no carry-over effects during the second growing season on galleta herbage yield (Fresquez et al. 1990), blue grama standing crop (Cooley 1998), or tobosagrass herbage yield (Benton and Wester 1998) were observed in once-a-year biosolids applications because of dry growing season conditions.

Carry-over effects of biosolids on %TKN into the second growing season were observed by Aguilar et al. (1994) with 1-

time biosolids topically-applied at 45 Mg ha⁻¹yr⁻¹ to blue grama in semiarid rangelands in New Mexico and by Wester et al. (unpublished data) in tobosagrass nitrogen after 2 growing seasons with autumn applications of biosolids in western Texas. Pierce et al. (1998) also observed carry-over effects on plant nitrogen concentration into the second and fifth growing seasons on cool-season grasses in Colorado.

These carry-over effects in both herbage yield and %TKN could be attributed to the beneficial impact of biosolids on soil fertility that may last for several years (White et al. 1997). Carry-over effects in herbage yield were always present with twice-a-year biosolids application from 18 to 34 Mg ha⁻¹ regardless of dry or normal growing conditions in this study. However, carry-over effects in %TKN apparently depended on growing conditions. The long-term beneficial effects of biosolids will eventually disappear as indicated by White et al. (1997), who did not observe soil or plant quality beneficial effects after 8 years of biosolids application to blue grama on a semiarid rangeland in New Mexico.

Conclusions

Twice-a-year biosolids surface application for 1-year-only increased herbage yield and plant %TKN. Herbage yield increased linearly with increasing biosolids rates during the 4 years of the study. Supplemental irrigation also increased tobosagrass herbage yield during the study. In general, winter and summer applications had more beneficial effects on herbage yield than spring and summer applications, except in 1995 (a year with atypical rainfall distribution). Plant %TKN increased (at a decreasing rate) in three out of four years of this study as a result of biosolids application. Irrigation did not affect %TKN in dry years, and decreased %TKN in wetter years. In general, seasons of biosolids application benefited %TKN similarly, except in 1996 (a normal rainfall year) where spring and summer applications increased %TKN compared to winter and summer applications.

These results suggest that biosolids application has a beneficial effect on tobosagrass herbage yield, and plant nitrogen concentration. Thus, biosolids application in this ecosystem may be beneficial for waste disposal and rangeland improvement.

Literature Cited

- Aguilar, R., S.R. Loftin, T.J. Ward, K.A. Stevens, and J.R. Gosz. 1994.** Sewage sludge application in semiarid grasslands: Effects on vegetation and water quality. Technical completion report 285. New Mexico Water Resources Research Institute-USDA Forest Service- Univ. of New Mexico-New Mexico State Univ. Las Cruces, N.M 75 pp.
- AOAC. 1990.** Official Methods of Analysis, 15th ed. Association of Official Analytical Chemists, Arlington, Virg.
- Beauchamp, E.G., G.E. Kid, and G. Thurtell. 1978.** Ammonia volatilization from sewage sludge applied in the field. *J. Environ. Qual.* 1:141-146.
- Benton, M.W. and D.B. Wester. 1998.** Biosolids effects on tobosagrass and alkali sacaton in a Chihuahuan desert grassland. *J. Environ. Qual.* 27:199-208.
- Black, A.L. and J.R. Wight. 1979.** Range fertilization: nitrogen and phosphorus uptake and recovery over time. *J. Range Manage.* 32:349-353.
- Brenton, C.M. 1995.** Evaluation of soil water quality following the application of biosolids on a semiarid rangeland in Texas. M.S. Thesis, Texas Tech Univ., Lubbock, Tex.
- Britton, C.M. and A. Steuter. 1983.** Production and nutritional attributes of tobosagrass. *Southw. Natur.* 28:347-352.
- Brown, R.W. 1995.** The water relations of range plants: adaptations to water deficits, pp. 291-413. *In:* D.J. Bedunah and R.E. Sosebee (eds.), *Wildland plants-Physiological ecology and developmental morphology.* Soc. for Range Manage., Denver, Colo.
- Brown, D.R. and J.G. Houston. 1993.** The nutritive value of range grasses in northern Brewster county, Texas. *Texas J. Agr. Nat. Res.* 6:109-116.
- Casby-Horton, S.M. 1997.** Soil genesis and soil-geomorphic relationships in an area near Sierra Blanca, Texas. Ph. D. Diss., Texas Tech Univ., Lubbock, Tex.
- Cooley, P.E. 1998.** Biosolids and chemical fertilizer application on the Chihuahuan Desert grasslands. M.S. Thesis, Texas Tech Univ., Lubbock, Tex.
- Day, D.A. and K.L. Ludeke. 1993.** Plant nutrients in desert environments. Springer-Verlag, Berlin, Germany.
- Dennis, G.L. and P.R. Fresquez. 1989.** The soil microbial community in a sewage sludge amended grassland. *Biol. Fertil. Soils* 7:310-317.
- Dwyer, D.D. 1971.** Nitrogen fertilization of blue grama range in the foot-hills of south-central New Mexico. *New Mexico State Univ. Agr. Exp. Sta. Bull.* 585.
- Ettershank, G., J. Ettershank, M. Bryant, and W.G. Whitford. 1978.** Effects of nitrogen fertilization on primary production in a Chihuahuan desert ecosystem. *J. Arid Environ.* 1:135-139.
- Freeman, B.N. and R.R. Humphrey. 1956.** The effects of nitrates and phosphates upon range production of a southern Arizona desert rangeland. *J. Range Manage.* 9:176-180.
- Fresquez, P.R. and G.L. Dennis. 1990.** Composition of fungal groups associated with sewage sludge amended grassland soils. *J. Arid Soil Res. Rehab.* 4:19-32.
- Fresquez, P.R., R.E. Francis, and G.L. Dennis. 1990.** Soil and vegetation responses to sewage sludge on a degraded semiarid broom snake weed/blue grama plant community. *J. Range Manage.* 43:325-331.
- Fuller, W.H. 1991.** Organic matter applications, p. 507-541. *In:* J. Skujins (ed.), *Semiarid lands and deserts. Soil resource and reclamation.* Marcel Dekker Inc., New York, N.Y.
- Gass, W.B. and J.M. Sweeten. 1992.** Benefits of applying sewage sludge on agricultural land. Pub. B-1637. Texas Agr. Ext. Serv. The Texas A&M Univ. System. College Station, Tex.
- Goodall, D.W. 1970.** Statistical plant ecology, p. 99-124. *In:* R.F. Johnston, P.W. Frank and C.D. Michener (eds.), *Ann. Rev. Ecol. Syst.* 1:99-124.
- Harmel, R.D., R.E. Zartman, C. Mouron, D.B. Wester, and R. Sosebee. 1997.** Modeling ammonia volatilization from biosolids applied to semiarid rangeland. *Soil Sci. Soc. Amer. J.* 61:1794-1798.
- Harris-Pierce, R.L., E.F. Redente, and K.A. Barbarick. 1993.** The effect of sewage sludge application on native rangeland soils and vegetation: Fort Collins-Meadow Springs Ranch. Tech. Rep. TR93-6. Colorado Agr. Exp. Sta., Colorado State Univ. Fort Collins, Colo.
- Harris-Pierce, R.L., E.F. Redente, and K.A. Barbarick. 1995.** Sewage-sludge application effects on runoff water quality in a semiarid rangeland. *J. Environ. Qual.* 24:112-115.
- Herbel, C.H. 1963.** Fertilizing tobosa on flood plains in the semidesert grassland. *J. Range Manage.* 13:133-138.
- Holecheck, J.L., R.D. Pieper, and C.H. Herbel. 1989.** Range management. Principles and practices. Regents/Prentice Hall. Englewood Cliffs, N.J.
- Holt, G.A. and D.G. Wilson. 1961.** The effect of commercial fertilizers on forage production and utilization on a desert grassland site. *J. Range Manage.* 14:252-256.
- Jager, J.C., and C.W.N. Looman. 1987.** Data collection, p. 10-28. *In:* R.H.G. Jongman et al. (eds.), *Data analysis in community and landscape ecology.* Pudoc, Wageningen, The Netherlands.
- Khaleel, R., K.R. Reddy, and M.R. Overcash. 1981.** Changes in soil physical properties due to organic waste applications: A review. *J. Environ. Qual.* 10:133-141.
- Kirk, R.E. 1995.** Experimental Design-procedures for the behavioral sciences, 3rd. ed. Brooks/Cole Publishing Co., Pacific Grove, Calif.
- Levene, H. 1960.** Robust tests for equality of variance. *In:* Contributions to probability and statistics, ed. I. Olkin. Palo Alto: Stanford Univ. Press.
- Ludwig, J.A., W.G. Whitford, and J.M. Cornelius. 1989.** Effects of water, nitrogen and sulfur amendments on cover, density and size of Chihuahuan Desert ephemerals. *J. Arid Environ.* 16:35-42.
- Mauchley, J.W. 1940.** Significance test for sphericity of a normal multivariate distribution. *Ann. Math. Stat.* 11:204-209.
- Moffet, C.A. 1997.** Quantity and quality of runoff from two biosolids-amended Chihuahuan Desert grassland soils. M.S. Thesis, Texas Tech Univ., Lubbock, Tex.
- Nelson, J.T. and M.L. Johnson. 1987.** Effect of phenology on total available carbohydrates and crude protein in tobosagrass. *Texas J. of Agr. and Nat. Res.* 1:44-46.
- N.O.A.A. 1993.** Climatological Data Annual Summary Texas. U.S. Dept. of Comm., Natl. Oceanic and Atmospheric Admin./Natl. Environ. Satellite, Data and Info. Serv./Natl. Climatic Data Center, Asheville, N.C.
- Noy-Meir, I. 1973.** Desert ecosystems: Environment and producers. *Ann. Rev. Ecol. Syst.* 4:25-51.
- Pieper, R.D., R.J. Kelsey, and A.B. Nelson. 1974.** Nutritive quality of nitrogen fertilized and unfertilized blue grama. *J. Range Manage.* 27:470-472.
- Pierce, B.L., E.F. Redente, K.A. Barbarick, R.B. Brobst, and P. Hegeman. 1998.** Plant biomass and elemental changes in shrubland forages following biosolids application. *J. Environ. Qual.* 27:789-794.
- Rostagno, C.M. 1998.** Biosolids application on southwest Texas rangelands: its influence on the soil and sediment properties and on runoff water quality. Ph. D. Diss., Texas Tech Univ., Lubbock, Tex.
- Seaker, E.M. and W.E. Sopper. 1988.** Municipal sludge for minespoil reclamation: II. Effects on organic matter. *J. Environ. Qual.* 17:598-602.
- Shapiro, S.S. and M.B. Wilk. 1965.** An analysis of variance test for normality (complete samples). *Biometrika* 52:591-611.
- Stephens, G. and W.G. Whitford. 1993.** Responses of *Bouteloua eriopoda* irrigation and nitrogen fertilization in a Chihuahuan Desert grassland. *J. Arid Environ.* 24:415-421.
- Steel, R.G.D. and J.H. Torrie. 1980.** Principles and procedures of statistics, 2nd. ed. McGraw-Hill Book Company, New York, N.Y.
- Strait, R. 1996.** Effects of temperature and soil water on biosolids degradation. M.S. Thesis, Texas Tech Univ., Lubbock, Tex.
- Stroehlein, J.L., P.R. Ogden, and B. Billy. 1968.** Time of fertilizer application on desert grasslands. *J. Range Manage.* 21: 86-89.
- Stubbendieck, J.S., S.L. Hatch, and C.H. Butterfield. 1992.** North American Range Plants, 4th. ed. Univ. of Nebraska Press, Omaha, Neb.
- U.S. Environmental Protection Agency. 1989.** Environmental regulations and technology. Use and disposal of municipal wastewater sludge. Office of Water (WH-595). EPA 625/10-84-003. Cincinnati, Ohio.
- U.S. Environmental Protection Agency. 1996.** Part 503-Standards for the use or disposal of sewage sludge. Washington, D.C.
- West, N.E. and J.O. Klemmedson. 1978.** Structural distribution of nitrogen in desert ecosystems, p. 1-16. *In:* N.E. West and J. Skujins (eds.), *Nitrogen in desert ecosystems.* Dowden Hutchinson and Ross Inc., Stroudsburg, Penn.
- White, C.S., S.R. Loftin, and R. Aguilar. 1997.** Application of biosolids to degraded semiarid rangeland: Nine-year responses. *J. Environ. Qual.* 26:1663-1671.
- Whitford, W.G., E.F. Aldon, D.W. Freckman, Y. Steinberger, and L.W. Parker. 1989.** Effects of organic amendments on soil biota on a degraded rangeland. *J. Range Manage.* 42:56-60.
- Wright, H.A. 1969.** Effect of spring burning on tobosagrass. *J. Range Manage.* 22:425-427.

Book Review

Riding the Higher Range: the Story of Colorado's Coleman Ranch and Coleman Natural Beef. By Stephen M. Voynick. 1998. Glen Melvin Coleman, Saguache, Colorado. 272p. US\$18.00 paper. ISBN: 0-9662331-0-7.

The energy crisis of the 1970's fueled much of the environmental movement of that decade with an emphasis on reducing consumption of and dependence upon fossil fuels. Consequently, at that time it was not surprising to see an article appear in the *Journal of Range Management* highlighting the inefficiency of feedlot livestock production in contrast to forage-based beef finishing systems (Cook et al, 1976, *J. Range Manage.*).

Today, for both environmental and personal health reasons, grass-fed beef is receiving new attention. Many health-conscious consumers, if they haven't renounced beef completely, are demanding a product that is free of antibiotics, hormones, and excess fat. This has led some ranchers to experiment with new production and marketing tactics to attract the growing number of socially conscious, well-off baby boomers who vote with their pocket books for health, environmental protection, humane treatment of animals, and social justice (Meeker-Lowery 1995, New Society Publisher).

Mel Coleman is one of a number of market-savvy ranchers attempting to capture the dollars of the environmental beef consumer. In *Riding the Higher Range*, Steve Voynick follows the settlement of the San Luis Valley in Southern Colorado by the ancestors of Mel and Polly Coleman, and the conception and development of Coleman Natural Beef, from a debt-ridden cow operation to a highly profitable business in the natural foods industry.

The "higher range" refers both to Coleman's purportedly lofty morals and the 10,000-foot plus elevations of the ranch's summer range in the Sangre de Cristo Mountains. "There is a right way and a wrong way to raise cattle", asserts Mel Coleman, "The right way demands environmental awareness, sustainable range management, and humane treatment. It emphasizes grass rather than grain for feed, preservation of rural lifestyles and open land, and reduction of America's agriculture's reliance on chemicals and drugs."

Voynick's story begins and ends with the present-day Coleman Ranch, taking the reader through waves of historical events that shaped the settlement of the San Luis Valley and the development of cattle ranching in the state. Jumping back to the valley's earliest human inhabitants and its settlement by a number of Indian peoples, most prominently the Ute, the author then describes the arrival of the first ranchers, Hispanic settlers from Mexico, and the subsequent arrival of Anglo-Americans.

The next 2 chapters portray Anglo life in the 1870's in the town of Saguache and the preceding forces that shaped the cattle industry including the establishment of military forts and Indian agencies, the onslaught of the Pike's Peak gold rush, and the completion of the Rio Grande Railroad. A chapter entitled "The New Century" describes the closing of the open range in the early 1900's, while another entitled "The New Agriculture" relates the rising use of chemicals and hormones in beef production in the 1940's and 50's. Throughout,

the author highlights events of family history that connect the Colemans to the general history of the area.

The second part of the book describes the conception and development of Coleman Natural Beef. Voynick traces the Colemans' first steps in entering the natural foods market and the preliminary obstacles they faced in getting their business rolling. Labeling regulations, the volatile nature of the meat packing industry, and the public's lack of knowledge regarding the differences between grass-fed and ordinary beef all posed new challenges; but eventually the Colemans' triumph becomes a "\$55-million-a-year company" and the largest natural beef producer in the United States.

While family photos and local newspaper articles lend authenticity to Voynick's tale, they do not mask an underlying sense that the purpose of this book is to sell the Coleman product. As Adler and Van Doren (1972, Simon & Schuster) noted, authorized biographies may lack the verisimilitude of definitive biographies because they are "often carefully written so that the errors the person made and the triumphs he achieved are seen in the best light possible." The Coleman family image is an important part of the Coleman product and in this book, published by Mel Coleman, Voynick is selling cowboy bravado, homespun values, and the legitimacy of ranching as Western cultural heritage.

What *Riding the Higher Range* does tell us indirectly is much about what has become acceptable to the public in this day and age. Ranchers, in order to stay in business, must profess that they practice "sustainable range management"—whatever that may be. Unfortunately, the author's treatment of the Colemans' "modern range management" practices lends limited credibility to the story. Perhaps a range manager would have better been able to define and verify what constitutes "sustainable range management". As Fairfax and Huntsinger noted (1997, *Arizona Quarterly*), Western historians such as Voynick too often employ "nature as backdrop" for their stories, failing to convey the complexity of western ecosystems and the difficulties inherent in "judging the relative impact of human and natural forces on the landscape." To Voynick, the San Luis Valley is a place for a story and the pristine "head of the creek" marketed by Coleman is a static entity. With the exception of an occasional drought and a vague reference to hydrologic changes, there is little explanation of ecosystem dynamics or how the Colemans practice modern range management.

The real value of Voynick's work lies in the lessons it can provide to ranchers wishing to enter the growing natural foods market. Labeling regulations, meat packing facilities, and public education remain major concerns in the marketing of grass-fed beef. *Riding the Higher Range* can help newcomers to avoid the major pitfalls while inspiring them to "make a difference in American agriculture." With some careful planning, ranchers may be able to produce a healthier, more environmentally friendly product, while fetching a premium for their beef. In May 2000 in Tucson, Arizona, a Coleman Choice grade sirloin tip steak sold for \$5.99/lb. That same steak produced through the regular beef industry fetched only \$3.49/lb. For this reason the Coleman story is worth telling.—*Julie L. Conley*, University of Arizona, Tucson, Arizona.

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.