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The Trail Boss

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Livestock-guarding dogs in Norway: Part I. Interactions

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Abstract

We documented behaviors of Great Pyrenees livestock-guarding dogs toward people, livestock, dogs, horses, reindeer, and bear to determine if they might be suitable for protecting livestock in Norway. None out of 13 dogs showed aggressive behavior towards unfamiliar people, and aggressiveness towards dogs and livestock was also low. However, 91% of the dogs tested chased reindeer. A willingness to chase bears was apparent in all 3 dogs tested. Although the Norwegian strains of the Great Pyrenees are bred mainly for exhibition, they obviously have retained some behavioral patterns important for the livestock-guarding function. Their nonaggressive behavior towards people, dogs, and livestock, and their active reaction towards bears suggest that this breed could be suitable for use as livestock-guardians in Norway. However, the dogs' tendency to chase reindeer is a trait that may cause conflicts in reindeer-herding areas.

Key Words: Great Pyrenees, behavior, strangers, cattle, sheep, horses, reindeer, bear, predation

Resumen

Documentamos el comportamiento de los perros guardianes de ganado de raza "Great Pyrenees" hacia la gente, ganado, perros, caballos, renos y osos para determinar si ellos pudieran ser apropiados para proteger el ganado en Noruega. Ninguno de los 13 perros mostraron comportamiento agresivo hacia la gente desconocida y la agresividad hacia perros y ganado también fue baja. Sin embargo, 91% de los perros bajo prueba persiguieron los renos. La disponibilidad para perseguir osos fue aparente en los 3 perros probados. Aunque la líneas noruegas de la raza "Great Pyrenees" son criados para exhibición, ellos obviamente han retenido algunos patrones de comportamiento importantes para la función de proteger el ganado. Su comportamiento no agresivo hacia la gente, perros y ganado y su reacción hacia los osos suguieren que esta raza pudiera ser apropiada para usarla en Noruega como perros guardianes de ganado. Sin embargo, la tendencia de los perros a perseguir renos es una característica que pudiera causar conflicto en áreas donde hay manadas de renos.

In Norway, 2.5 million sheep (*Ovis aries* L.) are grazed on mountain and forest summer range (SSB 1995), and more than 100,000 of these disappear each year. In some areas depredation on sheep may exceed 70% (Kvam et al. 1995b; Mysterud et al. 1994) of the total loss. Scandinavian brown bears (*Ursus arctos* L.), lynx (*Lynx lynx* L.) and wolverines (*Gulo gulo* L.)) are the main predators of livestock in Norway. Only bears and wolves are fully protected. Wolverines are hunted by licence in northern Norway and a quota of lynx are hunted during a regular hunting season.

Livestock-guarding dogs may be an effective way of protecting sheep from predators (Andelt 1992; Coppinger et al. 1988; Green and Woodruff 1990; Lorenz et al. 1986), but widely dispersing sheep make using guarding dogs difficult in Norway. In addition, rangeland is by law publicly accessible (Lov om friluftslivet 1957), and wildlife (Viltloven 1981), free-ranging livestock (Lov om ansvar for skade på bufe ved hund m.v. 1926), and domestic reindeer (Reindriftsloven 1978) are legally protected from stray dogs. Consequently, before the use of livestock-guarding dogs can be considered in Norway, we need to know the behavioral traits of the dogs which could cause conflicts with people, wildlife, and other animals.

Significant differences in success between breeds of livestock-guarding dogs were not found (Green and Woodruff 1983; Green and Woodruff 1988), but among different breeds evaluated, the Great Pyrenees was one of the least aggressive towards people, livestock, and other dogs. For this reason, we started with the Great Pyrenees before examining other breeds. However, there is no tradition for using livestock-guarding dogs in Norway, so the Norwegian lines of the Great Pyrenees are mainly bred as show dogs.

This publication focuses on interactions between Great Pyrenees and strangers, livestock, dogs, horses, reindeer, and bear. Different ways of using guarding dogs under Norwegian conditions will be reported in a Part II paper.

This project was funded by the Directorate of Nature Management and the Department of Agriculture. We would like to thank Ole Jakob Sørensen (Norwegian Inst. for Nature Science) and Even Bjørnes (County Governor, Dept. of Environmental Affairs) for valuable support during trial III. We also wish to thank the dog handlers; Katrine Eldegaard, Hildebjørg Haugan, Torill Jørgensen, Brynjulf Liland, Aud Ringsø, and Hanne-Brith Vold for indispensable assistance. Thanks are also due to the private Pyrenees owners.

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Material and Methods

Dogs

A total of 13 Great Pyrenees from 7 litters and 2 breeders were tested. They were all reared on sheep farms, but due to the strong influence of the breeders and Kennel Club, the dogs were not reared with sheep until the age of 12–16 weeks and were handled a lot by people. Consequently, they were more socially bonded to people than to sheep. The dogs were sired by the most common stud males and should therefore represent the major genes of Great Pyrenees lines in Norway. All males were castrated, whereas none of the females were spayed.

Trial 1. Test of Interactions between Pyrenees and "Strangers"

Of the 13 dogs tested, 11 were males. Seven were 1 year old and 6 were 2 years old. The test was performed inside a 4-ha enclosure, which was part of a pasture for 40 ewes and lambs that were familiar with Pyrenees. The dogs were tied to a long chain inside the enclosure the night before being tested.

The dogs were tested 3 times each at different days on 5 types of "stranger" in the following sequence: an unfamiliar man; an unfamiliar dog guided by a man; a herd of 6 sheep that were not used to dogs; an unfamiliar horse; and an unfamiliar Hereford cow with calf. The livestock were followed by a shepherd. The unfamiliar man wore 3 types of clothings: hunting clothes while bearing a shotgun, hiking clothes with a large backpack, and a rainsuit with a bucket used for picking berries. The 3 unfamiliar dogs were males of different breeds: a Kleiner Münsterländer (bird dog), a Siberian Husky, and a medium-sized mixed breed. The horse and the cow/calf pair were not the same in all presentations, however they were identical for all dogs within the same repetition number.

The strangers entered the open field from 2 different entrances, all following a path that turned 90 degrees at a distance of 50 m from the test dog. In this way the stranger was assumed not to have provoked the dogs by entering their personal space. The test dog was tied to a long leash at a starting-point located 150 m from both entrances, but was released by a dog handler at the moment it became aware of the unfamiliar being.

The following observations were recorded: the dog's behavior when the stranger entered the arena (behav.1); the behavior when the stranger left the arena (behav.2); the minimum distance between dog and stranger (min.dist); the latency time from when the dog discovered the stranger until the former sought physical contact (cont.time); and whether the dog barked (bark) or urinated (uri). In cases where the dog did not make contact with the stranger, the cont.time was recorded as a maximum time of 300 seconds. The behavioral repertoire (behav.1 and behav.2) was categorized into 13 behavior patterns including defensive aggression; fleeing; uninterested; staying/lying/sitting motionless, but attentive; ambivalent; approaching, but keeps a distance and makes no contact; approaching and making contact; non-aggressive greeting; playful; playfully jumping upon the stranger; chasing without attacking, the dog stops by itself; chasing without attacking, but the observer has to stop the dog; and aggressive attack. Because these behaviors could be categorized on a scale from strongly defensive to strongly offensive, they were evaluated statistically by both nonparametric and parametric tests.

Trial II. Interactions between Pyrenees and Reindeer

Ten male Pyrenees and 1 female were tested on a small flock of 20 reindeer on an island. None of the dogs had previous experience with reindeer. A maximum of 3 dogs were tested per day, and each dog was tested only once. The dogs were released one-at-a-time and, as long as no critical situations occurred, they were allowed to follow/chase the reindeer until the dogs stopped themselves. Distance to the reindeer at the moment the dog became aware of them, minimum distance between dog and reindeer, and total time of the chase were recorded.

Trial III. Interactions between Pyrenees and Bear

The Norwegian Institute of Nature Research allowed us to arrange the first controlled confrontation between a radio-tracked bear and 3 radio-tracked dogs. The dogs tested were a 2-year-old female and two 3-year-old males (male A and B). The female and male B might have had earlier experience with bears during a field study (Hansen. 1996). The bear was a 150 kg, 3-year-old male (Kvam et al. 1995b; Kvam et al. 1996) that previously had killed sheep, and sheep were grazing in a mountain area 5 km south of the bear's location. The dogs were released at 5-minutes intervals at a distance of approximately 100 m from the bear, which was hidden in dense vegetation.

Statistics

Unless otherwise stated, data are presented across breeding line, age, sex, and rearing conditions. Standard SAS procedures (SAS 1987) are used. Categorized behavioral data were tested by non-parametric tests (Mann-Whitney U-test, Spearmann's ranked correlation, and Chi-square), whereas variables following the normal-distribution were treated by analysis of variance (GLM) and two-tailed t-tests. Except for the descriptive presentation in Table 1, data regarding Trial I are pooled across the 3 repetitions for each type of stranger. All differences discussed are statistically significant at the 5% level unless otherwise stated.

Results

Trial 1. Test of Interactions between Pyrenees and Strangers

None of the 13 dogs showed any kind of aggressive behavior towards unfamiliar people (Table 1). Two Pyrenees displayed a highly dominant/threatening posture toward the husky and the mixed breed, but without fighting. One dog behaved aggressively towards the cattle, and 4 dogs chased the flock of 6 sheep that were unsocialized to dogs. One dog displayed fear towards cattle.

Table 1. The most common behavior pattern displayed by the dogs (N=13) when the different types of "stranger" entered the arena (behav. 1) and when they left (behav. 2), as shown by the number of dogs performing these behaviors at least twice[1] (N=13), and by the percentage of total trials per stranger type (N=39).

Stranger	Variable	Most Common Behavior Pattern	No. of Dogs	% of Total Trials
Man	Behav. 1	Standing/lying/sitting motionless, but attentive	5	39
	Behav. 1	Uninterested	2	21
	Behav. 2	Uninterested	7	44
	Behav. 2	Non-aggressive greeting	5	33
Dog	Behav. 1	Approaching to make contact	9	72
	Behav. 2	Non-aggressive greeting	9	59
Sheep	Behav. 1.	Approaching, but keeps a distance and makes no contact	3	28
	Behav. 1	Standing/lying/sitting motionless, but attentive	3	26
	Behav. 2	Uninterested	5	41
	Behav. 2	Chasing	3	18
Horse	Behav. 1	Approaching, but keeps a distance and makes no contact	3	36
	Behav. 1	Standing/lying/sitting motionless, but attentive	2	36
	Behav. 2	Uninterested	4	31
	Behav. 2	Approaching, but keeps a distance and makes no contact	3	26
Cattle	Behav. 1	Standing/lying/sitting motionless, but attentive	5	39
	Behav. 1	Approaching, but keeps a distance and makes no contact	5	39
	Behav. 2	Uninterested	4	26
	Behav. 2	Standing/lying/sitting motionless, but attentive	3	28

[1]These 2 measures will not correspond, because each dog may show different behavioral patterns during the 3 trials.

Each dog showed consistency in behavior pattern between the 1st, 2nd and 3rd meeting with same stranger type ($P>0.05$). Therefore, the 3 repetitions for each dog were pooled (df = 64).

Of the 5 stranger types, unfamiliar dogs elicited the most offensive behavior pattern regarding behav.1 and behav.2 (Table 1). They also triggered the fastest contact time (Fig. 1) and the least minimum distance (Fig. 1). In addition, the strange dogs induced the Pyrenees to urinate more often and to follow them out of the pasture more often. The contact time and minimum distance between the other stranger types were not significantly different (Fig. 1). The Pyrenees barked most frequently at cattle and least often at sheep (15% versus 3%).

The dogs detected the entering stranger at ≤ 50 m in 8% of the trials, at 51–100 m 67% of the trials, and at ≥ 100m (200m max.) in 25% of the occasions. In 62% of the trials, the dogs did not seek physical contact with the stranger at all (cont.time = max = 300sec.). In 15% of the times the contact time was <30 seconds.

Dogs that showed the most offensive behavior when the stranger entered the arena (behav.1) also were the most offensive when the stranger left (behav.2, r_S=0.78). The faster the Pyrenees approached to investigate the stranger (cont.time), the closer contact they established (min.dist., r_S = 0.86). No significant differences in behav.1, behav.2, cont.time or min.dist between 1-year-old and 2-year-old dogs were found.

Trial II. Interactions between Pyrenees and Reindeer

Ten of 11 dogs chased reindeer (Table 2), and all were interested in the unfamiliar scent. However, none of the dogs achieved physical contact with the reindeer. One dog was afraid of the flock. This dog also displayed fear towards the cattle in Trial I.

Our observer had to intervene and stop 2 dogs during the testing. The first had chased a reindeer for more than 1 km, and the second chased a female out into the sea. Most often, singles or small family groups were chased. The reindeer had no problems outrunning the dogs, and the reindeer were often found in the same area immediately after being chased. Panic among reindeer was observed only during the 2 occasions described above.

Table 2. Distance to the reindeer at the moment the dog discovered it (discovery distance), the closest distance between dog and reindeer (minimum distance) and chasing time.

	Mean	Minimum	Maximum
Discovery distance(m)	86	10	300
Minimum distance(m)	59	5	100
Chasing time(sec)	176	60	400

Trial III. Interactions between Pyrenees and Bear

When first released and after smelling the bear, the dogs ran about rather unsystematically, trying to locate the bear. The bear started moving in a circle around the dogs and observers at 60–100 m away, but out of sight. Ten minutes after the last dog was released, they finally began chasing the bear. The chase lasted approximately 25 minutes, by which time the bear moved about 1 km away. However, radio-tracking revealed that the bear was already on its way back to the starting-point one hour later. Of the 3 dogs, the female was consistently the most offensive and remained closest to the bear, whereas male B returned to the observers twice. The dogs' response towards the bear was modest compared with other breeds bred for bear hunting as the Laika, Karelsk bjørnehund or Jämthund (Sørensen, pers. comm.). None of the dogs were injured during the test.

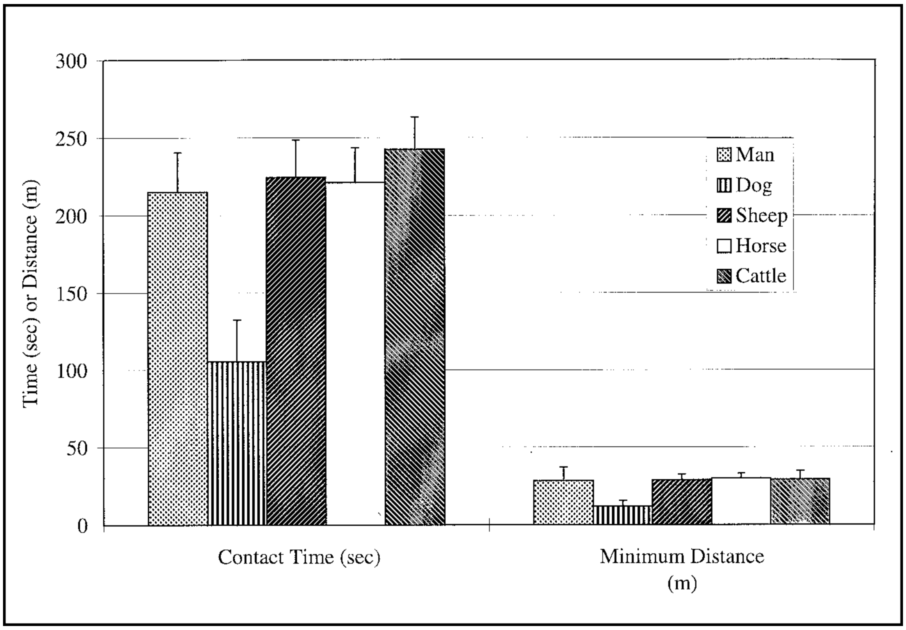

Fig. 1. Time from when the dog discovered the "stranger" until it sought physical contact with the unfamiliar being (contact time) and minimum distance between dog and "stranger" after discovery (mean ± SE).

Discussion

The Pyrenees tested showed no aggressive behavior towards unfamiliar people and only slight aggressiveness towards dogs and livestock. These findings agree partly with characteristics of the breed documented by Green and Woodruff (1983), who found that 4% of 437 Pyrenees injured people, 7% injured sheep and 67% were aggressive to dogs. These results are of course dependent on the quality and the strength of the socialization to other species during rearing. Further, the dogs in this study did not show any offensive protective behavior, i.e. they did not seem to be highly protective of the sheep. A stronger bonding to the sheep and a longer habituation period inside the test area would probably have resulted in more aggressive behavior towards the intruders.

When the sheep that were unfamiliar with dogs discovered the Pyrenees, they immediately turned and ran out of the arena. This flight behavior triggered a chase by some of the youngest dogs. Nevertheless, none of the 40 grazing sheep that were familiar with dogs were ever chased. These episodes indicate that there could be difficulties involved in using guarding dogs on open rangeland where different herds graze together, as seen elsewhere (Green and Woodruff 1990; Lorenz and Coppinger 1986). This problem will be focused further in Part II.

In Norway, sheep and reindeer grazing areas often overlap. Reindeer farmers are, in general, opposed to the use of dogs since stray dogs often chase their reindeer. More than 90% (10 dogs) of the Pyrenees that participated in this trial chased reindeer; thus the use of guarding dogs in reindeer grazing areas could result in conflicts. Indeed, the mere presence of a dog can be enough to cause reindeer to avoid an area. This was observed during another field trial, where dogs barked frequently at night (Hansen 1996). The problem should be discussed with the Reindeer Farmers' Association. Perhaps, through cooperative efforts, methods for preventing dogs from chasing reindeer could be found. One solution to this problem could be aversive conditioning of the dogs using electric shock collars. A better solution might be to expose pups regularly to reindeer. Because reindeer are also subject to severe predation (20% of the flock can be preyed upon annually (Kvam et al. 1995a)), one could even try using dogs to guard reindeer herds. This might help change the attitude of reindeer farmers towards guarding dogs.

The dogs proved their bear-chasing capacity. They chased the bear away from the close surroundings and returned to their flock (the observers) relatively soon after the encounter, which is typical for canine guardians (Green and Woodruff 1990). However, the bear returned soon thereafter. This observation corresponds to a very similar trial in Pasvik (Norway) during the summer of 1994, where 3 other Pyrenees were allowed to chase bears (Wikan 1996). A bear needed at least 4–5 encounters with dogs before it finally left the area. This is also in accordance with the experiences of encounters between livestock-guarding dogs and grizzlies (Green and Woodruff 1989). The 2 Norwegian trials show that the willingness to chase bears is latent in all 6 Pyrenees tested thus far.

The behavior displayed towards bears is also applicable toward lynx and wolverines. In another study (Staaland et al. 1998) we documented that the female from the bear-dog interaction chased a wolverine in much the same way that she chased the bear. Furthermore, losses of lambs due to lynx were reduced in the presence of guarding dogs (Hansen et al. 1997). Due to the strict legislations for dog-keeping, predation by stray dogs is not a large problem in Norway. This study shows, however, that the Pyrenees may be less effective against stray dogs. Under Norwegian conditions this could be best, since hikers might walk their dogs through the sheep herding area.

Livestock-guarding dogs have behavioral characteristics that distinguish them from other breeds. They are submissive and show no predatory behavior towards livestock; they are strongly bonded to their flock-mates whom they will protect; and they show ambivalent behavior (barking and approach/withdrawal) rather than aggression when something novel approaches (Lorenz and Coppinger 1986). The result is a "preventive" defense, usually without physical contact between dog and predator. Because the livestock-guarding dogs' way of working is more subtle than that of the bear-hunting dogs, which are generally bred to be extremely eager hunters, the guarding dogs' working capacity is often misinterpreted.

Conclusions

Although the Great Pyrenees in Norway are bred mainly for exhibition, they have obviously maintained some of the behavioral patterns important for their use as livestock-guarding dogs. Based on their calm and nonaggressive behavior towards people, dogs and livestock, and their conservative (i.e., minimal physical contact) way of chasing predators, we believe the Great Pyrenees breed has a good potential for use as livestock guardians in Norway. Still, there may be other breeds, yet to be tested, that are as good or better. The problems with dogs chasing reindeer must be solved before guarding dogs are used on rangeland used by both sheep and reindeer.

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Use of livestock and range management practi ces in Utah

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Abstract

Despite large efforts to generate and extend management innovations for rangeland operators, little is known about the degree to which practices are used. We determined what influenced use of 26 management practices among 340 permittees using data from a mailed survey. Five, co-dominant socioeconomic groups of permittees were identified by cluster analysis: "Large-Scale Operators," 2 types of traditional "Ranchers," and 2 types of "Hobbyists." The main concern across groups was losing access to public land, and coping strategies overall included passivity (64%), intensification of private-land use (27%), and enterprise diversification (5%). Across all groups the 4 highest use rates uniformly occurred for livestock cross-breeding (92%), livestock supplementation (80%), planting improved forages on private land (76%), and interaction with extension personnel (73%). The 4 lowest rates (3 to 12%) occurred for use of futures markets, range-trend monitoring on private land, estrus synchronization, and short-duration grazing (SDG). Groups varied in use of feed and financial consultants, prescribed fire on private land, forward contracting, and controlled grazing systems other than SDG, with Large-Scale Operators tending to use these the most. Larger operation size and higher levels of formal education and income for managers were positively associated with using more practices. Hobbyists tended to use practices the least. Practices which were less complex, clearly linked to animal production, potentially more cost-effective, and had greater compatibility with operational goals were favored. Socioeconomic groups and coping strategies have utility for better targeting research and extension. Understanding why some seemingly beneficial practices are rarely used requires improved communication with rangeland operators.

Key Words: socioeconomic diversity, ranching, hobby ranching, private grazing land, grazing permittees, technology transfer, sustainability, coping strategies

Resumen

A pesar de los grandes esfuerzos para generar y difundir las inovaciones de manejo entre los manejadores de pastizales poco se sabe acerca del grado de uso de estas prácticas. A través de una investigación enviada por correo a 340 usuarios del pastizal determinamos que influye en el uso de 26 prácticas de manejo. Mediante el análisis de conglomerado se dentificaron 5 grupos codominantes de usuarios: "Manejadores a gran escala", 2 tipos de "rancheros" tradicionales y 2 tipos de manejadores "aficionados". La principal preocupación entre grupos fue perder acceso a las tierras públicas y las estrategias generales de solución incluyeron pasividad (64%), intensificación del uso de tierras privadas (27%) y diversificación de la empresa (5%). En todos los grupos las 4 prácticas más uniformemente utilizadas fueron: El uso de ganado cruzado (92%), la suplementación de ganado (80%), la siembra de forrajes mejorados en tierras privadas (76%) y la interacción con personal de extensión (73%). Las prácticas menos usadas (3–12%) fueron: el uso de mercados futuros, el monitoreo de la tendencia de la condición del pastizal en tierras privadas, la sincronización del estro y el pastoreo de corta duración. Los grupos variaron en el uso de consultores en nutrición y financieros, el fuego prescrito en tierras privadas, contratos por adelantado y sistemas de pastoreo controlado diferentes al sistema de corta duración, siendo los manejadores a gran escala los que tienden a usar estos sistemas. El mayor tamaño de la operación y los altos niveles de educación formal e ingresos de los manejadores fueron positivamente correlacionados con el uso de más prácticas. Los aficionados tendieron a utilizar menos prácticas. Las prácticas menos complejas, claramente ligadas a la producción animal, más efectivas en términos de costos y de mayor compatibilidad con las metas de la explotación fueron favorecidas. Conocer los grupos socioeconómicos y las estrategias de solución tienen utilidad para enfocar mejor la investigación y extensión. El entender porque algunas prácticas aparentemente tiles son raramente utilizadas, requiere de una mejor comunicación con los manejadores del pastizal.

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Range and animal scientists often seek to develop technologies and management practices that promote sustainability of range livestock operations. One measure of the effectiveness of applied research and extension is the extent that technologies and management practices are used by target populations. Higher use rates can be interpreted to suggest that a technology or practice has been successfully transferred and has utility for producers, while lower use rates can be interpreted to indicate the opposite. Constraints which preclude use can include attributes of a given technology or practice (i.e., cost, complexity, effectiveness), behavior of potential end-users, and socioeconomic features of whole production systems (Rogers 1983). Little such research has been conducted in rangeland systems. A few studies indicate that adoption rates of technology and management practices for rangeland operations are often below the expectations of range professionals (Lacey et al. 1985, Hanselka et al. 1991, Banner et al. 1993). Assuming innovations are beneficial, why do low adoption rates occur?

We wanted to assess the extent to which a variety of livestock and range management practices were used among a specific subpopulation of rangeland operators in Utah. We therefore undertook a broad, exploratory investigation. Our objectives were to determine: (1) use rates for 26 management practices, and (2) social, economic, and other factors that most affected overall use rates. To meet the second objective we first had to assess socioeconomic diversity to see if the target population could be broken-out into distinct groups (Jamtgaard 1989). This included analysis of the primary concerns, goals, coping strategies, and felt needs of key decision-makers who manage rangeland operations.

Methods

Sampling

Grazing resources in Utah occur on public lands (> 70% of land acreage) and private lands (Anderson 1989). The target population for this study was range livestock producers who rely on both public and private lands. We focused on permittees with access to BLM, USFS, and Utah State Trust Lands. We ended-up with a list of 2,520 permittees. We hoped that many of these operations would also significantly rely on their private grazing land. This would allow us to better evaluate uptake of selected animal- and land-based practices in the absence of regulations common for public lands.

Thirty-six percent (900) of the 2,520 operations were selected via a simple random sample and were mailed a survey questionnaire in October 1993. Nine hundred was based on our desire to obtain at least 270 responses for a cluster analysis (see below) in conjunction with an anticipated response rate of 30%. The survey was designed and implemented following guidelines in Dillman (1978) with 2 small modifications; namely, we used a 7-week survey period rather than 12 weeks and 2 follow-up mailings instead of 3. The survey contained 46 multiple-choice and short-answer questions. Completed surveys were to be returned to us via pre-paid envelopes.

Survey Structure, Hypotheses, and Statistics

Defining Socioeconomic Subgroups

About half of the survey sought descriptive information about the operations. These data were largely to be used in a cluster analysis to categorize respondents into varied socioeconomic groups. Permittees were expected to be socially and economically diverse (Workman 1986) and such diversity could affect use of livestock and range management practices. Cluster analysis has been used elsewhere to establish typologies among livestock producers and provide recommendation domains for research and extension (Jamtgaard 1989).

Descriptive information was collected on 30 attributes for each operation. These attributes included personal features of key decision-makers (e.g., formal education, age, goals, self-perceived innovativeness, etc.), features of operating environments (i.e., levels of income, access to physical and capital resources, etc.), and primary concerns, felt needs, and coping strategies of operators. It was hypothesized that attributes of operating environments (i.e., income, indebtedness, public-land dependence, enterprise diversity, and/or scale of operation) would emerge as key variables defining groups. We assumed we could reveal up to 9 groups in the cluster analysis, and with a minimum of 30 observations per group for valid statistical procedures we therefore would need at least 270 respondents.

The clustering procedure followed a K-mean procedure (Romesburg 1990, Wilkinson 1990). Groups that emerged were then considered as treatments and contrasted among themselves with respect to some ancillary social and economic attributes using 2 approaches. A one-way ANOVA was used to assess variability among groups for continuous response variables. Mean separation tests were conducted using Kramer's modification of Tukey's test, suitable for unplanned comparisons with unequal sample sizes (Day and Quinn 1989). Pearson's Chi Square test was used to assess variability among groups for categorical response variables. Standardized residuals for cells that exceeded 2.5 units in size were used to identify significant ($P \leq 0.05$) contributors to lack of fit for homogeneity models (Wickens 1989, p. 136; SAS 1987).

Use of Livestock and Range Management Practices

The other half of the survey dealt with experiences operators had with 26 livestock and range management practices. Practices were selected after consulting with local experts and were intended to be diverse given the exploratory nature of the research. We wanted highly used and rarely used practices in order to enhance resolution of our analyses. Three animal-based practices included use of nutritional supplements, cross-breeding, and estrus synchronization. Four sets of land-based practices included use of range-trend monitoring, grazing systems, planting improved forages, and shrub control, all with respect to the private-land component of each operation. Three types of finance-based practices broadly included activities relevant to economic management and planning. Use of technical advisors and consultants, participation in government agricultural programs, and livestock marketing methods are examples of each type of finance-based practices.

In accordance with work of Lacey et al. (1985), Hanselka et al. (1991), and expert opinion (i.e., R.E. Banner, K.C. Olson, G.A. Rasmussen, and J.P. Workman, all of Utah State University, pers. comm.; R.L. Dorigatti, CPA of Cook, Dorigatti & Associates, Logan, Utah, pers. comm.) we anticipated that rates of use for all land- and finance-based innovations, as well as that for 1 animal-based innovation (e.g., estrus synchronization) would be low (i.e., < 50%). We expected, however, that other animal-based innovations (i.e., nutritional supplements, cross-breeding) would be highly used because these were either less expensive or had a greater likelihood of achieving desired outcomes (Lacey et al. 1985).

Rates of use of livestock and range management practices could be affected by many factors. These include attributes of a specific practice or technology [i.e., it's accessibility, cost, ease of use, compatibility, etc., (Rogers 1983)], personal attributes of potential end-users [i.e., a person's formal education, age, income-level, risk-aversiveness, etc. (Fliegel and van Es 1983, Rogers 1983)], and aspects of operations [(i.e., land, labor, information, and capital controlled; Rogers 1983)]. Our main goal was to discern which combinations of factors were most important overall in explaining use of livestock and range management practices. We used 3 complementary approaches. The first approach was to involve analysis of any socioeconomic groups emerging from the cluster analysis. For any such group we wanted to see if it was associated with variation in use of livestock and range management practices. These groups would presumably be characterized by aggregates of operation-level attributes. The second approach focused on key personal and operation-level attributes as explanatory factors. We selected income, formal education, and operation scale. Higher income, more formal education, and larger operations are often associated with innovative behavior in other production systems (Fliegel and van Es 1983, Rogers 1983). The third approach was the most direct in terms of respondent participation and was comprehensive in terms of tackling attributes of individuals, operations, and practices in tandem. In the second half of the survey, if respondents had not used a particular practice they were directed to questions listing 6 possible reasons why. Respondents were asked to pick the one best answer. The list of possible answers was derived from Rogers (1983) and included lack of information, capital, or time to implement, excessive risk or complexity of the practice, and incompatibility between the practice and acute needs of their operation. We predicted that incompatibility would be the most common explanation for not using innovations based on opinion of local experts (R.E. Banner and G.A. Rasmussen, Utah State University, pers. comm.).

Statistical procedures varied for each approach above. Pearson's Chi Square test was used to assess variability in observed use rates among socioeconomic groups using use rates across the target population as expected values. The same test was also used to analyze primary constraints perceived by non-users of practices; the null hypothesis was that non-users would select equally from among 6 choices identifying why they did not use a given practice. In both applications, Chi Square standardized residuals for cells that exceeded 2.5 units in size were used to identify significant ($P < 0.05$) contributors to lack-of-fit for homogeneity models (Wickens 1989, p. 136; SAS 1987). We used 2 methods to determine if groups could be ranked in terms of aggregated use rates for livestock and range management practices. The Page Test (Hollander and Wolfe 1973, p. 147; SAS 1987) was first employed to discern non-random, rank-ordering among groups. This test examined repeatibility of rank for groups across the 26 innovations. Each innovation was represented by a vector having groups ordered from 1 (highest) to 5 (lowest) based on the proportion of their members who used the practice. While the Page Test could gauge likelihood of non-random rank-ordering across groups, it could not be used to assess significant differences in ranked position between any given pair of groups. For the latter we used Fisher's distribution-free Sign Test (Hollander and Wolfe 1973; p. 39). Here each group was represented by a vector of 26 ordered values. Each value was the proportion of group members who had used a given practice. Contrasts of vectors involved pair-wise comparisons of proportions; proportions in 1 vector had to exceed those of another at least 18 out of 26 times to refute the null hypothesis that vectors were similar at $P = 0.01$. A Bonferroni adjustment was used to control the overall Type I error rate to $P = 0.10$ across all 10 paired vector comparisons (Day and Quinn 1989). Isolation of effects of income, education, and operation scale on overall use of management practices was conducted by using the 1-way ANOVA. Income class, educational level, and operation scale (Animal Units) were used as treatments while percentage of 26 innovations used was the response variable. Kramer's modification of Tukey's test was used for mean separation.

All statistical differences cited as significant in this paper were at the $P \leq 0.05$ probability level. Means in the text are accompanied by standard errors.

Results

Sampling Effectiveness

We obtained 522 mailed responses from November, 1993, through January, 1994, for a response rate of 58%. Only two-thirds of the responses (340 or 39% of the original sample) were completely filled-out, however, and these were used for the analysis. A follow-up telephone survey in April, 1994, of 52 randomly selected, non-respondents confirmed a high similarity among respondents and non-respondents in key attributes. Survey results were thus interpreted as being unbiased and can be extrapolated to the target population (Birkenfeld 1994).

Table 1. Socioeconomic groups and defining variables of Utah permittees based on a cluster analysis of 340 survey respondents.

Variables	Group				
	Large-Scale Operators	Private Hobbyists	Public Hobbyists	Private Ranchers	Public Ranchers
Annual labor supplied by family (%)	≤50	≥80	≥85	≥80	≥90
Annual income from non-agricultural sources (%)	0 to 100[1]	≥50	≥50	≤35	≤35
Annual AUMs supplied by public land (%)	0 to 100[1]	≤33	≥50	≤40	≥50
Sample count	56	96	66	66	56

[1]Figures include operations having permits that were not used, hence the rare occurrence of either no non-agricultural income or no AUM's supplied by public land in the year of the survey.

General Features of the Target Population

Key decision-makers for operations in our survey were overwhelmingly male (99%) and middle-aged (average: 55 ±0.7 years old). Operations were all family owned and operated. On average, operations were held by the same families for 68 ±2.3 years. In general, cow-calf operations were the predominate animal-production activity (85% of operations); this was occassionally diversified to include sheep or (rarely) dairy. Most operations (86%) were involved in cultivated forage production. All respondents owned private grazing land, and 7 ±0.1% of this private grazing land had surface or subsurface irrigation. Over 80% of operations had a source of income not related to livestock production.

Socioeconomic Diversity

Only 3 of 30 variables (i.e., relative dependence on family labor, income from non-livestock sources, and public forage) were needed by the cluster analysis to define 5 socioeconomic groups. Groups were inclusive, as only 1 of 340 operations failed to be categorized. We named groups in an attempt to concisely convey identity. These names reflect our interpretation of the blends of economic and social features revealed in our analyses. Groups are described below.

Large-Scale Operators

The "Large-Scale Operators" were primarily distinguished in the cluster analysis by their greater reliance on hired labor, which was a proxy for operation scale (Table 1). They exhibited a wide range of dependence on public grazing and income from non-livestock sources. Compared to other groups, the Large-Scale Operators tended to have: (1) a greater percentage of members in the highest income bracket, (2) a higher percentage of members having an open line of bank credit, (3) higher absolute assets, (4) larger cattle herds and sheep flocks, (5) an average of 5-times more privately owned land, (6) more hay production, and (7) nearly 3-times more AUMs on public lands (Tables 2, 3). A larger proportion of Large-Scale Operators tended to have college degrees and over half considered themselves as managerial innovators (Table 4). Profit and lifestyle were often stated as important motivations that Large-Scale Operators had for being involved with range livestock production. Despite comprising just 16% of the permittee population, Large-Scale Operators owned over one-third of permitted brood cows, over three-fourths of permitted ewes, and dominated use of public and private grazing lands (Table 5).

Smaller-Scale Hobbyists and Traditional Ranchers

The other 4 groups all relied heavily on family labor and were largely comprised of small- to medium-sized operations. These groups were primarily distinguished among themselves by variation in their relative dependence on income from non-livestock sources, and secondarily by variation in relative dependence on public versus private grazing.

Two groups were categorized as "Hobbyists" because they obtained >50% of their income from non-livestock sources (Table 1). Although both groups of Hobbyists relied on both public and private grazing, they markedly varied in terms of permitted AUMs. Therefore, we called one group "Public Hobbyists" and the other "Private Hobbyists." The Public Hobbyists had 3.5-times more permitted AUMs than the Private Hobbyists, and permitted sheep were an important component of this difference (Table 3). Both groups of Hobbyists tended to regard themselves as less-innovative managers. Hobby factors (i.e., use of livestock to generate ancillary income) were prominent in their production motivations (Table 4). Although both groups of Hobbyists out-numbered Large-Scale Operators almost 3:1, Hobbyists controlled far fewer animal and land resources (Table 5).

We called the last 2 groups "Ranchers" because they obtained relatively more income from livestock production than Hobbyists, were highly dependent on family labor to run medium-sized operations, and had social features that appeared more "traditional" in nature (Tables 1–4). For example, profit was the dominant production motivation. Ranchers tended to have received less formal education than members of other groups. Ranchers were more heterogenous in how they perceived their degree of managerial innovativeness. Like Hobbyists, Ranchers were also divided into Public and Private groups based on relative dependence on public grazing. "Public Ranchers" on average ran 3.7-times more AUMs on public lands than "Private Ranchers" (Table 3).

Except for the Private Hobbyists that comprised 28% of the sample, the other groups were similar in representation (i.e., from 16 to 19%). Extrapolating back to the target population, this translates into about 415 Large-Scale Operators, 712 and 489 Private and Public Hobbyists, respectively, and 489 and 415 Private and

Table 2. Economic features of Utah permittees statewide and by socioeconomic group.

Variable	All (n = 340)	Group: Large-Scale Operators (n = 56)	Private Hobbyists (n = 96)	Public Hobbyists (n = 66)	Private Ranchers (n = 66)	Public Ranchers (n = 56)	Chi-Square	F-ratio
	(%)							
Annual labor supplied by family	85	34a[1]	95b	95b	96b	96b		**
Annual AUMs supplied by public land	39	39b	18a	63c	23a	66c		**
Income sources	(%)							
Livestock production	49	58b	24a	23a	80c	78c		**
Crop production	6	6ab	2a	2a	11b	8ab		**
Non-agricultural activities	45	36b	74c	75c	9a	14a		**
Total Annual gross income	(% earning)						**	
≤$25,000	26	20	19	39	29	28		
$25,001–$60,000	49	40	57	52	43	46		
$60,001–$100,000	14	11	20	9	12	17		
>$100,000	11	29[2]	4	0[2]	16	9		
Credit access	(% having)						*	
Open line of credit	39	53	38	37	46	24		
To complete loan process	41	35	36	45	42	51		
Never applied for agr. loan	16	9	22	18	7	18		
Other	4	3	4	0	5	7		
	($000's)							
Debt	98	159b	68a	46a	101ab	150ab		**
Assets	747	1,784b	440a	330a	664a	832a		**

*,**Significant at the 0.05 and 0.01 levels, respectively. Significance of F-ratio is row-specific, while significance of Chi-square is specific to a set of rows associated with a variable. For example, the Chi-Square for total income was significant at P ≤ 0.01, and the analysis was based on 12 degrees of freedom for cells representing 4 income levels across all 5 groups.

[1]For groups within a row, means with the same lower case letters are not significant at P≤ 0.05.

[2]Indicates significantly large (P ≤ 0.01) standardized residuals; these are the main contributors to significance of respective Chi-square tests. The null distribution is represented by data collated for all respondents.

Public Ranchers, respectively. Each group has an associated 95% confidence interval of ±19 operations.

Concerns, Coping Strategies, and Felt Needs of Respondents

Respondents were asked to identify important threats to their livelihood, coping strategies, and felt needs (Table 6). Increased restrictions in access to public lands were by far the greatest perceived threat overall; groups more dependent on public lands were most uniform in this response. Far behind public-land access were concerns about continued availability of private land and lack of suitable information and technology for production and management.

Only 32% of respondents had what we referred to as a "pro-active" coping strategy for the future. Most of these operators planned to intensify use of private-land resources; this was 5-times more common than plans to diversify the household economy. The high, overall percentage of those with non pro-active coping strategies (64%) had 2 components. About one-quarter planned either to turn over decision-making to someone else in the family or simply get out of livestock production in the near future; we labeled these respondents as "passive." The remaining three-quarters desired to be pro-active managers but were constrained from doing so by lack of resources (unspecified); we labeled these as "semi-passive."

Despite high variation among socioeconomic groups in access to resources and production motivations, it is notable that incidence of coping strategies did not differ among groups. Overall, the primary unfulfilled need of pro-active respondents was for improved information and technology. This was most prominent for groups having a greater incidence of profit motivations and higher dependence on privately owned land.

Use of Livestock and Range Management Practices

There was high variability in the use of 26 livestock and range management practices overall (Tables 7, 8). About half of the practices had been used by <25% of the sampled operations. These included low rates of use for private consultants, estrus synchronization, marketing of livestock based on futures market pricing, participation in several government programs, technical methods for monitoring range trend, and rest rotation or short-duration grazing. One out of every 4.5 operators still relied on continuous grazing. Eight practices were used by over 50% of the population. Notable were the exceptionally high use of livestock nutritional supplements and cross-breeding. Three out of 4 operators had planted improved forages and 6 out of 10 used herbicides. Operators often had substantive contact with government advisors concerning management of public or private land.

Table 3. Livestock and land resources held by Utah permittees statewide and by socioeconomic group.

Variable	All (n = 340)	Large-Scale Operators (n = 56)	Private Hobbyists (n = 96)	Public Hobbyists (n = 66)	Private Ranchers (n = 66)	Public Ranchers (n = 56)	F-ratio
		Group					
Livestock[1]	(head)						
Pure-bred beef cows(n)	59 (19)	97 (3)	61 (5)	16 (2)	61 (4)	50 (5)	NS
Other beef cows(n)	169 (278)	392 c[2] (42)	74 a (78)	85 a (56)	161 ab (55)	238 bc (47)	**
Yearlings(n)	166 (105)	587 (19)	40 (29)	34 (21)	113 (21)	134 (15)	NS
Stockers(n)	321 (47)	1,042 (10)	72 (14)	23 (5)	181 (12)	227 (6)	NS
Ewes(n)	1,074 (67)	2,912 b (19)	196 a (14)	675 ab (12)	263 a (14)	263 a (8)	**
Dairy cows(n)	36 (12)	160 (1)	1 (1)	26 (2)	47 (5)	2 (3)	NS
Land resources[1]	(hectares)						
Owned grazing land(n)	983 (340)	2,969 b (56)	436 a (96)	398 a (66)	808 a (66)	855 a (56)	**
Irrigated grazing land(n)	72 (332)	152 c (56)	46 ab (92)	31 a (65)	109 bc (64)	38 a (55)	**
Crops(n)	114 (195)	283 b (29)	49 a (56)	44 a (37)	132 a (40)	134 a (33)	**
	(metric tons)						
Hay produced(n)	497 (294)	939 b (49)	233 a (82)	256 a (51)	598 ab(61)	617 ab (51)	**
Hay sold(n)	405 (76)	882 b (11)	180 a (24)	191 ab (12)	385ab (16)	640 b (13)	*
Hay purchased(n)	123 (111)	248 b (26)	74 a (27)	53 a (22)	109 ab (21)	113 ab (15)	*
	(AUM's)						
Private land forage(n)	1,629 (340)	5,086 b (56)	887 a (96)	421 a (66)	1,597 a (66)	904 a (56)	**
Public land forage(n)	1,043 (340)	2,466 b (56)	223 a (96)	832 a (66)	507 a (66)	1,904 b (56)	*

*,** Significant at the 0.05 and 0.01 levels, respectively.

[1]Average resources were calculated only across those respondents involved in each enterprise. Numbers in parentheses indicate respective sample size (e.g., there were 19 pure-bred cattle operations in the sample overall, with an average size of 59 head. Three of these operations were held by Large-Scale Operators with an average size of 97 head).

[2]For variables analyzed using an ANOVA, means within the same row having the same lower case letter are not significant at $P \leq 0.05$.

Table 4. Social features of Utah permittees statewide and by socioeconomic group.

Variable	All (n = 340)	Large-Scale Operators (n = 56)	Private Hobbyists (n = 96)	Public Hobbyists (n = 66)	Private Ranchers (n = 66)	Public Ranchers (n = 56)	Chi-Square
		Group					
Education	(% receiving)						*
High school diploma or less	34	29	30	38	35	41	
Some post high-school education	38	27	39	35	48	38	
College degree	28	44	31	27	17	21	
Innovativeness	(% saying they)						*
Are the first to use new practices	42	56	38	31	41	51	
Are cautious and watch others before adopting	38	26	34	48	46	33	
Avoid new methods if possible	20	18	28	21	13	16	
Production Motivation	(%)						**
Profit	49	49	29[1]	35	82[1]	59	
Profit and lifestyle	27	36	23	27	15	39	
Hobby	20	2	46[1]	29	3[1]	2[1]	
Investment/tax shelter	4	13[1]	2	9	0	0	

*,** Significant at the 0.05 and 0.01 levels, respectively. Significance is specific to a set of rows associated with a variable. For example, the Chi-Square for education was significant at $P \leq 0.05$, and the analysis was based on 8 degrees of freedom for cells representing 3 levels across all 5 groups.

[1]Superscripted entries indicate significantly large ($P \leq 0.01$) standardized residuals; these are the main contributors to significance of the respective Chi-Square test. The null distribution is represented by data collated for all respondents.

There was a moderate level of use of grazing exclosures to serve as benchmarks for monitoring range trend. Deferred rotational grazing was about 3-times more common than the next most frequently used grazing system on private land.

Group membership appeared to influence use of 9 out of 26 practices (Tables 7, 8). Compared to most other groups, the Large-Scale Operators appeared to make greater use of certain technical advisors, forward contracting to sell livestock, and prescribed fire. Large-Scale Operators tended to use rest-rotation grazing to the highest degree, but often had more than one grazing system compared to other groups. Hobbyists occassionally exhibited the lowest rates of use for practices like deferred rotation grazing or grazing for weed control. Ranchers or Hobbyists more dependent on private land appeared to use rest rotation grazing less often than other groups.

Considering use rates across all 26 practices, results of the Page Test were

Table 5. Ownership or control (%) of livestock and land resources by socioeconomic groups of Utah permittees.

Variable[2]	Large-Scale Operators (16%)[1]	Private Hobbyists (28%)	Public Hobbyists (19%)	Private Ranchers (19%)	Public Ranchers (16%)
	(%)				
Permitted cows	35	13	10	19	23
Permitted ewes	77	4	11	5	3
Private grazing land	51	12	6	16	15
Private, irrigable grazing land	36	17	8	30	9
Public land AUMs	39	6	16	9	30
Private land AUMs	51	15	5	19	9

[1]Percentages that group made-up of the sample of 340 permittees.
[2]Percentages based on 48,133 beef cows, 71,995 ewes, 325,349 ha of total private grazing land, 23,756 ha of private, irrigable grazing land, 118,152 AUMs on public land, and 184,612 AUMs on private land.

interpreted to reveal that groups were ordered non-randomly (P = 0.01). The group with the highest overall use of the 26 practices was the Large-Scale Operators ranked first with a score of 2.2, followed by the Private Ranchers (2.9), Public Hobbyists (3.0), Public Ranchers (3.1), and Private Hobbyists (3.8). Paired comparisons using the Sign Test were interpreted to indicate that the Large-Scale Operators had higher overall use rates than the Private or Public Hobbyists (P = 0.01). All other comparisons did not significantly differ. Increased income, formal education, or operation scale were each positively associated with increased rates of use for the 26 management practices (Table 9).

Survey respondents indicated that incompatibility between a given practice and acute needs of operations was the most frequently given reason why practices were not used for 8 out of 10 innovations. In such cases incompatibility was mentioned 2 to 4-times more often than the next most important constraint (Table 10). In contrast, lack of information was offered as the greatest constraint limiting use of technical range-trend monitoring, while risk was mentioned as a co-dominant constraint with incompatibility for adoption of novel practices for livestock marketing. Cost was more frequently mentioned as a constraint for land-based innovations involving new forages or brush control.

Discussion

Socioeconomic Diversity

We feel that the groups identified by cluster analysis are logical and distinctive. As we hypothesized, the variables that were most important in the cluster analysis were features of the operating environment. The 3 discriminatory variables of income distribution, private versus public land access, and use of family labor reflect aspects

Table 6. Perceived threats, coping strategies, and future needs of Utah permittees statewide and by socioeconomic group.

Variable	All (n = 340)	Large-Scale Operators (n = 56)	Private Hobbyists (n = 96)	Public Hobbyists (n = 66)	Private Ranchers (n = 66)	Public Ranchers (n = 56)	Chi-Square
Greatest perceived threat	(% saying their greatest threat is)						**
Reduced public-land access	60	61	46	73	48	82	
Reduced private and public land access	13	16	18	6	19[1]	4	
Loss of water rights	5	2	6	6	6	0	
Financial problems	6	2	7	5	8	6	
Lack of information and technology	12	16	16	8	11	6	
Other	4	3	7	2	8	2	
Coping strategy	(% planning to)						NS
Take a passive approach	17	13	15	23	15	20	
Take a semi-passive approach	47	47	50	47	40	49	
Intensify production on ranch	27	29	29	21	35	20	
Diversify on- or off- ranch	5	2	4	3	6	7	
Other	4	9	2	6	4	4	
Primary future need	(% saying their greatest need is)						**
None	9	4	17[1]	8	2	7	
Continued public land access	17	13	14	31[1]	16	9	
More private land access	11	20	8	8	16	7	
Financial assistance	12	9	12	15	5	19	
Information and technology	33	40	30	16	44	39	
Labor or time savings	13	7	17	16	11	7	
Other	5	7	2	6	6	12	

**Significant at the 0.01 level. Significance is specific to a set of rows associated with a variable. For example, the Chi-Square for greatest perceived threat was significant at P ≤ 0.01, and the analysis was based on 20 degrees of freedom for cells representing 6 threat categories across all 5 groups.
[1]Indicates significantly large (P ≤ 0.01) standardized residuals; these are the main contributors to significance of the respective Chi-Square test. The null distribution is represented by data collated for all respondents.

Table 7. Use rates (%) for animal- and finance- based innovations by Utah permittees statewide and by socioeconomic group.

Innovation	All (n = 340)	Large-Scale Operators (n = 56)	Private Hobbyists (n = 96)	Public Hobbyists (n = 66)	Private Ranchers (n = 66)	Public Ranchers (n = 56)	Chi-square
			Group				
Animal-based	----------	----------	----------	(%)	----------	----------	
Nutritional supplements	80	84	80	82	77	79	NS
Cross-breeding	92	98	91	92	88	95	NS
Estrus synchronization	11	6	7	13	18	15	NS
Finance-based[1]							
Technical advisor							
Loan officer	25	36	16	28	18	35	**
Accountant	31	45	22	35	30	29	*
Private range consultant	9	16	6	5	8	13	NS
Private feed consultant	6	15	3	2	6	5	**
Government personnel[2]	73	75	72	74	76	67	NS
Government Programs[3]							
Agricultural Conservation Program (ACP)	42	38	38	41	48	48	NS
Long-Term Agreement (LTA)	11	14	10	6	14	14	NS
Water Quality Incentive Program (WQIP)	8	9	6	11	3	11	NS
Conservation Reserve Program (CRP)	12	7	7	15	14	16	NS
Marketing Practices							
Forward contracting	38	50	31	32	39	45	*
Direct sales to public	51	48	50	55	50	55	NS
Futures markets	3	2	3	6	3	2	NS

*,**Significant at the 0.05 and 0.01 levels, respectively. In no cases were standardized residuals significant (P≤0.01) for individual cells. Groups which most contribute to significance of Chi-Square tests can be identified by comparing group entries with respective entries for all respondents because the latter served as expected values for each Chi-Square test.

[1]Where finance-based innovations are related to economics and planning on privately owned lands, unless indicated otherwise.

[2]Includes interaction with agencies dealing with private lands such as county extension agents and personnel of the Natural Resource Conservation Service (NRCS).

[3]Where the ACP, LTA, and WQIP are short- or long- term cost-share projects that can be targeted as specific range resource problems, typically on private lands. Participants in the LTA were commonly also participants in ACP. The CRP deals with protection of highly erodible lands by excluding them from cultivation or grazing.

Table 8. Use rates (%) for land-based practices on privately owned land by Utah permittees statewide and by socioeconomic group.

Innovation	All (n = 340)	Large-Scale Operators (n = 56)	Private Hobbyists (n = 96)	Public Hobbyists (n = 66)	Private Ranchers (n = 66)	Public Ranchers (n = 56)	Chi-Square
			Group				
Range trend monitoring:	----------	----------	----------	(%)	----------	----------	
Fenced exclosures	57	55	57	58	55	61	NS
Photo points	8	16	6	6	9	4	NS
Transects	7	12	6	7	6	5	NS
Grazing systems:[1]							
Deferred rotation only	59	67	61	44	70	55	*
Rest rotation only	19	29	11	24	14	20	*
Short duration only	12	15	19	9	7	6	NS
Multiple rotations[2]	15	29	16	9	13	10	*
Continuous grazing only	22	21	22	27	18	22	NS
Improved forages	76	80	74	69	85	71	NS
Prescribed fire	18	27	20	22	12	9	*
Herbicides	62	64	59	57	69	61	NS
Mechanical shrub control	29	34	27	34	26	23	NS
Grazing for weed control	17	23	7	26	15	18	**

*,** Significant at the 0.05 and 0.01 levels, respectively. In no cases were standardized residuals significant (P ≤ 0.01) for individual cells. Subgroups which most contribute to significance of Chi-Square tests can be identified by comparing subgroup entries with respective entries collated for all respondents because the latter served as expected values for each Chi-Square test.

[1]Percentages within columns exceed 100%; this is because some operations used more than 1 grazing system (i.e., use of different systems on different types of land or on the same parcel of land over time). About 5% of permittees did not use their private land for grazing (not tabulated). Note that "multiple rotations" or "continuous grazing" are not included among the 26 total innovations; they are tabulated here for illustration purposes only.

[2] Includes various combinations of deferred rotation, rest rotation, and short duration grazing.

Table 9. Factors affecting use of 26 livestock and range management practices.

Factor[1]	n	Use Rate(%[2])
Annual Gross Income:		
≤ $25,000	88	38a
$25,001-$40,000	93	40ab
$40,001-$60,000	70	40ab
$60,001-$100,000	48	39ab
>$100,000	35	45b
Formal Education:		
Did not complete high school	26	33a
Received high school diploma	83	36a
High school diploma and trade school	26	43b
Attended university	94	42b
Received university degree	94	42b
Operation scale (Animal Units):		
Very small (≤ 39)	72	35a
Small (40-99)	92	38a
Medium (100-239)	91	40b
Large (≥ 240)	83	45c

[1]Subcategories of factors defined on the basis of respondents answers to multiple-choice or short answer questions.
[2]Rates of innovation adoption were calculated as 100 x (no. innovations adopted/26). Means accompanied by the same letter within a factor (i.e. income, education, or operation scale) were not significantly different (P > 0.05) in a 1-way ANOVA, with mean separation provided by using Kramer's modification of Tukey's test.

of capital, land, and labor considered by economists to be primary drivers for production decisions (Workman 1986).

Other important social features also tended to vary among groups including level of formal education, innovativeness, and operational goals. Our work therefore confirmed a high degree of social and economic diversity among Utah permittees. Such variation in resources and production goals among rangeland operators has been noted elsewhere (Smith and Martin 1972, Grigsby 1980, Bartlett et al. 1989, Rowan 1994, Rowan and Connor 1995, Rowan and White 1994). Although the groups exhibited marked variation in terms of resource access and operational goals, the prominent concerns, coping strategies, and felt needs were remarkably similar across groups. This similarity may have been a corollary of the period when the survey was conducted. The early 1990s were a time of intense "Range Reform rhetoric." We suspect that this highly charged atmosphere served to focus a diverse array of operators on the prospect of losing public land access and how they could deal with such change.

Under conditions of high risk and uncertainty agricultural producers are often advised to sustain themselves by diversifying the household economy and/or reducing indebtedness (National Research Council 1989, Holechek et al. 1994). While the large percentage of Utah permittees who are generally passive (64%) may reflect a lack of resources, pessimism, and/or dearth of options, many may also be embracing a conservative "wait and see what happens" strategy appropriate for dealing with high uncertainty (Holechek et al. 1994). One possible strategy in risk management is to avoid making private-land investments if there is uncertainty that public land access would really be reduced. Under this strategy passiveness may confer a greater chance of economic survival for low- and middle-income operators. Under this strategy passiveness should not necessarily be viewed as an impediment to "progress," but rather as a conscious means for managing risk.

At the other extreme we have the pro-active minority. Only 5% of permittees planned to diversify their enterprises. This small number runs counter to prevailing expert opinion that diversification is the main course of action for pro-active managers under pressure (L. Butler, NRCS, pers. comm.). It remains unclear what constrains operators from attempting to diversify their operations in Utah.

Although enterprise intensification is not recommended by experts as a form of risk management, it appears to be the main strategy for pro-active operators here. This apparent paradox may be explained by the need of some operators to intensify use of private land in order to partially or fully compensate for anticipated losses in public grazing. If an operator was unable to compensate, the vulnerability of the household would increase as livestock-based income declined. If operators can tolerate the investment risks, the decision to intensify now could help ensure a viable income stream from livestock production in the future and reduce uncertainties associated with dependence on public lands. In this sense, some operators could be intensifying now in order to mantain economic diversity of the household in the future.

Felt needs reflected concerns and coping strategies and only slightly varied among subgroups. We lack details on felt needs for improved information and technology and are pursuing this in on-going research. We speculate, however, that many of the pro-active operators are seeking ways to intensify use of private land via intensive grazing on irrigated and subirrigated sites. Such topics have not traditionally received much attention from applied research or extension in the Intermountain West. This could partially explain the gap in technology and information that was indicated by survey respondents.

Use of Livestock and Range Management Practices

Our assessment of the use of livestock and range management practices has several limitations. For example, due to the broad and exploratory scope of our study, we were unable to collect details regarding the extent to which management practices had been used. We also do not know whether practices have been properly implemented. Despite such problems we feel this work provides a useful, initial overview.

Use of management practices is affected by attributes of given practices, potential end-users, and whole production systems (Rogers 1983). We begin by examining empirical data

Table 10. Primary reasons given by Utah permittees for not using livestock and range management practices.

Variable	n	Nonadopters Saying Primary Reason Was: Incompatibility	Lack of Information	Lack of Time	Cost	Risk	Complexity	Chi Square
Animal based		(%)						
Nutritional supplements	54	59[1]	5	0[1]	22	12	2[1]	**
Cross-breeding	23	78[1]	0	4	0	18	0	**
Estrus synchronization	284	37[1]	19	14	9[1]	14	7[1]	**
Finance-based								
Technical advisors	52	56[1]	4	7	9	19	5	**
Government programs	115	57[1]	21	9	3[1]	5[1]	5[1]	**
Marketing practices	33	31	18	10	0	31	10	*
Land-based[2]								
Range trend monitoring	87	21	37[1]	25	4[1]	10	3[1]	**
Improved forages	51	45[1]	7	2[1]	23	19	4[1]	**
Grazing systems	31	45[1]	10	6	16	23	0	**
Brush control	53	40[1]	5	11	27	11	6	**

*,** Significant at the 0.05 and 0.01 levels, respectively.
[1]Indicates significantly large ($P \leq 0.01$) standardized residuals; these are the main contributors to significance of the Chi-Square test for the respective row. The null hypothesis was that responses would be equally distributed among the 6 choices.
[2]Implemented on private land.

for those practices that were either widely used or rarely used, regardless of socioeconomic group. This allows us to isolate important attributes of practices that could help explain their utility (or dis-utility) for our target population.

Four practices (i.e., cross-breeding of livestock, livestock nutritional supplementation, planting forages, and herbicide application) were reportedly widely used, with overall rates of 62 to 92%. In contrast to the widely used practices, about 6 others (i.e., use of futures markets, technical range-trend monitoring, selected government programs, range consultants, estrus synchronization, and short-duration grazing) were rarely used, with overall rates of 3 to 12%. Comparative data from elsewhere are rare, which precludes much generalization. Some of our figures, nevertheless, are remarkably similar to survey results among private-land operators in Texas (Hanselka et al. 1991, Rowan 1994, Rowan and Connor 1995).

What are some important contrasts between practices that were widely used versus those that were rarely used? We speculate that the widely used practices share some common features. These include: (1) relatively straight-forward modes of implementation, (2) relatively lower costs of implementation and/or continuing use, (3) a more-direct link to animal-based production concerns, and/or (4) they appear to offer a higher chance that users can control outcomes and thus promote effectiveness over the short term. Cross-breeding seems to be the one practice that embodies most of these characteristics. Cross-breeding was also (by far) the most praised of the 26 practices in terms of user satisfaction (Coppock and Birkenfeld, unpubl.). The practices that were rarely used are more heterogeneous in character, but they generally appear to have features different from those listed above. These prominently include: (1) greater complexity, including more interaction with unfamiliar people, (2) higher expense to implement, (3) more nebulous links to animal production, and/or (4) more nebulous prospects for user control of outcomes and short-term effectiveness.

Our main opportunity to disentangle why certain practices were not used came from survey respondents, who had a menu of reasons to choose from concerning 10 representative practices. In contrast to our tidy dichotomy above focusing on cost, complexity, risk, and short-term effectiveness, it was incompatibility between available practices and priority needs of operations that dominated responses as to why some practices were not used. The major exceptions to this pattern were that: (1) risk was acknowledged to be a co-dominant constraint with incompatibility for use of novel marketing procedures for livestock and (2) lack of information constrained use of technical methods for monitoring range trend. There are paradoxes in these 2 responses. First, the livestock marketing procedures (i.e., use of futures markets) are supposed to reduce producer risk of income fluctuation by "locking-in" sale prices. This suggests that some operators did not understand what they were for. In the range-trend monitoring case, local experts contend that rural Utah has been saturated with information on how to monitor range trend. In both cases, therefore, it appears that information is either still not reaching respondents or is not being understood and effectively used. Some recent evidence supports the latter in the case of range-trend monitoring. A different survey effort was conducted in which 300 land managers were contacted after participating in short courses on traditional methods for range-trend monitoring in Utah (G.A. Rasmussen, Utah State Univ., unpubl. data). It was found that at 2 years following the short-courses only 1 person was still monitoring range trend. Subsequent analysis revealed that the main problems in transfering this practice were that the justification for monitoring range trend was ineffective and field methods were much too complex. It was concluded that the extension approach needed to be re-thought and re-packaged. One idea, for example, was to develop a better justification based on the value that range-trend monitoring has for sustaining the animal production system (Rasmussen et al. 1997). This outcome is in accordance with the concept that innovations that are simpler and more clearly linked to animal production will be more readily used.

The dominant response that available management practices are often incompatible with priority needs of operations supported predictions of our extension experts. This result also ran counter to a prevailing view that producers need larger doses of extension information to exhibit more progressive behavior (Hanselka et al. 1991). We can interpret the incompatibility message in several ways. First, it could reflect that common technical problems are still not being addressed. For example, problems with soil salinity or water management may preoccupy managers and such situations still pose many technical challenges for research. Second, it could also be that development of management practices and technologies is out of sync with dynamic producer strategies. The previous example of irrigated pasture as a non-traditional intensification tactic may be relevant here. Third, that acute problems of operations are really broad and social or economic in nature. For example, the spectre of unfavorable government policies, adverse public opinion towards ranching, and simply the daunting task of managing complex operations under uncertainty and risk may make isolated technical issues seem increasingly trivial. Clarifying felt needs and possible remedies for those needs is a major focus of on-going research.

Besides attributes of specific practices, attributes of managers and production systems appeared to influence use of livestock and range management practices. This was revealed by cases where use of practices varied among socioeconomic groups. For example, use of 5 practices (i.e., financial advising, feed consulting, forward contracting, and deferred- and rest-rotation grazing systems) varied among groups. In general, Larger-Scale Operators (and in some cases Ranchers) appeared to use these practices more often while Hobbyists used them less often. This pattern was a major contributor to the significant ranking of groups for use of all 26 management practices, with Large-Scale Operators using the most practices and Hobbyists using the fewest. Ancillary predictions that innovative managers would have more formal education and higher incomes (Rogers 1983) was also supported. Operation scale, therefore, with the concomitant factors of profit motives, managerial expertise, and entrepreneurism, appears to be the critical factor associated with increased use of management practices in our study. The presumed mechanism is that the production goals and greater resources of larger operations allows them to take more risks and make innovative investments. Larger range operations elsewhere have been associated with more land investment in Montana (Lacey et al. 1985), and innovative, technology-seeking behavior in Nevada (Harris et al. 1995). Small-acreage operators in Texas have been associated with the opposite features (Rowan 1994, Rowan and Connor 1995).

Conclusions

We focus our summary conclusions around answers for 3 questions: (1) what determines use rates for the spectrum of technologies and management practices included in our study, (2) are the socioeconomic groups useful for understanding variation among rangeland operators and improved targeting of research and extension, and (3) what can we do to enhance the up-take of practices that are rarely used?

Our work confirmed that use rates are jointly influenced by attributes of production systems and potential adopters as well as those of technologies or management practices. Attributes of production systems and potential adopters, however, were often confounded and difficult to segregate. Because technologies and management practices exhibited a very wide range in use rates (i.e., from 3 to 92%), attributes of technologies and management practices appear to be most critical. Those which variously exhibit less complexity, have more predictable or controllable outcomes, potentially greater cost-effectiveness, and a clear and direct compatibility with production goals appeared most favored– the best example is livestock cross-breeding. A marked contrast to cross-breeding is provided by use of futures markets and technical range-trend monitoring. Interaction between attributes of production systems and managers is secondary, but also important, in affecting use rates. Polar opposites incorporating socioeconomic group and coping strategy provide a good example: use rates for a given technology or management practice could be expected to be lowest among a subpopulation of passive Hobbyists versus a subpopulation of pro-active, Larger-Scale Operators. Pro-active, Larger-Scale Operations may offer the greatest scope for rapid impact and more natural resources may be affected in absolute terms. Passive Hobbyists, however, also merit attention from research and extension because of their abundance.

Our answer to the second question is a “qualified yes.” Groups significantly differed in many social and economic aspects, and the fact that group membership of a given operator could be approximated by knowing only 3 variables is fortuitous. Groups have different resources, goals, and vulnerability to changes in federal land policy. The practical problem, however, is that group membership was not synonymous with variation in primary concerns, coping strategies, or felt needs. The overall picture is therefore clarified by focusing more on coping strategy, operation scale, and production goals, because these are the features that should largely dictate the ability and motives of a given operation to alter management practices and make effective use of improved information and technology.

Our answer to the third question will always be open to debate, but we sense that continuing to do what we have always been doing may not be effective in all cases. In other words, our survey respondents did not appear to think they needed more of the same information or technology to be more innovative, and this may be best exemplified by range-trend monitoring. Our respondents often seemed to think they were "hip-deep" in information. This may not always be the "right" information, however, or it may be the "right" information but ineffectively packaged or marketed. Making a practice easier to use, less expensive, more effective, and more relevant to an operator's values and goals is the common-sense message here. If this still fails to improve use rates, challenge the validity of a given practice from the perspective of a potential user. The overwhelming response that most unused practices were incompatible with priority needs of operations was an eye-opener. Research and extension therefore need to focus more on what the evolving and priority needs of different classes of operations really are and why. This involves more attention towards how management decisions are made and improving 2-way communication with a customer-driven agenda. It also challenges a common assumption that we have all (or most) of the answers already. More attention to identifying overall producer goals and strategy, balancing production concerns versus the need to manage risks, and finding out how specific innovations fit operations in a holistic sense could be fruitful. Similar perspectives have been voiced elsewhere (Banner et al. 1993, Holechek 1996, Richards and George 1996). Such an approach requires more attention to a "mentoring and mutual learning" style of interaction with rangeland users.

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Animal and plant response on renovated pastures in western Canada

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Abstract

Extending the present 4 month grazing season in the Aspen parklands of western Canada is of major economic interest to cow-calf producers. A long-term experiment was conducted on 375 ha to compare the present practice of continuous grazing with no fertilizer to a rotational grazing system of 4 paddocks fertilized in alternate years with 90 kg N, 45 kg P_2O_5, 10 kg S ha^{-1} and a 6 paddocks rotational grazing system including fertilizing and species replacement by cultivation and reseeding. Compared to the continuously-grazed control, the grazing period was extended by 14-days on the 4-paddock rotation system, and by a further 15-days on the 6-paddock rotation system, divided about equally between spring and fall. Forage yield, cow weight gains and calf growth were significantly improved, and year-to-year variation in forage yield and animal weight gain was reduced. In the 6-paddock rotation system, breaking 1 paddock at a time in summer after grazing, and reseeding the following spring caused no noticeable reduction in grazing capacity. Replacing the bromegrass (*Bromus inermis* Leyss.) dominated vegetation in 1 of the 6 paddocks with an early-growing grass contributed to the grazing season extension. Crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.) performed well in this role; Russian wildrye (*Psathyrostachys juncea* (Fisch.) Nevski) died out within 6 years of seeding.

Resumen

Extensión del período de pastoreo cuatro meses practicado en la zona del parque de lamo tremblón (chopo) del oeste del Canadá, es de mucho interés para los criadores de vacas y terneros de la región. Un experimento de larga duración fue establecido y conducido en 375 ha para comparar los efectos de pastoreo rotativo en un sistema de cuatro parcelas fertilizadas en años alternados con 90kg N, 45 kg P_2O_5 y 10 kg S ha^{-1}, con la practica presente de pastoreo continuo y con una combinación de pastoreo rotativo, fertilización y reemplazo de especies por medio de labranza y resiembra en un sistema de 6 parcelas. Comparado con el testigo de pastoreo continuo, el período de pastoreo fue extendido por 14 días en el sistema de 4 parcelas y por otros 15 días adicionales en el sistema de 6 parcelas; la extensión del período de pastoreo fue dividido igualmente entre primavera y otoño. Rendimiento de forraje ,ganancia de peso de las vacas y crecimiento de los terneros fueron mejorados significativamente y la variación anual fue reducida. En la rotación de 6 parcelas, labranza de una parcela al año después de concluido el pastoreo seguida de resienbra en la próxima primavera no causó una disminución perceptible del la capacidad de pastoreo del sistema. Reemplazando bromo liso (*Bromus inermis* Leyss.) en una de las parcelas por una especie con crecimiento temprano en la primavera contribuyó substancialmente a extender el período de pastoreo. Agropiro (*Agropyrum cristatum* (L .)Gaertn.) cumplió muy bien esta función; *Psathyrostachys juncea* (Fisch.) Nevski desapareció de la pastura dentro de 6 años de sembrado.

Key Words: *Bromus inermis, Medicago sativa, Agropyron cristatum, Psathyrostachys juncea, Poa pratensis,* pasture management

The Aspen Parkland of Western Canada stretches from southern Manitoba through central Saskatchewan to northern Alberta, and in its native state consists of poplar (*Populus* spp.) groves intermixed with rough fescue [*Festucahallii* (Vasey) Piper grasslands (Beacom 1991a, McCartney 1993). Abandoned farmlands and cleared poplar groves have been seeded with mixtures of bromegrass (*Bromus inermis* Leyss .), creeping red fescue (*Festuca rubra* L.), alfalfa (*Medicago sativa* L.), alsike clover (*Trifolium hybridum* L.) and sometimes small amounts of other species. The areas have been fenced into fields of varying sizes and grazed continuously from late May to early October, depending on rainfall. The term ‘roughland bush pasture’ well-describes these areas of uneven topography, stony soils, lakes, swamps, and poplar groves.

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Most of the research demonstrating the benefits of legumes, fertilizer, rotational grazing, etc. has taken place using steers and heifers on high quality, more uniform and flat land than that used for much of the grazing in the region (Cooke et al. 1968, Robertson et al. 1979). Since many of the commercial operations in the Aspen parkland are on low-quality land and concentrate on calf production, acceptance of the findings has been limited.

Fertility on these grazing lands is inherently low and the sward declines to low producing bromegrass-bluegrass (*Poa pratensis* L.) mixtures (McCartney 1994, McCartney and Bittman 1994, Nuttall et al. 1991). Increases in production were obtained by breaking up the old sward and reseeding with the same species as originally seeded. The falling response to repeats of this process, and the increased cost provided an opportunity to test the applicability of other rejuvenation methods on poor quality land (Cooke 1964).

A long-term large-scale rotational grazing study was established using cow-calf pairs on a working Aspen Parkland pasture to evaluate the application of fertilizer and rotational grazing for increasing forage production and animal performance on these depleted soils and to evaluate if the replacement of some of the resident vegetation with earlier-growing species would further increase pasture performance over the long term.

In keeping with current producer trends, cow-calf units were used for grazing along with January and April born calves. Since this was a working pasture it was essential to not reduce grazing capacity while rejuvenating the pastures.

Materials and Methods

Experimental site

In 1974, approximately 375 ha of Aspen Parkland pasture on a stony Orthic Gray Luvisol (Typic Cryoboralf, USDA-SCS 1975) was selected at Pathlow Community Pasture in northeastern Saskatchewan (52°41'N, 104°58'W). This was typical of the many government operated pastures in the Aspen Parkland. The topography consists of small hills and depressions intermixed with flat and gently sloping areas, typical of glacial stagnation areas. The pasture was developed from abandoned farmsteads and aspen bushland in the mid 1960's by clearing most of the bush, and cultivating and seeding to a mixture of bromegrass, alfalfa, red fescue, and alsike clover. The area had been grazed continuously each growing season since, and by 1974 its carrying capacity had declined significantly. Soil fertility was extremely low (Nuttall et al. 1991).

Experimental design

In 1975 the area was cross-fenced to create 4-paddock and 6-paddock rotational grazing systems, each replicated 4 times, and a continuously-grazed area replicated twice. Each paddock in the rotational system was approximately 8 ha, and the continuously-grazed areas were each approximately 16 ha. The cow-calf pairs used to graze the paddocks were randomly selected from groups that had calved in January–February (Early) or March–April (Late). They were allocated separately to the rotational grazing systems so that 2 replicates of each had early-born calves and 2 had late-born calves. The continuously-grazed paddocks used cow-calf pairs from both early-and late-calving groups. All the paddocks in the 4- and 6- paddock rotational systems were fertilized with 90 kg N, 45 kg P_2O_5 and 10 kg S ha^{-1} in fall 1975. Following this, to avoid large swings in productivity, half of the paddocks were fertilized at the same rates in late fall in 1977, 1979, 1981,1983, and 1985, and the other half were fertilized in fall 1978, 1980, 1982, and early spring 1985.

At some point in time, between 1975 and 1985, each paddock in the 6-paddock system was cultivated in summer to destroy the resident vegetation and reseeded the following spring. This was the standard procedure used in the region. The exception was the fall of 1984 when glyphosate at 2.2 kg ha^{-1} was used instead of cultivation. Vegetation was replaced in sequence by paddock so that the same number of animals could be maintained on the pasture for the duration of the experiment. Two paddocks per replicate were seeded in 1976 to Russian wildrye (*Psathyrostachys juncea* (Fisch.)Nevski 'Swift') at 5.6 kg ha^{-1} and oats (*Avena sativa* L.) at 19 kg ha^{-1}. In 1979 and in 1981, a paddock in each replicate was seeded to smooth bromegrass ('Carlton') at 9 kg ha^{-1}, and alfalfa ('Rambler') at 2.2 kg ha^{-1}. In 1983, one paddock per replicate was seeded to crested wheatgrass (*Agropyron cristatum* (L.) Gaertn. 'Parkway') at 9 kg ha^{-1}. The remaining paddocks were sod-seeded in 1985 to meadow bromegrass (*Bromus riparius* Rehm. 'Regar') at 9 kg ha^{-1} and alfalfa at 2.2 kg ha^{-1}.

Each year, grazing commenced when the grass reached 10–15 cm in height, usually during the last week of May. Cows with calves born in January-February were stocked at 1.33 ha/cow calf pairs, and those with the smaller calves born in March–April at 1.11 ha/cow calf pair. This resulted in a stocking rate of 1.15 ha/cow calf pair for the 4-paddock system, 1.18 for the 6-paddock system and 1.84 for the continuously grazed control group. These densities were set to maximize the length of the grazing season for each grazing system. In 1976, the first year of grazing, insufficient cow-calf pairs were available for the control areas, so results are reported starting in 1977.

Due to heavy snow pack and the poor digestibility of over-wintered forages in the area, carry over of plant material is not practiced. In the 4-paddock rotational system, grazing commenced in a different paddock each year. In the 6-paddock rotational system, grazing started in 1 of the Russian wildrye paddocks, or in later years, in the crested wheatgrass paddocks. Cattle grazed in a paddock for 1 to 3 weeks and were moved to the next paddock when most of the forage had been consumed. Each paddock was grazed once or twice during the grazing season depending on forage production. Cows and calves were weighed separately before entering a paddock and on leaving it. At the start and end of the grazing season, animal weights were taken with water being restricted overnight. Calves were weaned about 2 weeks prior to completion of the grazing season, and removed from the pasture. Male calves were left intact until 1 month before weaning.

Forage dry matter yield was estimated each year using the double sampling cage technique (Cooke 1969). Six portable metal cages (1.8 × 2.7 m), pup tent style, were used in a paddock. Samples (0.9 × 2.7 m) were harvested by clipping to about 5 cm stubble under the cage after cattle had been moved to the next paddock. A comparable area from outside the caged area was harvested for residual yield. In 1977 and 1987, samples from cage 1 and cage 4 were frozen, and later hand-separated into grasses, legumes, and weeds. All samples were dried to 100% dry matter and weighed. Using the same procedure, 2 areas located in an adjacent pasture outside the experimental area were also sampled to obtain additional forage yield and component information under the local producer's grazing management system.

Statistical procedures

The data analyzed consisted of forage dry matter yield, the proportions of grasses, legumes, and weeds, animal gains, and length of grazing season. Statistical analyses, all of which were performed using Genstat 5, release 2 (Lawes Agricultural Trust 1987), used generalized linear models. The structure within which each analysis consisted first of the block structure (years, paddocks etc.) and then the applied treatments. Forage yields, animal gains and number of grazing days were analyzed assuming a constant coefficient of variation (McCullagh and Nelder 1989), which is to be preferred over an analysis of variance when there is a positive association between the mean and the variance as is typical for these measures. The species composition was analysed assuming a "pseudo-binomial" distribution and a logit link, but with the dispersion factor estimated from the residual mean deviance rather than assuming the unity value of the true binomial distribution. Tests of significance of responses were based on the ratio of the factors and interaction mean deviances to that of the residual mean deviance; these ratios were referred to the F-distribution. Probabilities less than 0.05 are deemed to be significant. Year and grazing system means separated by more than the sum of their standard errors were considered different.

Results

Dry matter yield

An analysis of deviance summarizes the effects of the various factors (Table 1). The significance of the main factors: year, grazing system, and fertilizer application is clear even without tests. The significant interaction between year and fertilizer is probably a result of the year-to-year variation in precipitation (Table 2). This did not significantly affect the relative forage production among the 3 grazing systems.

Annually over the period 1977 to 1986, there were no significant differences between production in the continuously-grazed experimental areas and the adjacent pasture (data not shown). Fields fertilized the previous fall averaged 160 percent more yield, and those fertilized 18 months previously yielded 58% more than the mean of 1,160 kg ha^{-1} produced in the unfertilized continuously grazed paddocks (Table 3). The 4-paddock rotation system produced a significant 88% more forage than the continuously-grazed, non-fertilized areas, and the 6-paddock system with the reseeding produced a significant 18 percent more than the 4-paddock system. The 6-paddock system produced little more than the 4-paddock system until 1981 as the cumulative effect of reseeding did not occur until that time.

In general, grazing systems and treatments produced the least forage in 1980 and the most in 1984, although there were other years in which production was not significantly different from one of the high or low values. It

Table 1. Analysis of deviance for dry-matter yield in a pasture in northeastern Saskatchewan between 1977 and 1986.

Source of variation	Degrees of Freedom	Mean deviance Ratio[1]
Year	9	35.1**
Grazing Systems[2]		
Rotation vs. Continuous	1	182.51**
Four vs. Six-Paddock	1	17.08**
Year × Grazing System	18	1.2
Year × (Rotation vs. Continuous)	9	1.58
Year × (Four vs. Six-Paddock)	9	0.89
Fertilizer	1	179.01**
Year × Fertilizer[3]	8	6.08**
Residual	397	

Analysis of deviance for average daily gain for cows

Source of variation	Degrees of Freedom	Mean deviance Ratio[1]
Rep	1	0.37
Year	8	6.65**
Calving time	1	0
Year × calving time	8	1.55
Rotation vs. Continuous	1	5.49**
Four vs. Six-Paddock	1	5.23**
Year × (Rotation vs. Continuous)	8	1.42
Year × (Four vs. Six-Paddock)	8	2.78
Calving time (Four vs. Six-Paddock)	1	2.67
Residual	52	

[1]Equivalent to the variance ratio of an ANOVA
[2]Grazing methods were: continuous, 4-Paddock system, 6-Paddock system
[3]Because of aliasing the degrees of freedom are less than with a balanced design

Table 2. Precipitation at Melfort Research Station, 25 km northeast of Pathlow Community Pasture.

Year	Winter (Oct. prev. yr. – 30 April)	Growing Season May	June	July	August	Sept.	Total	Total for Year
	-----	-----	-----	(mm)	-----	-----	-----	-----
1976	93	47	90	123	42	6	306	401
1977	96	120	28	63	77	73	361	457
1978	162	22	99	47	62	50	280	442
1979	205	40	68	26	42	14	190	395
1980	170	2	82	41	79	24	228	398
1981	115	7	40	105	12	77	241	356
1982	187	73	34	88	63	19	277	464
1983	143	23	67	130	50	68	338	481
1984	137	101	104	51	18	68	342	479
1985	215	73	66	21	48	33	241	456
1986	97	49	40	109	33	77	308	405
1987	64	42	20	78	86	13	239	303
Mean (12 yr)	140	50	62	74	51	44	280	420

was impossible to detect a positive relationship between the precipitation in any particular period and forage production. Very low precipitation in May 1980 (2 mm) clearly reduced forage production, but the low precipitation in May 1981 did not, even though precipitation the previous winter was lower than in 1979–80. Applying fertilizer and grazing rotationally resulted in 2.3 to 2.6 times more forage in the best-yielding year than in the poorest year, compared to a best: worst yearly production ratio of 3.4:1 in the continuously-grazed treatment without fertilizer.

The effects of grazing systems on forage constituents.

Significant changes occurred in the proportions of forage constituents between 1977 and 1987 with significant interactions between years and grazing systems, and years and species seeded (Table 4). In 1977, all paddocks except those seeded to Russian wildrye in 1976 contained the original species mix. In general, a decline in the proportion of legume dry matter and an increase in weeds is evident, with no change in grass content. In the 4-paddock system, the doubling of the weed component between 1977 and 1987 mirrored the decline in alfalfa. The proportion of grass in the forage did not change. In the 6-paddock system, reseeding to change the dominant species from the original bromegrass and creeping red fescue had mixed success. In paddocks seeded to Russian wildrye, this grass made up 70% of the total dry matter in 1977. In the years following, all the species previously present, except alfalfa, re-established with smooth bromegrass and Kentucky bluegrass being dominant. By 1987 Russian wildrye was confined to dry knolls. After establishment in 1983, crested wheatgrass dominated the vegetation, produced 97% of the forage in 1987, and provided excellent early spring and late fall grazing. The contrast in weed content with the Russian wildrye paddocks probably reflects the more competitive nature of crested wheatgrass. Reseeding with brome-alfalfa prevented the reduction in alfalfa that occurred in the 4-paddock system, but did not prevent an increase in weeds. Kentucky bluegrass, present in low quantities in all paddocks at the beginning of the study, increased, and by 1987 was estimated to contribute up to 15% of the total yield.

The effects of management systems on grazing season length.

During the course of the study the earliest date when pastures were ready to graze varied from 16 May for the 6-

Table 3. Estimated dry matter production (standard error) by year and treatment in a pasture in northeastern Sakatchewan between 1977 and 1985.

Year	Grazing system: 6-paddock system (fertilized)		4-paddock system (fertilized)		Continuosly grazed system (not fertilized)		Fertilization time: Previous fall		18 mos. previously	
	-----	-----	-----	-----	(kg ha^{-1})	-----	-----	-----	-----	-----
1977	1830	(127)	1750	(149)	1080	(184)	--	--	1800	(97)
1978	2150	(153)	2020	(175)	1190	(182)	2920	(223)	1420	(108)
1979	2020	(141)	1990	(171)	1210	(184)	1930	(147)	2080	(158)
1980	1450	(102)	1370	(117)	580	(88)	1760	(134)	1140	(87)
1981	1860	(136)	1410	(121)	820	(125)	2310	(182)	1150	(88)
1982	3120	(218)	2290	(196)	1070	(164)	3390	(259)	2270	(174)
1983	3290	(251)	2870	(250)	1390	(211)	4460	(341)	2000	(173)
1984	3750	(262)	2990	(255)	1980	(303)	4190	(320)	2810	(215)
1985	3200	(244)	2610	(223)	1120	(170)	3580	(273)	2440	(211)
Mean	2540	(65)	2160	(65)	1160	(63)	3050	(86)	1900	(51)

Table 4. **Mean values (standard errors) of proportions of dry matter of species groups present on a pasture in northeastern Saskatchewan in 1977 and 1987 before and after reseeding.**

Forage and year seeded	Paddocks fertilized					Paddocks not fertilized (original species)[1]	
	Original[1] species (4-paddock system)	Russian wildrye 1976	Brome alfalfa 1979	Brome alfalfa 1981	Crested wheatgrass 1983	Continuous graze (control)	Pathlow community pasture
	(%)						
Grass							
1977	77 (3)	98 (7)	87 (5)	83 (5)	65 (7)	63 (12)	66 (17)
1987	78 (4)	80 (5)	69 (7)	79 (7)	97 (2)	54 (13)	69 (13)
Legume							
1977	17 (2)	1 (1)	6 (3)	16 (5)	30 (6)	34 (10)	32 (15)
1987	7 (2)	4 (2)	21 (6)	10 (5)	0 (1)	17 (10)	17 (11)
Weeds							
1977	6 (1)	1 (1)	7 (2)	1 (1)	5 (2)	3 (2)	3 (3)
1987	14 (2)	16 (2)	10 (3)	12 (3)	2 (1)	20 (6)	5 (3)

[1]Original species mix was: smooth bromegrass, creeping red fescue, Russian wildrye, alfalfa, alsike clover, ladino clover.

paddock system to the latest date of 17 June for the continuously grazed, non-fertilized system. On average cattle commenced grazing in the 6-paddock system 5 days earlier than in the 4-paddock system and 11 days earlier than in the continuously grazed control treatment. In the 6-paddock system this was due to the earlier growth of the Russian wildrye and in later years the crested wheatgrass, and in the 4-paddock system, to fertilizer application. The latest day for fall grazing was 1 November for the 6-paddock system. The average length of grazing season for the 4-paddock system was 1 June to 8 October (129 days), the 6-paddock system was 26 May to 17 October (144 days) and for the continuously grazed system, 6 June to 29 September (115 days).

Cow performance during the grazing season

Over the experimental period, average daily gain (ADG) was significantly greater on the rotational grazing than on the continuous grazing treatments, and the 4 paddock system was superior to the 6 paddock system (Table 1). On a yearly basis there were no consistent differences between grazing systems (Table 5).

Overall, continuous grazing resulted in poorer gain ha^{-1} than rotational grazing (Table 6). On a yearly basis, weight gain ha^{-1} was consistently poorer on continuously grazed areas compared to the 4 paddock system but less consistent when compared to the 6 paddocks system. There were no clear differences in gain ha^{-1} between early and late calving cows.

Calf performance during the grazing season

Average daily gain (ADG) for the calves on the 4 paddock system and the continuously grazed treatments were significantly greater than the gain on calves on the 6 paddock system when averaged over the years (Table 7). However there were no consistent differences between grazing treatments on a yearly basis. Cows and calves heavily grazed the continuously grazed control area and grazing material was very short and usually consisted of regrowth material which was of high nutritional quality. The ratio of best: poorest year for average daily gains was 1.3:1 in the rotations and 1.6:1 in the control. On average, early-born calves had better rates of gain than late-born calves. However, this was not the case each year as ADG was similar in some years.

Average calf gain ha^{-1} was greater in the 6 paddock system than in the 4 paddock system, but this was not consistent on a yearly basis (Table 8). However both the 4 paddock and 6 paddock system had greater gains than the continuously grazed non-fertilized treatments except in 1977. Overall, and in 8 of 9 years, late-born calves gained more ha^{-1}.

It is recognized that animal-unit-months ha^{-1} is partly dependent on the beginning and ending dates of the

Table 5. **Cow average daily gain kg/d (standard error) by rotation in northeastern Saskatchewan.**

Year	Grazing system: 6-paddock system	4-paddock system	Continuously grazed
	(kg/d)		
1977	0.39 (0.05)	0.44 (0.06)	0.37 (0.07)
1978	0.29 (0.04)	0.35 (0.05)	0.31 (0.06)
1979	0.39 (0.05)	0.42 (0.05)	0.40 0.08)
1980	0.53 (0.07)	0.62 (0.09)	0.39 (0.07)
1981	0.47 (0.06)	0.60 (0.08)	0.25 (0.05)
1982	0.38 (0.05)	0.32 (0.04)	0.28 (0.05)
1983	0.38 (0.05)	0.38 (0.05)	0.36 (0.07)
1984	0.13 (0.02)	0.39 (0.06)	0.37 (0.07)
1985	0.32 (0.04)	0.45 (0.06)	0.31 (0.06)
Mean	0.37 (0.02)	0.41 (0.02)	0.34 (0.02)

Table 6. Cow weight gain kg per hectare (standard error) by grazing systems and calving time in northeatern Saskatchewan.

Year	Grazing system						Calving time			
	6-paddock system		4-paddock system		Continuosly grazed		Early (Jan.)		Late (Mar.)	
	--(kg ha)--									
1977	52	(5.4)	50	(5.2)	44	(6.5)	48	(4.3)	54	(5.6)
1978	44	(4.7)	50	(5.4)	32	(4.7)	47	(4.4)	40	(4.2)
1979	46	(4.8)	51	(5.5)	37	(5.5)	48	(4.4)	43	(4.5)
1980	45	(4.7)	45	(4.7)	19	(2.8)	39	(3.7)	47	(4.9)
1981	45	(4.7)	45	(4.7)	13	(1.9)	36	(3.5)	51	(5.3)
1982	51	(5.2)	33	(3.4)	15	(2.2)	35	(3.3)	45	(4.8)
1983	44	(4.6)	41	(4.3)	17	(2.4)	39	(3.4)	39	(4.7)
1984	23	(2.4)	35	(3.8)	18	(2.6)	28	(2.6)	29	(3.0)
1985	38	(3.9)	52	(5.4)	15	(2.3)	37	(3.6)	50	(5.2)
Mean	43	(1.5)	45	(1.6)	23	(1.3)	40	(1.2)	44	(1.6)

Table 7. Calf average daily gain kg/d (standard error) by grazing systems and calving time in northeastern Saskatchewan.

Year	Grazing system						Calving time			
	6-paddock system		4-paddock system		Continuously grazed		Early (Jan.)		Late (Mar.)	
	--(kg/d)--									
1977	0.89	(0.02)	0.99	(0.02)	0.83	(0.03)	0.93	(0.02)	0.91	(0.02)
1978	0.90	(0.02)	0.96	(0.02)	0.97	(0.03)	0.95	(0.02)	0.90	(0.02)
1979	0.91	(0.02)	0.98	(0.02)	0.97	(0.03)	0.97	(0.02)	0.92	(0.02)
1980	1.09	(0.02)	1.18	(0.03)	1.18	(0.04)	1.14	(0.02)	0.15	(0.02)
1981	1.15	(0.02)	1.18	(0.03)	1.11	(0.03)	1.16	(0.02)	1.15	(0.02)
1982	1.05	(0.02)	1..07	(0.02)	1.14	(0.04)	1.09	(0.02)	1.04	(0.02)
1983	1.07	(0.02)	1.07	(0.02)	1.29	(0.04)	1.12	(0.02)	1.05	(0.03)
1984	1.00	(0.02)	1.12	(0.02)	1.20	(0.04)	1.12	(0.02)	1.00	(0.02)
1985	1.15	(0.03)	1.19	(0.03)	1.20	(0.04)	1.22	(0.02)	1.18	(0.02)
Mean	1.02	(0.01)	1.08	(0.01)	1.10	(0.01)	1.08	(0.01)	1.02	(0.01)

Table 8. Calf weight gain kg per hectare (standard error) by grazing systems and calving time in northeatern Saskatchewan.

Year	Grazing system						Calving time			
	6-paddock system		4-paddock system		Continuosly grazed		Early (Jan.)		Late (Mar.)	
	--(kg/ha)--									
1977	78	(2.7)	72	(2.4)	70	(2.4)	72	(2.1)	77	(2.6)
1978	107	(3.7)	102	(3.5)	68	(3.3)	95	(2.8)	109	(3.7)
1979	86	(2.9)	91	(3.1)	60	(2.9)	82	(2.5)	89	(3.0)
1980	72	(2.4)	68	(2.3)	53	(2.5)	64	(1.9)	75	(2.5)
1981	90	(3.1)	86	(2.9)	50	(2.4)	78	(2.3)	93	(3.2)
1982	101	(3.5)	90	(3.1)	60	(2.9)	86	(2.5)	100	(3.4)
1983	98	(3.4)	91	(3.1)	51	(2.4)	86	(2.4)	95	(3.7)
1984	118	(4.1)	93	(3.2)	52	(2.5)	96	(3.0)	104	(3.5)
1985	110	(3.8)	105	(3.7)	54	(2.8)	101	(3.1)	99	(3.4)
Mean	96	(1.1)	89	(1.0)	58	(0.9)	84	(0.8)	93	(1.1)

Table 9. Animal-Unit-Month's /ha grazing capacity (standard error) by rotation and calving time in northeatern Saskatchewan.

Year	Grazing system						Calving time			
	6-paddock system		4-paddock system		Continuosly grazed		Early (Jan.)		Late (Mar.)	
	(AUM/ha									
1977	4.8	(0.13)	4.2	(0.12)	3.8	(0.15)	4.1	(0.10)	5..0	(0.14)
1978	5.1	(0.14)	4.8	(0.13)	3.6	(0.15)	4.6	(0.11)	5.2	(0.14)
1979	4.2	(0.12)	4.3	(0.12)	3.3	(0.13)	4.0	(0.10)	4.4	(0.12)
1980	2.8	(0.08)	2.6	(0.07)	1.7	(0.07)	2.4	(0.06)	2.9	(0.08)
1981	3.1	(0.09)	2.8	(0.08)	1.7	(0.07)	2.5	(0.06)	3.2	(0.09)
1982	3.7	(0.10)	3.2	(0.09)	1.7	(0.07)	3.0	(0.07)	3.7	(0.10)
1983	3.3	(0.09)	3.2	(0.09)	1.3	(0.05)	2.8	(0.07)	3.4	(0.09)
1984	4.4	(0.12)	3.5	(0.10)	1.4	(0.06)	3.3	(0.08)	4.2	(0.12)
1985	3.6	(0.10)	3.3	(0.09)	1.5	(0.06)	2.9	(0.07)	3.7	(0.10)
Mean	3.9	(0.04)	3.5	(0.03)	2.2	(0.03)	3.3	(0.03)	4.0	0.04)

grazing season and should be interpreted with some caution. They were established at the beginning of each grazing season on the expected forage production for the year. Producers in Canada traditionally use their historical AUM information and establish their stocking rates accordingly at the start of each grazing season.

By the animal-unit-months ha^{-1} measure for cow calf pairs, the 6-paddock system was significantly better than the 4-paddock system, 3.9 vs. 3.5 (Table 9). Both rotations were superior to the control at 2.2 animal-unit months ha^{-1}. The ratio of best: poorest year was 1: 1.8 in the rotations compared to 1: 2.9 for the control treatment. Each year there were significantly more animal-unit-months of grazing for late calves than early calves.

Discussion

The maximum possible length of grazing season in northeastern Saskatchewan is about 170 days. There is never sufficient growth to sustain grazing before mid-May, and by the end of October forage quality has deteriorated to below maintenance requirement of the beef cow. In addition, a late spring snowstorm may prevent early grazing, as occurred in 1977, and snow cover may prevent grazing the standing forage in October, as occurred in 4 of the 9 years of study. The 6-paddock system achieved 85% of this maximum, compared to 76% by the 4-paddock system and 68% by the continuously-grazed control treatment. In both systems, slightly less than half the additional time was gained in spring when forage quality is very high, and the rest gained in fall when forage quality is usually low. It seems likely that the 6-paddock system is at the maximum practical limit of grazing period for standing forage in the aspen parkland. This applies only to grazing cows after the calves have been removed. Stocker steers as used by Cooke et al.(1973) and Robertson et al. (1979) are not allowed to graze as long in fall because they lose weight on the poor-quality grass.

The extension of the grazing season from 115 days on the continuously-grazed control to 129 days on the 4-paddock system and 144 days on the 6-paddock system is of great significance to cow-calf producers in the northern area of western Canada. Stored feed accounts for the greatest proportion of winter costs, so extending the grazing season is beneficial economically (Beacom 1991b). As well, all cows entered the winter in good body condition regardless of grazing system.

Pastures dominated by smooth bromegrass can be regarded as a more-or-less stable 'climax' vegetation of well-adapted introduced grasses (Looman 1976). The native broadleaf plants which form the 'weed' component occupy the same niches as they do in native grassland communities. Fertilizing bromegrass in fall, which results in faster growth of more vigorous, better quality tillers the following spring (Waddington 1968), probably accounts for the earlier readiness for grazing of the 4-paddock system compared to the unfertilized control paddocks. The additional 5-day gain in readiness for grazing of the 6-paddock system, due to the earlier growth of Russian wildrye and crested wheatgrass, was slightly better than that observed by Cooke et al. (1973).

The use of the double-sampling cage technique allowed us to estimate forage disappearance. Because cows grazed until almost all the forage had disappeared, utilization ranged from 80 to 90%. Losses from trampling, senescence, etc. which are included in this estimate, were observed to be low. Based on forage estimates and cow gains, daily forage disappearance averaged 3.7% of their body weight. When the weight of the calf over the grazing period was included, forage disappearance averaged 2.8% of the total cow-calf weight. It appears that the present value used to estimate forage requirements of 2.6% of body weight for a 454 kg cow or 11.8 kg forage dry matter per day (Jacoby 1989, NRC 1984), is too low for east-central Saskatchewan conditions.

Although the early-born calves had greater daily rates of gain than the late-born calves, the slightly higher stocking rate on the paddocks with late calves resulted in significantly greater gain per hectare than on the others. Producers in the region who are moving their calving season to February–March from April–May to get heavier calves for the fall sales, may find gains on an area basis to be lower than before.

Most of the performance measures used, but forage production in particular, showed less year-to-year variation in fertilized and rotationally grazed areas than in the control. This is a very useful finding, because one of the major problems producers face is balancing cattle numbers with the year-to-year variation in forage production caused by weather vagaries (Bittman et al. 1997). In the 6-paddock system, renovating one paddock at a time in succession had little negative impact on productivity because the paddock was grazed before breaking in early summer, and was grazed in late summer the following year after seedlings were well-established.‘

Much of the variation in cow performance on the control areas was caused by the large difference between results from 1977–79 and from 1980–85. Apparently, these areas were unable to recover following the stress caused by drought in 1980. The low cow weight gain in the 6-paddock system in 1984 was caused by a severe snow storm the day before the cattle were due to be removed. Consequently, they spent 2 days without food and water which resulted in a large shrink.

In summary the use of fertilizer and rotational grazing significantly increased forage yield and animal gain, and decreased year to year variability. Crested wheatgrass and Russian wildrye fertilized and rotationally grazed extended the grazing season, and could be established without any reduction in grazing capacity. Russian wildrye established well but did not persist.

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A chamber design for measuring net CO_2 exchange on rangeland

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Abstract

Net carbon exchange of terrestrial ecosystems will likely change as atmospheric CO_2 concentration increases. Currently, little is known of the annual dynamics or magnitude of CO_2 flux on many native and agricultural ecosystems. Remoteness of many ecosystems has limited our ability to measure CO_2 flux on undisturbed vegetation. Today, many plant ecologists have portable photosynthesis systems with which they make single-leaf photosynthesis measurements. Utility of this equipment is enhanced when canopy-level CO_2 flux is also measured. We designed a portable 1-m^3 closed chamber for use in measuring CO_2 exchange in short statured vegetation with widely varied canopy structure. The design includes external ductwork equipped with doors which are used to open the chamber for ventilation with outside air between measurements. The chamber was tested on a Wyoming big sagebrush (*Artemisia tridentata* ssp. *Wyomingensis* Nutt.)/Thurber's needlegrass (*Stipa thurberiana* Piper) community using 10 plots equally divided between shrub and interspace. The ductwork and doors provided adequate ventilation to allow consecutive measurements of CO_2 flux without removing the chamber from the plot. The chamber could differentiate CO_2 flux between plots with sagebrush and those with grass only, even at relatively low fluxes. Net CO_2 uptake per unit ground area was greater ($P = 0.04$) on sagebrush-grass plots (7.6 ± 1.4 µmol m^{-2} s^{-1}) than on interspace plots without sagebrush (3.1 ± 1.0 µmol m^{-2} s^{-1}). Chamber and leaf temperature increased by an average of 0.5 and 1.2°C, respectively, during measurements.

Key Words: photosynthesis; respiration; carbon dioxide flux, sagebrush

Resumen

El intercambio neto de carbón de los ecosistemas terrestres probablemente cambiará conforme la concentración atmosfrica de CO_2 se incremente. Actualmente se sabe poco acerca de la dinámica anual o de la magnitud del flujo de CO_2 de muchos de los ecosistemas nativos y agrícolas. La localización remota de muchos de los ecosistemas ha limitado nuestra capacidad para medir el flujo de CO_2 en vegetacion sin disturbio. Hoy, muchos ecólogos de plantas cuentan con sistemas portátiles para medir fotosítesis, con los cuales hacen mediciones de fotosítesis en una sola hoja. La utilidad de este equipo aumenta cuando el flujo de CO_2 a nivel de la copa también es medido. Nosotros diseñamos una cámara cerrada portátil de 1 m^3 para utilizarla en la medición del intercambio de CO_2 en vegetación corta saturada con una estructura de copa muy variada. El diseño incluye ductos externos equipados con puertas que son utilizadas para abrir la cámara para ventilarla con aire del exterior entre mediciones. La cámara fue probada en una comunidad de "Wyoming big sagebrush" (*Artemisa tridentata* ssp. Wyomigensis Nutt)/ "Thurber's needlegrass" (*Stipa thuberiana* Piper) utilizando 10 parcela divididas igualmente entre los arbustos y los espacios entre ellos. Los ductos y puertas suministraron una ventilación adecuada para permitir medidas consecutivas del flujo de CO_2 sin remover la cámara de la planta. La cámara pudo diferenciar el flujo de CO_2 entre parcelas con arbustos ("sagebrush") y con solo pasto, aun en flujos relativamente bajos. La toma neta de CO_2 por unidad de terreno fue mayor ($P = 0.04$) en parcelas con arbustos y zacate (7.6 ± 1.4 µmol m^{-2} s^{-1}) que en los espacios sin arbustos (3.1 ± 1.0 µmol m^{-2} s^{-1}). Durante las mediciones, la temperatura de la cámaray hoja se incrementaron en promedio 0.5 y 1.2°C respectivamente.

There is renewed interest in evaluating terrestrial CO_2 fluxes and ecosystem productivity as a basis for understanding the global carbon cycle and ecosystem responses to increasing CO_2. At present, there is a significant "missing sink" in most global carbon budgets (Gifford 1994). Schimel (1995) suggests there is "increasingly strong evidence for terrestrial sinks, potentially distributed between Northern Hemisphere and tropical regions, but conclusive detection in direct biomass and soil measurements remains elusive." More complete data on ecosystem CO_2 fluxes will help identify some of these missing sinks.

The temporal and spatial aspects of CO_2 flux and responses to increasing atmospheric CO_2 are also of interest. Modeled predictions of ecosystem-level responses to CO_2 provide interesting insights, but fall outside the realm

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of traditional science because rigorous tests are not usually possible (Rastetter 1996). Traditional CO_2 response studies usually involve a short-term (< 2 yr) comparison of current ambient CO_2 concentration to about twice ambient levels. However, it is difficult to know if responses to an immediate doubling of CO_2 will approximate responses to the slow, long-term elevation of CO_2 (about 1.5 μmol mol^{-1} yr^{-1}) that ecosystems actually will experience. An alternative approach is to study long-term responses of ecosystems to changes in climate and CO_2 as they occur (Rastetter 1996). Such an approach requires patience, but would be a useful complement to ongoing modeling and CO_2 enrichment work. The chamber approach can also be used in conjunction with soil respiration measurements to construct community or ecosystem carbon budgets (e.g., Norman et al. 1992). Chamber measurements are also a useful complement to larger-scale techniques for quantifying carbon fluxes (i.e. Bowen ratio or eddy correlation). One major advantage of the chamber technique is that comparisons of small-scale treatments are possible. Thus the effects of species composition, prescribed fire, grazing, etc. on carbon budgets can be investigated. This would be more difficult with larger-scale techniques because of the treatment size required.

Reicosky (1990) reviewed the use of closed transparent chambers in the field and discussed their advantages. Closed chamber techniques have been developed for ecosystem and crops research (Sebacher and Harris 1982, Wagner and Reicosky 1992, Pickering et al. 1993), and have proven to be a practical method when limitations of the design are taken into account.

Battery powered, portable photosynthesis systems have also been developed for single-leaf photosynthesis measurements. Recently, these systems have been used with passive closed chambers. Passive chambers do not maintain steady-state conditions by active dehumidification and cooling, whereas active closed chambers use equipment to cool and dehumidify the chamber air. Passive chambers have successfully measured CO_2 flux in widely varied settings including native arctic ecosystems (Vourlitis et al. 1993) and peanut crops (Pickering et al. 1993). Vourlitis et al. (1993) utilized a LI-COR 6200 portable photosynthesis system (LI-COR, Inc., Lincoln, Nebr., USA[1]) to measure CO_2 concentration within the chamber. They reported that the system, which included a base inserted into the turf, had minimal effect on ecosystem CO_2 flux.

One major difficulty with large passive closed chambers is that the chamber must be physically lifted from the plot between measurements to prevent excessive CO_2 depletion. Venting capability provided with the LI-COR 6200 works well on leaf cuvettes, but is inadequate for use on chambers such as the one discussed here. A chamber design which allows chamber ventilation without removal from the plot could greatly enhance the utility of closed systems.

The design presented here provides a new approach whereby air exchange through the chamber is accomplished using ductwork, a fan, and doors. These innovations permit the chamber to be operated as a closed system for measurement, and as an open system for ventilation. We designed the chamber for use on both shrub and grass dominated plots. The plot area (1 m^2) is sufficient for whole-plant measurements, but small enough to characterize spatial variability, which is critical in assessing landscape productivity (e.g., Whiting et al. 1992, Gilmanov and Oechel 1995). This chamber is relatively inexpensive, easy to use, commercially available, and adaptable to a wide array of non-forested ecosystems, both native and agricultural.

Materials and Methods

Chamber Design

Air within closed chambers departs from ambient temperature and relative humidity (RH) through time, but these changes can be minimized either by actively cooling and dehumidifying chamber air (e.g., Whiting et al. 1992), or by using a passive design that reduces sampling time (Wagner and Reicosky 1992). Our passive closed chamber system was designed to provide rapid measurement of carbon dioxide exchange rate (CER) in shrub and grassland communities. Minimized sampling time eliminated the need for additional equipment and weight compared with actively cooled and dehumidified chambers, which is a major advantage on remote sites.

The chamber was fabricated commercially (Bend Plastic Supply, Bend, Ore.) for about U.S. $1,500 and has a mass of about 20 kg. The design incorporates upper and lower air channels (6 x 16 cm). These are attached on their inner surfaces to the 1 x 1 m Lexan® (6-mm thick) walls of the chamber (Fig. 1). The top of the 1m x 1m cube is open, and the front and sides have 60 x 60 cm openings, each of which is covered with plastic film (propafilm® C; ICI Americas, Inc., Wilmington, Del.). The openings minimize chamber mass thereby enhancing portability. Additionally, the film may help reduce heat buildup because it transmits about 70% in the 2.5–20 µm (thermal) wavelengths, while the Lexan walls are opaque to thermal radiation. The back wall is solid and provides a surface on which to mount sensors. Top, front, and side openings are closed by taping propafilm to the Lexan surfaces. A detachable Lexan duct is mounted directly to the upper and lower air channels on the back of the chamber. The duct has upper and lower doors, which can be opened to allow air exchange between inside and outside the chamber. A fan (rated at 11 m^3 minute^{-1}) is mounted inside the duct on the lower air channel. The fan can circulate air through the chamber by 2 pathways: When the upper and lower doors on the duct are open, ambient air is blown into the bottom of the chamber through holes on the lower air channel. Air exits the 1-m^3 chamber through holes in the upper air channel and leaves the upper channel through the upper door. Alternatively,

[1]The use of trade, firm, or corporation names in this publication is for the information and convenience of the reader. Such use does not constitute an official endorsement or approval by the USDA Agricultural Research Service of any product or service to the exclusion of others that may be suitable.

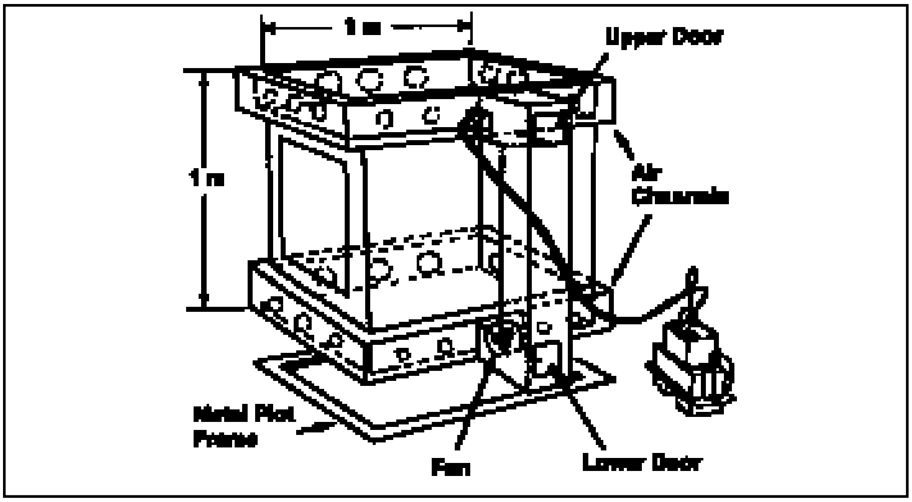

Fig. 1. Schematic drawing of a 1 m^3 chamber, approximately to scale. The chamber is constructed of Lexan® and propafilm® C.

when both doors are closed the duct provides a closed loop whereby air circulates from the upper chamber, through the duct, to the lower chamber.

In the field, permanent study plots were established by pressing a 1-m^2 angle-iron frame into the soil. The vertical angle is pressed into the soil and seals the soil surface, while the horizontal angle provides a flat mounting surface for the chamber. Closed-cell foam mounted on the chamber's lower air channel provides a gas-tight seal between chamber and frame. Chamber mass is sufficient to compress the foam and close the joint between chamber and frame. Scale drawings of both chamber and frames are available from the authors. We use a small trailer and an all-terrain vehicle (ATV) to transport the chamber and associated equipment between plots.

CO_2 Sampling

Carbon dioxide exchange is estimated by operating the chamber with the fan on and the doors closed (i.e. as a passive closed system). The fan directs air into the chamber at the soil surface. Air then flows upward through the chamber into the upper air channel. A LI-6200 sensor head mounted on the upper end of the duct samples air exiting the upper air channel (Fig. 1). We used LI-COR equipment, however the chamber design should be adaptable to other commercially available portable photosynthesis systems. Sensor tubing and cables are routed to a LI-6250 infrared gas analyzer and system console. The analyzer measures CO_2 concentration at 60 samples min^{-1}, providing rapid measurement of CO_2 concentration. Carbon dioxide exchange rate is then estimated from the rate of change in CO_2 concentration. Details regarding the IRGA and associated equipment were presented by McDermitt (1987). Chamber air temperature and humidity are measured at the sensor head, while leaf temperature is measured by a fine wire thermocouple attached to a leaf within the chamber, similar to Pickering et al. (1993). Alternatively, leaf temperature can be measured remotely by infrared thermometry. Incident PAR is measured by a quantum sensor mounted on the inside back wall of the chamber. Chamber shading is minimized by positioning the back wall away from the sun.

Chamber Volume

Chamber volume and mixing time were determined by injecting a known amount of pure CO_2 into the chamber during a data collection period. Total system volume was determined to be 1,020 ± 6 liters, including chamber, air channels, duct, tubing, and IRGA. Total volume is needed for calculating CER, and can be entered into the LI-COR system tables. Mixing time was considered to be the time required for CO_2 to stabilize after injection. Approximately 10 seconds after injection, CO_2 concentration increased rapidly and stabilized at the new concentration in about 30 seconds (Fig 2a).

Field Testing

The chamber was tested at the Northern Great Basin Experimental Range (119° 43'W, 43° 29'N; 1,380 m elev.) approximately 67 km west of Burns, Ore. in a Wyoming big sagebrush (*Artemisia tridentata* Nutt. subsp. *Wyomingensis*) community. Understory species include Thurber's needlegrass (*Stipa thurberiana* Piper), bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve), Sandberg's bluegrass (*Poa sandbergii* Vasey.), bottlebrush squirreltail (*Sitanion hystrix* (Nutt.) Smith), prairie lupine (*Lupinus lepidus* Dougl.), hawksbeard (*Crepis occidentalis* Nutt.) and longleaf phlox (*Phlox longifolia* Nutt.) Soils are coarse-to-fine sandy loam Holte-Milican complex.

Ten frames were inserted into the soil and sealed by packing soil against the frame as needed. Measurements were taken no earlier than 7 days after placing the frames. Five of the 10 frames were centered over a sagebrush plant, and 5 were randomly located in an adjacent interspace containing no sagebrush. The chamber was lowered onto the frame with the doors open, and the fan was immediately started. When the system was in place, the doors were closed, and a measurement was initiated about 30 seconds later. During each measurement, the LI-6200 software was programmed to compute 2 consecutive flux rates, which are referred to as observations in LI-COR manuals (LI-COR 1990). Each observation was programmed to end after a 5 µmol mol^{-1} CO_2 change. Sampling time per observation varied from 15 to 90 seconds, depending on the CO_2 flux rate. At the end of the measurement period CER was calculated for each observation by the LI-6200 software, based on changes in CO_2 concentration and total system volume.

All reported flux rates are based on plot surface area (1 m^2), not green leaf area. We are currently evaluating a protocol for estimating leaf area index in shrub plots.

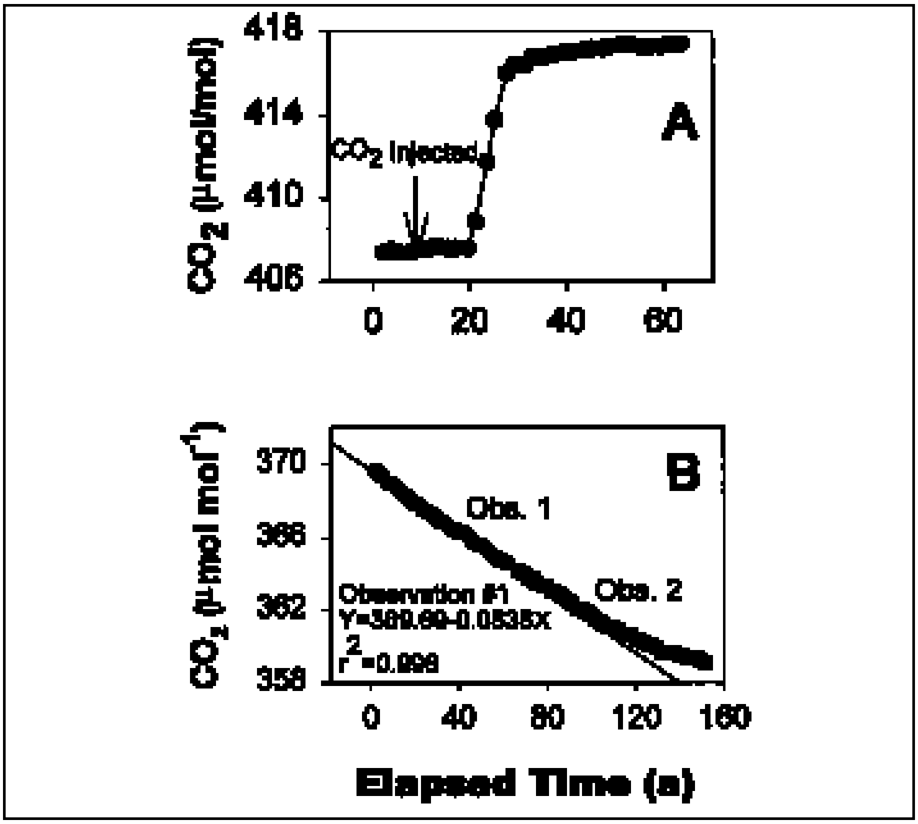

Fig. 2. Chamber CO_2 changes recorded during testing. (A) Mixing time of the chamber was determined by measuring time required to stabilize at the new concentration after injecting a known amount of CO_2. (B) Field data collected in full sun (1700 µmol m^{-2} s^{-1} over a grass\forb canopy on 25 May 1996. The solid line represents the least squares regression for data from observation 1.

Results

Chamber Leak Testing

The chamber was leak tested in the laboratory by flushing it with air from outside the building, thereby creating a 135 µmol mol^{-1} gradient between the chamber interior (375 µmol mol^{-1} CO_2) and room air (510 µmol mol^{-1} CO_2). Chamber doors were closed, and the fan was operated at full speed. Following a 30-seconds settling time, chamber CO_2 concentration was recorded for 2 min. Carbon dioxide increase averaged 0.03 µmol mol^{-1} sec^{-1} ($n = 5$). In the field, gradients between inside and outside are at least 10- to 30-times less than this, and CO_2 changes caused by leakage should be proportionately lower.

Field Testing

Carbon dioxide exchange rate of the 10 field plots was measured on 25 May 1996, during peak growth, when transpiration and CER are at seasonal maxima. Solar radiation measured inside the chamber averaged 1,655 µmol m^{-2} sec^{-1} and ranged from about 600 to 2,000 µmol m^{-2} sec^{-1}, depending on cloud cover. During these measurements, air temperature, leaf temperature and RH inside the chamber increased about 0.5 ± 0.1˚C, 1.2 ± 0.4˚C and 8 ± 1%, respectively ($n = 20$).

Later, on 30 May, we evaluated the ability of the fan and ductwork to ventilate the chamber between consecutive measurements by measuring CER in full sun followed quickly by a measurement of plant and soil respiration. Between the light and dark measurements, the chamber doors were opened and the chamber was ventilated with ambient air for 2 min during which the cover was placed over the chamber. Chamber air temperature and leaf temperature differences between full sun and dark measurements reflect the effect of covering the chamber with a shroud, which reduces heating (Table 1). Relative humidity at the start of the dark measurement was within 1% of the previous starting value in full sun.

The profile of CO_2 concentration change during a measurement is illustrated in Figure 2b for an interspace plot. On this plot, the first observation spanned a 5 µmol mol^{-1} CO_2 change, and lasted 60 seconds. The depletion of CO_2 was linear with time, with a slope of –0.08 ± 0.001 µmol mol^{-1} sec^{-1} ($r^2 = .996$, df = 29). The second observation lasted 90 seconds. The

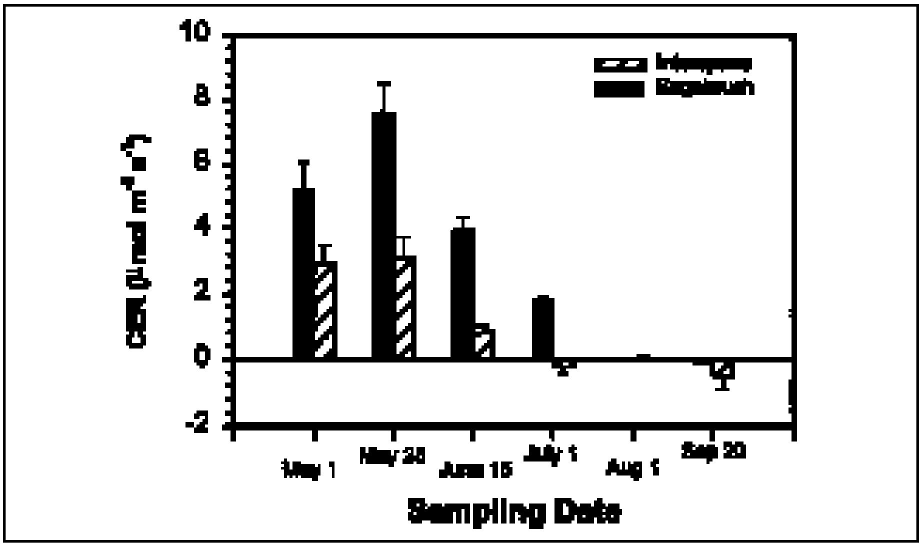

Fig. 3. Seasonal profiles of CO_2 exchange rate (CER) over sagebrush and interspace plots during 1996. Data are presented on a ground area basis and vertical bars represent 1 SE.

Table 1. Chamber air and leaf temperature initial conditions and associated SE measured on 5 sagebrush plots on 30 May. The range of each variable is the change recorded during the measurements. Full sun (light) measurements were separated from covered chamber (dark) measurements by about 2 min, during which the chamber remained affixed to the plot, and ambient air was circulated through the open chamber doors. For time, range is the length of the measurement.

	Light			Dark		
	Starting value		Range	Starting value		Range
Variable	$\bar{x}$	SE	$\bar{x}$	$\bar{x}$	SE	$\bar{x}$
Chamber PAR (µmol m^{-2} s^{-1})	1601	5	10	—	—	—
Air temperature (°C)	20.7	0.6	0.3	20.1	0.6	0.2
Leaf temperature (°C)	21.2	1.4	1	17.4	0.6	0.5
Relative humidity (%)	51	1.7	3.4	50.1	2	6.8
Carbon dioxide (µmol^{-1})	360	2	5.3	366	1	5.1
Measurement time (s)			13			50

slope was linear (-0.06 ± 0.001 µmol mol^{-1} sec^{-1}; r^2 = .98, df = 45), but was significantly ($P < 0.05$) less than for the first observation. Visual inspection of the figure shows that depletion rate slowed after about 90 seconds (about 2 min after door closure), likely because of increased humidity and lowered CO_2 concentration.

We were able to separate CER on shrub and interspace, even though rates in this area are low, and plant cover is variable. Seasonally, CER averaged 0.27 µmol mol^{-1} sec^{-1} on sagebrush plots, twice the rate measured on interspace plots (P = 0.04). During the period of maximum growth, mean CER on shrub plots was 7.6 ± 1.4 µmol m^{-2} sec^{-1} versus 3.1 ± 1.0 µmol m^{-2} sec^{-1} over interspace plots (Fig. 3). Even though CER on these plots was not large, we easily distinguished between shrub and interspace during this critical period of active growth.

Discussion and Conclusions

The chamber described here was designed to provide estimates of instantaneous CER on undisturbed rangeland, without incorporating specialized air conditioning equipment. The duct and fan arrangement allows the chamber to be ventilated without removing it from the frame. This arrangement facilitates measurement of CER in full sunlight, followed immediately by measurements of plant and soil respiration after covering the chamber with an opaque cloth. Based on measured CO_2 exchange in both sagebrush and interspace plots, precision is good. Standard errors of CER within a measurement period were generally less than 1% of the least squares slope for that measurement. Temperature increases were small, while humidity increases were somewhat larger. Both appeared to have only slight effect on CER during the first 60 seconds. We found that if chamber measurements were kept under 2 min and chamber conditions remained close to ambient, linear curves provided a good fit for CO_2 flux data. In cases where quadratic relationships occur, other approaches for analysis are available, and are discussed elsewhere (Reicosky et al. 1990). Cloud cover changes are always a problem, however if the measurement is split into more than 1 observation, cloud effects can be delineated. The chamber is sufficiently portable that 2 persons equipped with an ATV and trailer can easily set up and take a measurement within 10 minutes, even in remote areas. This arrangement allows wide separation of plots for treatment comparisons or characterization of spatial variation. The chamber we have described is easy to use, relatively inexpensive, and adaptable to a wide range of field conditions.

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Aerial films and solar angles: Influences on silver sagebrush inventory

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Abstract

Aerial photos in Alberta are generally acquired according to topographic mapping and forestry specifications. The parameters for interpreting rangeland vegetation, such as silver sagebrush (*Artemisia cana*-Pursch), need to be explored and condensed into an operational specification. Five aerial films and 3 solar angles were evaluated by 7 photo interpreters to determine the optimal conditions for interpreting silver sagebrush at a scale of 1:20,000. Interpreter accuracy and preference are determined for the 2 experimental conditions as to determine operational specifications. Kodak Panatomic-X 2412 achieved the highest interpretation accuracies for silver sagebrush cover detection and plant density estimation (91.0% and 94.4% respectively), while Kodak Aerochrome Infrared 2443 and Agfa Avicolor H100 performed best for estimating plant vigor (92.7% and 93.7% respectively). Photo interpreters also chose Kodak Panatomic-X 2412 as the preferred film for interpreting silver sagebrush (7.7 on a scale of 10). Positive correlations were obtained between combinations of interpretation accuracy, interpreter film preference and photographic density range measurements, indicating the trends for higher accuracy and preference are associated with higher density ranges. Solar angles of 20°, 37° and 54° were evaluated by photo interpreters with significant preference shown for 20˚. Recommendations for modifying Alberta's air photo operational specifications to include high resolution (Kodak Panatomic-X) imagery and decreasing the acceptable lower boundary for the operational solar angle from 30 to 20° for interpreting silver sagebrush at the 1:20 000 scale are proposed.

Key Words: Aerial photography, spectral sensitivity, film resolution, air photo specifications, air photo, interpretation

Resumen

Las fotografís aéreas en Alberta son generalmente adquiridas de acuerdo al mapeo topográfico y especificaciones forestales. Los parametros para interpretar la vegetación de pastizal, tal como "silver sagebrush" (*Artemisia cana* - Pursch), necesitan ser explorados y condensados en una especificación operacional. 7 fotointerpretadores evaluaron 5 tipos de pelíula area y 3 ángulos solares para determinar las condiciones óptimas para interpretar el "silver sagebrush" a una escala de 1:20,000. La exactitud y preferencia del interpretador son determinadas para las dos condiciones experimentales, así como para determinar la especificaciones operacionales. La película Kodak Panatomic-X 2412 logró la mayor exactitud de interpretación para la detección de la cobertura y densidad de plantas de "silver sagebrush" (91.0% y 94.4% respectivamente), en tanto Kodak Aerochrome Infrared 2443 y Agfa Avicolor H100 fueron mejores para estimar el vigor de la planta (97.2% y 93.7% respectivamente). Los fotointerpretadores también escogieron la película Kodak Panatomic- X 241 como la mejor para interpretar el "silver sagebrush" (7.7 en base a una escala de 10). Se obtuvieron correlaciones positivas entre combinaciones de exactitud de intrepretación , perferencia del tipo de película del fotointerpretador y las medidas del rango de densidad fortográfica, indicando las tendencias que una mayor exactitud y preferencia estan asociadas con los rangos de densidad mayores. Los ángulos solares de 20°, 37° y 54° fueron evaluados por los fotointerpretadores los cuales tuvieron una preferencia por el ángulo de 20°. Se proponen recomendaciones para modificar las especificaciones operacionales de la fotografía area de Alberta para incluir imagnes de alta resolución (Kodak Panatomic-X) y disminuir de 30° a 20° el límite inferior operacional del ángulo solar para interpretar "silver sagebrush" en la escala de 1:20,000. mentaron en promedio 0.5 y 1.2°C respectivamente.

Silver sagebrush (*Artemisia cana*-Pursch) has a ubiquitous presence on the Great Plains of North America. Its occurrence has led to strategies ranging from eradication to conservation and protection. It is a common native shrub, characteristic of the dry mixed grass natural region of Alberta (Achuff 1994). It also defines the habitat conditions for a range of wildlife species such as pronghorn antelope (*Antilocarpa americana*) and sage grouse (*Centrocercus urophasianus*) (Mitchell and Smoliak 1971, Wallestad 1976, Glaholt 1984, Kerley and Anderson 1995).

Silver sagebrush is a short shrub with typical heights around 0.25 to 0.75 m, but heights of 1.0 to 1.5 m are not

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uncommon in ideal soil moisture conditions. It tends to grow in mesic sites where it is often found in fairly dense distributions. The presence and abundance of silver sagebrush can reduce the production of associated grasses and forbes (White and Currie 1983, 1984). The shrub is also commonly found in low lying level, poorly drained clay soils and saline areas (Smoliak et al. 1981). In Alberta, it is frequently associated with the Orion (ORN) soil series (Contract Pedology-Lethbridge, personal communication, 1997), and is also the dominant species of sagebrush flats (Wershler and Wallis 1986). Silver sagebrush can usually be identified by its distinctive light blue-green and silvery hue that contrasts sharply among the greener or yellow-brown grasses and shrubs (depending on the moisture situation) on the prairie landscape (Wilkinson 1990).

The interest in the plant, whether for wildlife habitat preservation or for agricultural efficiency, has led investigators to explore various means for identifying and mapping its distribution on rangelands. Aerial photographs remain the most used and the highest resolution product able to capture the spatial and textural characteristics of the scene (Tueller 1989, Driscoll 1992). Although aerial photographs remain the traditional remote sensing tool, the technology associated with it has not been stagnant. Improvements in films, cameras, and lens have been particularly vigorous over the past 10 years (Fent 1990, Bahnmüller 1992, Fent and Brouwer 1993, Mussio and Light 1995, Light 1996).

The application of these advancements and innovations in aerial photography have been investigated to some degree in forestry (Hall and Fent 1991, Fent et al. 1995), however, specific details in optimizing aerial photographic product performance for identifying silver sagebrush (and for other rangeland applications) have been limited to large scale photographic studies (Nesby 1986, Werth and Work 1991). In addition to the spectral influences of aerial films in detecting silver sagebrush, other photographic variables will also impact the shrub's photographic recording identity. Image contrast, varied either photographically or by solar angle, has a major effect upon the quality of photo interpretation (Welch and Halliday 1975). Furthermore, human preference for specific film or contrast may also be an influencing factor in air photo interpretation (Hall and Fent 1991).

The objective of this study was to investigate whether 2 photographic variables, film type and contrast change associated with different solar angles, are factors in detecting and classifying silver sagebrush distributions. The study objective was addressed by the following 3 questions: is there a film type that leads to greater accuracies in interpreting silver sagebrush; is there a film type that is more preferred by interpreters for interpreting silver sagebrush, and; is solar angle a factor for air photo interpretation of silver sagebrush?

Study Area

The study area is located in Township 1 Range 2 west of 4 meridian in the southeast corner of the province of Alberta and adjacent to Montana (National Topographic System map sheets 72 E/1). It is located within the Dry Mixed Grass Ecoregion (Strong and Leggat 1981). A north-south 12 km flight line was flown along Sage Creek to capture a wide diversity in silver sagebrush distribution, density, and vigor.

Materials and Methods

Aerial Photography

The 5 aerial films[1] selected are described in Table 1 (Agfa-Gevaert 1990a, 1990b; Eastman Kodak 1992). The Kodak Aerographic Infrared 2424 (BWIR) is a near-infrared sensitive aerial film with a spectral sensitivity extending to approximately 900 nm. Agfa Aviphot Pan 50 (A50) and Kodak Panatomic 2412 (PANX) are classed as extended red sensitivity films with spectral sensitivities extending to approximately 750 and 720 nm, respectively (Table 1). The Agfa Avicolor H100 (H100) is a true color film manufactured by Agfa while the Kodak Aerochrome Infrared 2443 (CIR) is a standard false color infrared film manufactured by Kodak. Table 1 also outlines the spatial resolution of the aerial films; PANX and A50 are regarded as high resolution films while the other emulsions are general purpose films.

The aerial photography was acquired at 2 separate times. The first acquisition occurred on 14 July 1996 with all films flown at a scale of 1:20 000. The 5 films were flown and exposed with a forward motion compensation (FMC) equipped metric aerial camera (Zeiss Jena) and with minimal rate change in the solar angle (54˚ ± 1˚). Processing was conducted with the same processor (Kodak Versamat II) and chemicals (Kodak 885) for the black-and-white films. The color films were processed in their own respective processing environments (EA-5 for CIR and C-41 in high color saturation mode for H100). The contrast of the black-and-white films was further controlled sensitometrically by processing all the films to an average gradient of 1.40[2] and printing the negatives on grade 3 paper. The CIR film was sensitometrically evaluated to determine its IR balance value (Fleming 1979) and exposed such that an IR balance of 28 was achieved to compensate for altitude and inherent infrared film sensitivity. All films except the H100 were exposed with a minus blue (500 nm) cutoff filter to reduce haze effects, the H100 was exposed with a 420 nm haze compensating filter. These considerations served to reduce the effect of image motion, variable contrast, and film processing that would otherwise mask the differences among films and affect interpretation accuracies.

[1]The mention of trade names does not imply endorsement by the author.

[2]Average gradient (G) defines the ratio of the brightness range of objects photographed on the ground and the photographic density measured on the negative (International Standards Organization 7249, 1986). A brightness range to density ratio of 1:1 equals an average gradient of 1.0. An average gradient of 1.4, therefore, indicates that the photographic contrast (or density range) was enhanced by 40% relative to the ground contrast.

Table 1. Aerial films investigated and some defining characteristics.

Films	Type	Abbreviation	Film Resolution (lp/mm)	Spectral sensitivity (nm)
Kodak Infrared Aerographic 2424	black and white	BWIR	50	900
Agfa Aviphot Pan 50	black and white	A50	81	750
Kodak Panatomic Aerographic II 2412	black and white	PANX	125	720
Agfa Avicolor H 100	color	H100	40	670
Kodak Aerochrome Infrared 2443	color	CIR	32	900

The second air photo acquisition phase occurred on 8 July 1997 using the same camera and scale. The best performing film from the phase 1 analysis (PANX) was flown at 3 distinct solar angle conditions, 20˚ ± 0.5˚, 37˚ ± 0.5˚, and 54˚ ± 0.5˚, providing 3 unique solar angle contrast conditions to evaluate. The average gradient (1.40) and paper grade (3) were controlled to isolate the contrast changes due to solar angle. The 2 phase experimental design was deemed necessary to adequately control the continuously changing environmental light conditions.

Interpretation Procedure

Thirty-two polygons were selectively chosen along the flight path and among the different films for the interpretation procedure. The polygons varied in silver sagebrush coverage, density and vigor. This ensured each film type was represented by different polygons, and prevented photo interpreters interpreting the same stand more than once. Seven interpreters from various government and private agencies familiar with rangeland photo interpretation participated in the first phase of the study. The interpreters were asked to identify silver sagebrush for each of the polygons outlined on the aerial photographs by primarily noting the percentage of sagebrush covering the polygon and also stratifying the cover by density (in stems/ha) and plant vigor. Each of these 3 attributes were classed in 6 percentage intervals; the interpreter was asked to choose which of the 6 classes best represented the attribute in question (Table 2). The interpreters were provided with a photo interpretation key of silver sagebrush at a 1:20 000 scale as means to train themselves in recognizing the various silver sagebrush attributes. The ground reference information was obtained from field surveys of each of the 32 chosen polygons (used to determine vigor qualities) and from 35 mm reconnaissance photographs taken from a helicopter at a scale of 1:500 (use to determine density and ground cover percentage). The ground reference information was also categorized using classes described in Table 2.

Data compilation and statistical analysis

Interpretation accuracy was determined by calculating the difference between the interpreters' interpretation class of an attribute and the ground reference class. The difference indicated the number of classes the interpreter deviated from the ground truth (Fent et al. 1995). Since each of these classes were approximately 16.7%, an interpretation accuracy value (A_i) could be calculated by the following formula:

$$A_i = 100 - ((|I_i - G_i|)\ 16.7)$$

where

I_i = Interpreted class value
G_i = Ground reference class value

The 7 photo interpreters, interpreting 3 cover attributes, for 32 polygons created a database of 672 accuracy values which were then stratified by film type. A one-way analysis of variance (ANOVA) was conducted on the balanced data set (Table 3) and the Tukey multiple means comparison (SAS Institute 1985, Neter et al. 1990) was employed to determine if there were significant differences among the films (Table 4).

Interpreters were also asked to rank each of the film combinations for preference on a scale of 1 to 10 with the high score indicating high preference. The preference values were averaged and ranked, and associated to film interpretation accuracy and density range rankings. The ranks were analyzed using Spearman's Rank Correlation Coefficient (r_s) (Mosteller and Rourke 1973).The phase 2 data compilation required interpreters to rank the PANX flown at the 3 different solar angles. Five additional interpreters (total 13) participated in this process and the results were compared and analyzed for statistical significance using the Friedman Statistic (χ^2_r) (Mosteller and Rourke 1973) .

Results and Discussions

Interpretation Accuracy

The first question of this study was to determine which of the 5 films performed best when silver sagebrush cover, density, and vigor were interpreted. PANX was the highest performing film for interpreting silver sagebrush ground cover and density (Table 4), while the color films performed best when interpreting vigor (Table 4). PANX is distinguished from the other films by its superior resolution and apparently aids the interpreter in detecting and assessing the distribution of silver sagebrush. The relatively small scale (1:20 000) of the interpre-

Table 2. Silver sagebrush attributes that interpreters were requested for each of the 32 polygons.

Coverage Class	Density Classes (stems/hectare)	Vigor Classes
0 = no sagebrush	0 = no sagebrush	0 = no sagebrush
1 = 1–20%	1 = ≤ 500	1 = dead
2 = 21–40%	2 = 501–1000	2 = poor
3 = 41–60%	3 = 1001–2000	3 = average
4 = 61–80%	4 = 2001–4000	4 = good
5 = 81–100%	5 = ≥ 4001	5 = excellent

Table 3. Analysis of variance table for the films evaluated.

Dependent variable	Source	Degrees of Freedom	F value	Pr > F
Coverage	Film	4	26.61	0.0001
Density	Film	4	39.76	0.0001
Vigor	Film	4	20.71	0.0001

tation images may also favor a high resolving film such as PANX in detecting a small shrub such as silver sagebrush. The increase in interpretation accuracy associated with PANX is also noted in applications associated with forestry and photogrammetry (Becker 1988, Fent et al. 1995, Hall and Fent 1996). The higher results produced by CIR and H100 for interpreting plant vigor (Table 4) were not unexpected given the phenological properties of the plant in mid-summer. The vigor attribute is highly dependent on the plant's leaf reflective properties which are at optimum condition during the growing season (White and Currie 1984). Films that add a color dimension, such as the CIR and H100 have an inherent advantage over the black-and-white films in portraying hue differences. Moreover, a film such as CIR that has both color and infrared sensitivity, will have an added advantage over other films in detecting plant health attributes. The overall results suggest that PANX is the best film for assessing quantity attributes while the color films are better tools for assessing quality attributes.

Table 4. Tukey's Studentized Range Test* film results. Means with the same letter are not significantly different.

Variable	Tukey Grouping	Mean	Film
Coverage	A	91.0	PANX
	A B	86.9	A50
	B	85.4	CIR
	C	78.3	H100
	C	77.7	BWIR
Density	A	94.9	PANX
	A	91.0	A50
	B	80.2	CIR
	B	79.1	BWIR
	C	69.5	H100
Vigor	A	93.7	H100
	A	92.7	CIR
	B	85.2	PANX
	B	84.4	BWIR
	C	78.1	A50

*Significance at 0.05 level

Interpreter Film Preference

The second question in this study was to determine whether interpreter preference differed among the film types. The most preferred film was PANX, with the A50 and CIR also showing relatively high preference as noted by the 95% confidence interval bars in Figure 1. The least preferred films were the H100 and the BWIR. These results suggest that the superior resolution characteristics of PANX and A50 (125 and 80 lp/mm, respectively) are an important factor in the interpreter's assessment of 'good' quality or ease of interpreting sagebrush. In addition, slower speed and sharper films tend to have more contrast giving a further impression of sharpness and increased subjective preference (Pfenninger 1984). Although the resolution quality of CIR is relatively low, this film's higher ranking was most likely associated with its infrared sensing and color rendition qualities. It should be noted, however, that this film also showed the greatest ranking variation as indicated by the 95% confidence interval bars in Figure 1. The H100, although a color film, may be disadvantaged at a scale of 1:20 000 because of poor haze penetration abilities, while other films fare better in this regard due to either haze filtration or infrared sensitive properties. Haze will reduce contrast, detail, and apparent sharpness in aerial photographs leading to a lower preference rating.

BWIR's poor ranking may be associated with the phenology of silver sagebrush plant relative to the general reflective character of its immediate environment. The reflective characteristics of the light green-silvery hues of the leaves are an atypical feature of this plant and show a gradual and quasi-linear increase from the blue to the infrared portion of the electromagnetic spectrum (Tueller 1989). Most vegetation shows a defined 'red edge' where the infrared reflective portion is abruptly higher than the visible reflective component (Brandes 1994). It is this contrast between the visible and the infrared reflective character of plants that aids photo interpreters in identifying vegetative characteristics. In silver sagebrush, this marked difference is subdued and further reduced because the near infrared reflective character of the surrounding grasses is relatively low, especially when they are in the maturity stage or under water stress. The lack of spectral contrast among ground vegetation, the relatively lower resolution of the film, and the lack of color (CIR's advantage) all may be factors associated with BWIR's perceived non-utility in silver sagebrush interpretation.

Accuracy-Preference-Density Range

The photographic density range of an image is a good indicator of the image's contrast. The density range of the experimental film images will vary because image contrast in this experiment is being determined exclusively by the films' spectral attributes. These contrast differences provide further evidence for deciphering the film accuracy and preference results. Spearman's Rank correlation results (Table 5) indicate a positive ($r_s = 0.90$) and significant ($P < 0.05$) trend between density range and preference. Density range and accuracy correlations were also positive ($r_s = 0.80$) but insignificant ($P > 0.10$). Positive and significant correlations were, however, noted between interpreter preference and accuracy ($r_s = 0.90$, $P < 0.05$). These correlated trends suggest that interpreters are noting contrast as an interpretation aid influencing both interpreter preference and accuracy. Contrast variations in this experiment were attributable to the spectral differences between films; however, defining an ideal contrast requires that average gradient and paper grade variables also be investigated and related to the density range parameter.

Solar Angle Contrast

The third question in this study was to investigate whether solar angle was a factor in the interpretation of silver sagebrush. Interpreter assessments showed a highly significant preference (P<0.01) for the images flown at a solar angle of 20˚±0.5˚ followed by the 37˚±0.5˚ and the 54˚±0.5˚images (Fig. 2). The enhanced contrast resulting from longer shadows accentuates the vegetative and topographic ground pattern and allows the interpreter a better textural context for identifying silver sagebrush distribution. The shadow information also provides the interpreter with cues on appraising shrub height that would not be photogrammetrically possible given the minimal image displacement at the scale of the photo. The solar angle photo samples in Figure 3 depict this effect.The relatively low solar angle preferred by the interpreters, however, should be considered with some degree of caution. The topographic character of the landscape may be a factor in obscuring land detail where slopes greater than 20˚ are encountered and the practicalities of flying with such a restricted solar angle may not be economically feasible. In essence, the decision to fly at lower solar angles should acknowledge the enhancements of textural and topographic detail, but be wary of both the length of time required to fly the project and the terrain morphology.

Conclusion

The results of this study indicate that, at a scale of 1:20 000, PANX film (G=1.40) flown at relatively low sun angles provides the best results for interpreting silver sagebrush cover and density, with color films showing an advantage for interpreting plant vigor. These findings suggest that a modification in air photo specifications for rangeland applications, silver sagebrush inventory in particular, may be warranted in Alberta.

The recommended use of PANX, implies that higher spatial resolution and contrast, rather than spectral sensitivity, is the key factor in detecting

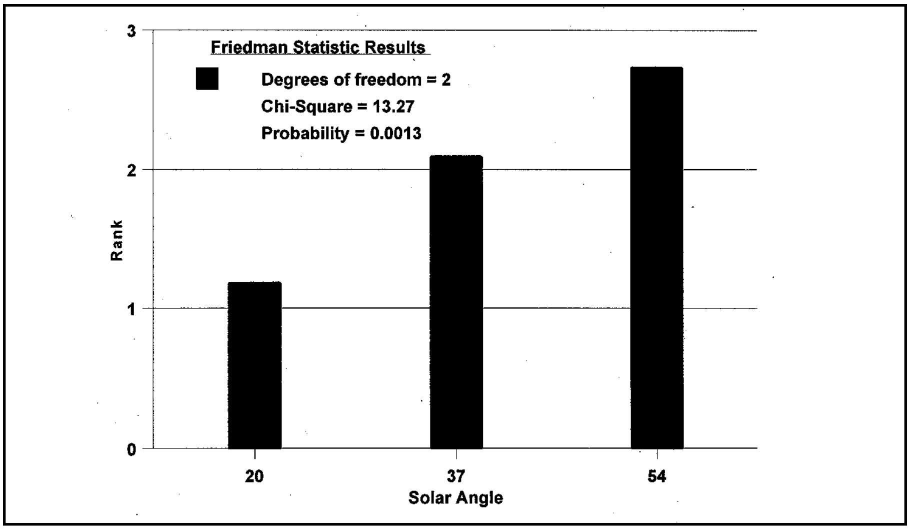

Fig. 1. Mean interpreter preference ranks with 95% confidence intervals the higher resolving films (PANX, A50) is indicated. CIR also shows relatively high preference but with more variation (less agreement among interpreters).

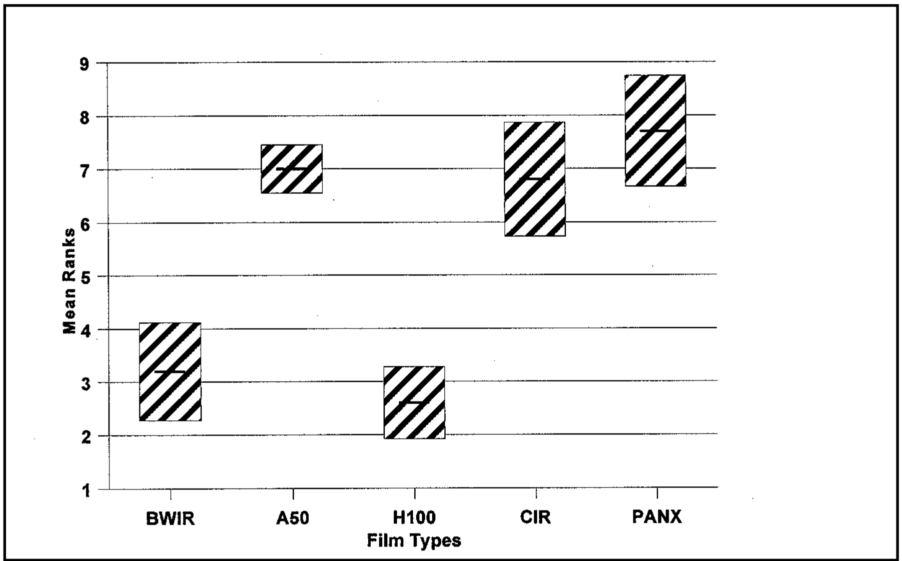

Fig. 2. Mean interpreter preference ranks of the PANX flown at the 3 different solar angles. The highly significant results (P < 0.01) indicate that interpreter preference increases as the solar angle decreases.

Table 5. Values for interpretation accuracy[1], preference and density range[2] are ranked and analyzed[3] for each film type.

Film	Preference		Interpretation accuracy		Density range	
	Value	Rank	Value	Rank	Value	Rank
BWIR	3.2	4	78.2	5	0.30	4
A50	7.0	2	81.1	3	0.54	3
PANX	7.7	1	90.4	1	0.76	1
H100	2.6	5	80.5	4	0.18	5
CIR	6.8	3	86.7	2	0.68	2

[1]Mean of the cover, density, and vigor accuracy values for each film
[2]Status M densiometry, visual filtration (1mm aperature)
[3]Spearman's Correlation Coefficients:

Preference X Interp. accuracy	r_S=0.90	Pr=0.0374
Preference X Density range	r_S=0.90	Pr=0.0374
Interp accurancy X Density range	r_S=0.80	Pr=0.1041

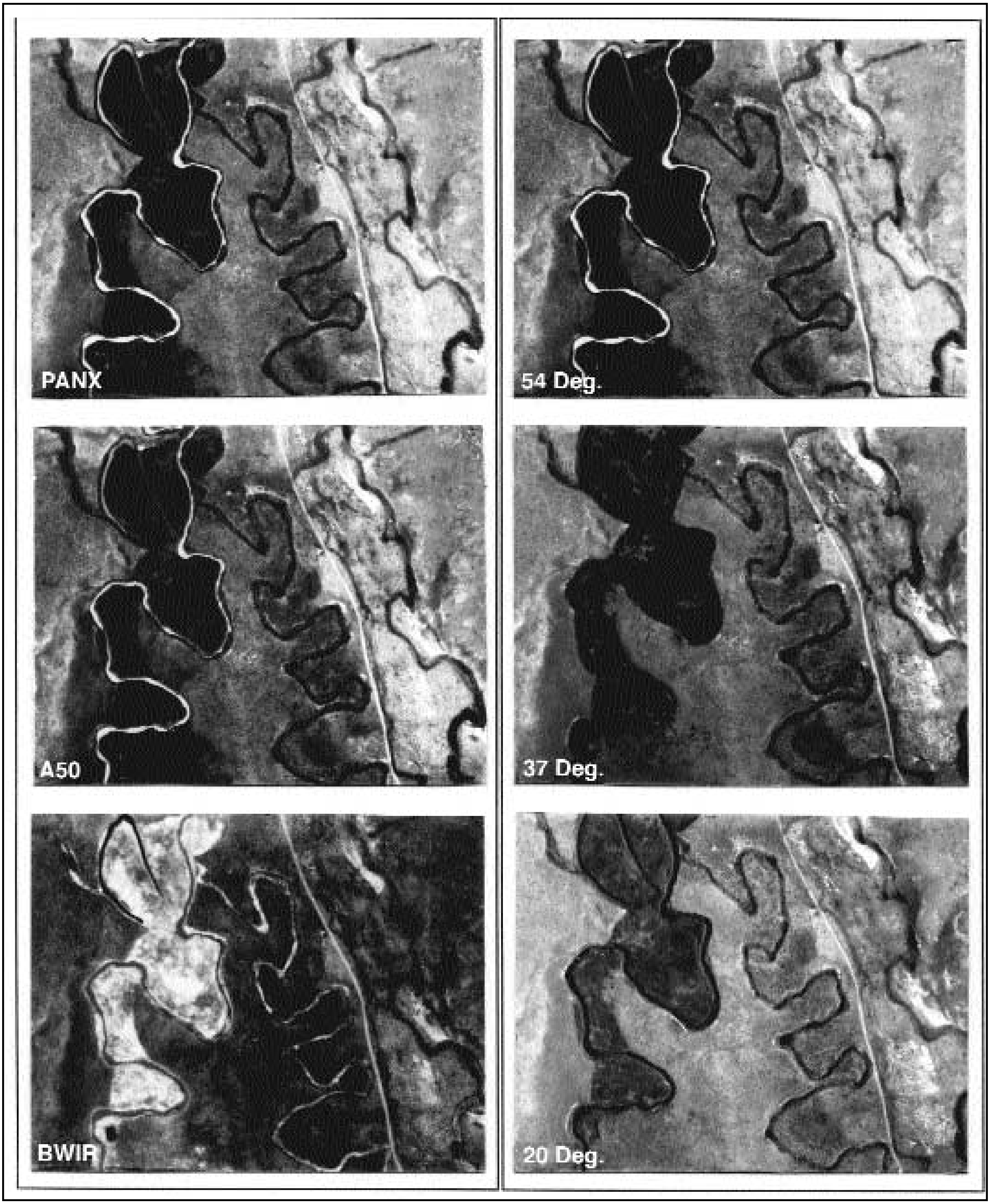

Fig. 3. A part of the study area as depicted by the 3 black-and-white films (left) and the 3 solar angle conditions using PANX (right). Significant occurrences of silver sagebrush are located along the dry creek bed along the center of the photos. The 20° solar angle condition is the only instance where the textural detail is sufficiently enhanced to show individual stands of silver sagebrush.

silver sagebrush at a scale of 1:20 000. Because this film is relatively low in sensitivity (40 ISO A), image motion effects must be addressed.

FMC cameras, thus, become essential in exploiting the film's resolution characteristics.

The interpreter preference for a lower solar angle needs to be implemented carefully. Adopting a lower solar angle would entail a change from the minimum current value in Alberta of 30˚ to about 20˚. Values lower than 20˚ would be impractical because of extreme shadows and low lighting conditions (especially when PANX is considered). The maximum value is defined only in that it should be below the second most preferred experimental level of 37˚±0.5˚. A working range of 20˚ to 35˚, with the understanding that the higher end values will diminish interpretability and lower end values may obscure some slope information is suggested. The operational range cannot be too narrow otherwise flying time is compromised.

The results and recommendations proposed suggest a modification in acquiring aerial photography for rangeland applications, or at least a consideration of the factors that will aid vegetation interpretation in prairie environments when relatively small scales are used. Optimizing these photographic factors should lead to more accurate initial stratifications of vegetation and more efficient methods for inventories of silver sagebrush.

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Sheep preference for leafy spurge from Idaho and North Dakota

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Abstract

Three trials were conducted to determine if low ingestion of some leafy spurge (*Euphorbia esula* L.) by sheep is primarily due to differences in sheep or in leafy spurge. In the first trial, pastures in Idaho and North Dakota were grazed by sheep originating from both states. Generally, sheep from both states grazed the leafy spurge growing in the Idaho pastures reluctantly but grazed the leafy spurge growing in the North Dakota pastures in proportion to its availability ($P = 0.003$). In the second trial, ingestion of air-dried leafy spurge by penned sheep was compared by offering samples from the 2 locations simultaneously. Sheep consumed more ($P = 0.0001$) leafy spurge from North Dakota than from Idaho. In the third trial, penned sheep were simultaneously offered Idaho leafy spurge harvested from fertilized and non-fertilized sites. Initially, equal amounts of fertilized and unfertilized leafy spurge were consumed ($P \geq .68$), but by the fourth day sheep had an obvious preference for leafy spurge from the fertilized site ($P = 0.01$). These trials indicate that preference for leafy spurge by sheep differs depending on site, and that using sheep to manage leafy spurge may be more successful on soils with relatively high fertility.

Key Words: diet selection, palatability, noxious weeds, *Euphorbia esula*

Resumen

Con el objeto de determinar si la baja ingestión de “leafy spurge” (*Euphorbia esula* L.) por parte de ovinos es debida principalmente a diferencias en ovinos o en “leafy spurge” se realizaron tres ensayos. En el primer ensayo, pasturas de Idaho (ID) y de Dakota del Norte (ND) fueron pastoreadas por ovinos originarios de ambos estados. En general, ovinos de ambos estados pastorearon renuentemente “leafy spurge” que creció en las pasturas de ID pero pastorearon “leafy spurge” que creció en las pasturas de ND en proporción a su disponibilidad ($P = 0.003$). En el segundo ensayo, se comparó la ingestión de “leafy spurge”, secada en corriente de aire forzado, por parte de ovinos en corrales que recibieron muestras de los dos lugares simultaneamente. Ovinos consumieron mas ($P = 0.0001$) “leafy spurge” originaria de ND que “leafy spurge” originaria de ID. En el tercer ensayo, ovinos en corrales recibieron una oferta simultanea de “leafy spurge” originaria de ID cosechada en lugares fertilizados y no fertilizados. Inicialmente fueron consumidas cantidades iguales de “leafy spurge” fertilizada y no fertilizada ($P \geq .68$), pero al cuarto dia los ovinos tuvieron una obvia preferencia por “leafy spurge” proveniente del lugar fertilizado ($P = 0.01$). Estos ensayos indican que la preferencia por “leafy spurge” en ovinos difiere dependiendo del sitio de establecimiento, y que el uso de ovinos para el manejo de “leafy spurge” puede ser mas exitoso en suelos con relativamente alta fertilidad.

Sheep and goats are used to help control and utilize the weed leafy spurge (*Euphorbia esula* L.) in many western states and Canadian provinces (Johnston and Peake 1960, Landgraf et al. 1984, Bartz et al. 1985, Faller et al. 1995). However, we have observed that the palatability of leafy spurge to sheep may vary among range sites. This could result from differences among animals, from differences in the environments where leafy spurge grows, from different plant phenotypes and chemical contents, or perhaps from interactions among these factors.

Several factors may account for differences in animal preference for leafy spurge. These include degree of previous experience with leafy spurge (Walker et al. 1992, Olson et al. 1995), whether individuals were exposed to leafy spurge when young or as adults (Squibb et al. 1990, Provenza et al. 1992), genotypic and consequently physiological differences among individual animals (Provenza 1995), and differences in the relative palatability of alternative vegetation to the animals. In a paired-choice study, goats preferred leafy spurge when it was offered with arrowleaf balsamroot (*Balsamorhiza sagittata* (Pursh) Nutt.) but preferred crested wheatgrass (*Agropyron crista-*

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tum (L.) Gaertn.) when it was offered with leafy spurge; sheep preferred both of these alternative plants when they were paired with leafy spurge. In southeastern Idaho, goats showed a relative preference for grazing leafy spurge while sheep avoided this plant (Walker et al. 1994).

Leafy spurge can elicit aversive feeding responses in cattle, sheep, and goats. This, response was strongest in cattle and weakest in goats with sheep intermediate (Kronberg et al. 1993, 1994). Also, individual sheep and goats vary in their tolerance for the aversive chemical(s) in leafy spurge (Kronberg and Walker, unpublished data).

Levels of aversive and other defensive phytochemicals can vary within a plant species as a function of soil fertility and shading (Bryant et al. 1983, 1991, Mihaliak and Lincoln 1985, Mihaliak et al. 1987, Fajer et al. 1992, Ruohomki et al. 1996). Carbon-based phytochemicals tend to occur at higher concentrations in plants that grow in infertile soils. Additionally, plant/water relations can affect levels of defensive phytochemicals (Briske and Camp 1982, Vrieling et al. 1993). Variability in phytochemical concentration can also have a genetic component (Fajer et al. 1992, Vrieling et al. 1993, Ruohomki et al. 1996). Leafy spurge has considerable genetic variability (Nissen et al. 1992); however, chloroplast DNA analysis of leafy spurge from our Idaho study site indicated that this leafy spurge is genetically similar to leafy spurge collected in North and South Dakota and Nebraska (Nissen, personal communication).

We conducted 3 trials to elucidate aspects of sheep response to leafy spurge. The overall objective of these trials was to determine if preference for leafy spurge differs because of sheep origin and (or) site location.

Material and Methods

Trial 1

A grazing trial was conducted to determine if relative preference by sheep for leafy spurge differed in Idaho and North Dakota. The trial was conducted on leafy spurge-infested pastures near Dubois, Ida. and Bismark, N.D. The Idaho pastures were 17 km northwest of Dubois (112˚ 22'W, 44˚ 15'N) on stream terrace near Medicine Lodge Creek. The North Dakota pastures were 6 km south of Bismark (100˚48'W, 46˚ 45'N) on bottomland beside the Missouri River. The alternative forages were primarily crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.) in Idaho and smooth brome (*Bromus inermis* Leyss.) in North Dakota. The trial was designed to test for differences in leafy spurge utilization and preference with the main effects of location (Idaho and North Dakota) and origin of sheep (Idaho and North Dakota). Ten yearling non-lactating female sheep from each state were placed on small, leafy spurge-infested pastures in southeastern Idaho and central North Dakota. All sheep had previous experience grazing leafy spurge in their state of origin before the trial began. All sheep grazed the Idaho pastures in early June then these sheep were transported to North Dakota where they grazed the pastures in mid-June.

At each location, 4 replicate pastures were grazed by sheep from Idaho and 4 were grazed by sheep from North Dakota. Sheep from the 2 states were pastured separately. Pasture size was 20 × 40 m in Idaho and 20 × 20 m in North Dakota. Five sheep were grazed in each pasture for 4 days in Idaho and 5 days in North Dakota. Four pastures (2 per origin of sheep) were grazed first until approximately 50% of the total standing crop was consumed, then the sheep were moved to the next set of 4 pastures. This design helped ensure that the number of sheep in each pasture was adequate for normal behavior while providing sufficient pasture replication to detect treatment effects.

The soil at the Idaho site was a gravelly loam and the soil at the North Dakota site was a sandy loam. Soil analysis was conducted by the Soil Testing and Plant Analysis Laboratory at South Dakota State University following their standard procedures (1995). The characteristics of these soils are described in Table 1.

Table 1. Soil characteristics at the Idaho and North Dakota sites where Trial 1 was conducted.

	Location	
	Idaho	North Dakota
	-----------(ppm)-----------	
NO_3-N (0-1.0)	0.79	1.3
P (0-0.9m)	24	2
K (0-0.9m)	156	159
	--------------(%)-----------	
Rock fragments (>2mm)	25-70	0.00

Standing crop was measured by clipping 5 randomly located 0.5 m^2 plots in each pasture at the beginning, middle and end of grazing. The number of grazed and non-grazed spurge stems were counted in 10 permanently marked, randomly located 0.25 m^2 plots per pasture at the beginning, middle and end of grazing. Percent utilization of leafy spurge stems was analyzed with the GLM procedure of SAS (1988) using a repeated measures design. The main effects were sheep origin and trial location (between experimental unit effects). Time of stem counting during the grazing period (middle and end) for each pasture was the repeated measure. The 4 replicate pastures were the experimental units and individual plot data were averaged for each pasture before statistical analysis.

Diet selection by sheep in each pasture was determined using the bite count technique and electronic data loggers (Sanders et al. 1980, Walker et al. 1992). All animals were observed while grazing using a focal animal sampling procedure (Altman 1974). Observations lasted 3 minutes per animal and multiple observations were made on each animal with the restriction that each animal in a pasture was observed once before an animal was observed another time. One observer recorded bites in each pasture. Bites were classified as leafy spurge, other forb, grass, or shrub. Bite count data were collected at the beginning and middle of the grazing time for each pasture but not at the end because we were interested in determining the extent to which the sheep would select leafy spurge when alternative vegetation was still available. Multiple observations for each animal at each time period (beginning and middle) in a pasture were averaged and then means for each animal by time period across pastures were calculated before further analysis. Bite count data were summarized in this manner because of missing data resulting from difficulties in observing sheep and some equipment malfunction. Because of missing data, bite count data were analyzed using individual sheep as experimental units. Preference for different forage classes was calculated as the difference between the percent of a class in the diet and the percent of that class in the available herbage (Strauss 1979). This is a normally distributed linear index with a range of preference and avoidance from +100 to –100 centered on 0 (for random feeding). Bite count data were analyzed with the GLM procedure of SAS (1988) for the main effects of sheep origin, trial location, time during grazing period and their interactions. Origin of sheep was a between animal effect while trial location and period of trial were within animal repeated measures.

Leafy spurge used for nutritional analysis for all trials was dried and ground to pass a 1-mm screen before analysis for Kjeldahl N (AOAC 1990) and nonsequential neutral detergent fiber (NDF) and acid detergent fiber (ADF) (Goering and Van Soest 1970). The percentages of crude protein (CP), NDF and ADF in samples are expressed on a dry matter basis.

Trial 2

This trial was conducted in pens with leafy spurge harvested from near the Idaho and North Dakota sites for Trial 1. A different group of sheep were used from those used in the first trial. Leafy spurge was in seed-ripening and seed-ripe growth stages when harvested at both sites and was air-dried and chopped to about 2-cm-long pieces.

During a 3-day pre-trial period, 8 adult white-faced wethers from Idaho were placed in individual pens (ca. 1.5 m^2) and offered water 24 hours • day^{-1} and alfalfa pellets between 0800 and 1800 hours in 2 adjacent feed boxes in each pen. The wethers had no previous experience with leafy spurge. Following the pre-trial period, consumption of Idaho and North Dakota leafy spurge by each wether was measured in a 2-day trial by placing leafy spurge from each state into the 2 adjacent feed boxes in each pen. Placement of the Idaho and North Dakota leafy spurge into the feed boxes was reversed on the second day of the trial. During the trial, the sheep had ad libitum access to water and were allowed to eat as much of the 2 leafy spurge types as they desired from 0800 to 1800 hours each day. They only had leafy spurge to eat during this trial. Intakes of the 2 leafy spurge types were compared by repeated measures analysis of variance (SAS 1988) with origin of leafy spurge a between animal effect and day of trial a within animal repeated measure.

Trial 3

The third trial was a pen trial in which sheep were offered Idaho leafy spurge that grew from soil that was or was not fertilized. In April, before the growing season began, a 500 m^2 area of leafy spurge-infested land was fertilized at the Idaho site (described by Walker et al. 1994). The site was fertilized at a rate of 300 kg • ha^{-1} with a mixture composed of 24% urea nitrogen (4.2% of this was coated slow-release nitrogen), 4% ammonia nitrate, 4% phosphoric acid, 8% soluble potash (K_20), 4% sulfur and 1% iron. Three months after the area was fertilized, leafy spurge was harvested from the site when it was primarily in seed-ripening and seed-ripe growth stages. Leafy spurge from an adjacent but unfertilized area with similar soil was also harvested at this time. Leafy spurge from both the fertilized and unfertilized sites was air-dried and chopped to 2-cm-long pieces.

In a 5-day pre-trial period, 10 weaned lambs with no previous exposure to leafy spurge were trained to eat alfalfa pellets from 2 adjacent feed boxes in individual (1.5 m^2) pens. During the 4-day trial period, lambs were placed in individual pens between 0800 and 1600 hours and each lamb's consumption of fertilized and unfertilized leafy spurge was measured. The location of the 2 leafy spurge types was alternated between left and right feed boxes. During the test period, the sheep had ad libitum access to water and were allowed to eat as much of the 2 leafy spurge types as they desired from 0800 until 1600 hours each day. They were offered only leafy spurge to eat during the trial period. Intakes of the 2 leafy spurge types were compared over days by repeated measures analysis of variance (SAS 1988).

Results and Discussion

Trial 1

When grazing began, grass comprised 61 and 74% of the standing crop in Idaho and North Dakota, respectively, whereas leafy spurge represented 30 and 24% of the standing crop in Idaho and North Dakota, respectively. Percent of leafy spurge stems grazed (Fig. 1) differed between locations ($P = 0.002$), period of trial ($P = 0.0001$), and the location $\times$ origin of sheep interaction was significant ($P = 0.06$). Sheep origin did not affect percent of leafy spurge stems grazed ($P = 0.33$), and all other interactions were not significant ($P > 0.20$). The effect of period (first half vs. second half) was simply an indication that utilization of leafy spurge increased as the trial progressed. The location x origin of sheep interaction ($P = 0.06$) resulted from a reversal of percent utilization of spurge stems by Idaho and North Dakota sheep in Idaho and North Dakota (Fig. 1). Idaho sheep had the lowest utilization in Idaho and the highest utilization in North Dakota. An explanation for this reversal is not apparent. Of greatest importance to this study was the significantly greater percent utilization of leafy spurge stems in North Dakota (100%) compared to Idaho (70%).

Preference for leafy spurge (Fig. 2) was not influenced by origin of sheep ($P = 0.14$), but it was affected by location of grazing ($P = 0.003$), grazing period ($P = 0.005$), and interactions of grazing period with origin of sheep ($P = 0.002$) and location ($P = 0.01$) and

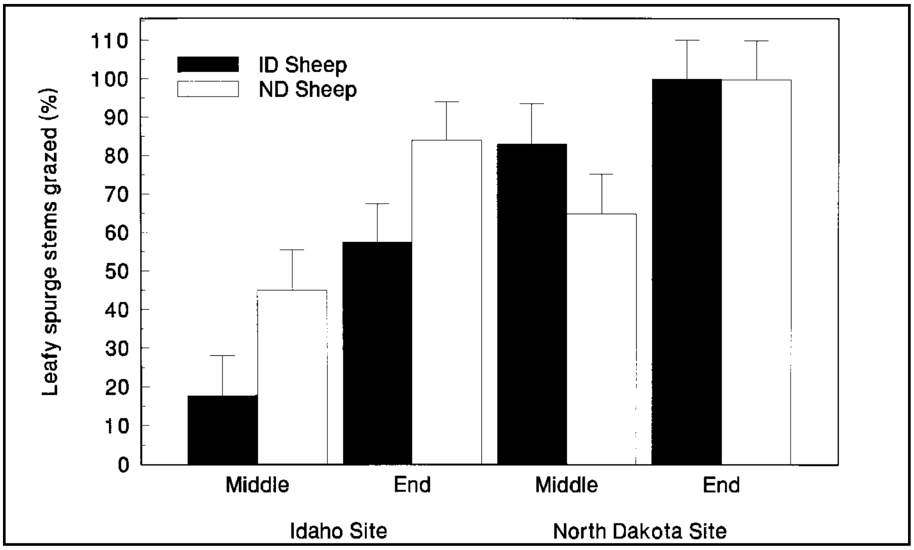

Fig. 1. Percentage of leafy spurge stems grazed at the middle and end of grazing trials in Idaho and North Dakota by sheep that originated from Idaho or North Dakota. Bars represent the standard error of the least squares mean.

by the 3-way period × origin × location interaction (P = .04). We believe the period × origin × location interaction shows the effect of learning on diet selection. This interaction was a result of the initial preference by North Dakota sheep for leafy spurge during the beginning time period in the first set of Idaho pastures. We suspect that this was due to their previous positive post-ingestive experiences with leafy spurge in North Dakota. Relative to the objectives of this study, the significant effect of location was the most important result of the analysis of sheep preference for leafy spurge. In Idaho, sheep grazed leafy spurge reluctantly while in North Dakota sheep consumed leafy spurge in proportion to its availability.

Trial 2

The sheep ate much more (P = 0.0001) of the leafy spurge from North Dakota (609 and 761 g on days 1 and 2, respectively) than from Idaho (148 and 82 g on days 1 and 2, respectively). These results were consistent with those from the first trial. The low relative palatablility of the Idaho spurge is also consistent with results from grazing trials in Idaho, which were conducted close to where spurge for Trial 2 was collected and where sheep grazed leafy spurge reluctantly (Walker et al. 1994). Crude protein levels were 16.3 and 8.2% for the Idaho and North Dakota leafy spurge, respectively. Neutral detergent fiber levels were 28.5 and 41.4% for the Idaho and North Dakota leafy spurge, respectively, and ADF levels were 27.1 and 37.2% for the Idaho and North Dakota leafy spurge, respectively. These results indicate that the North Dakota leafy spurge was more mature and less nutritious when it was harvested for the trial than was the Idaho leafy spurge. Based on their levels of CP, NDF and ADF we might have expected the Idaho leafy spurge to have been preferred by the sheep. Sheep preference for the North Dakota spurge apparently resulted from some other characteristic(s) and we suggest this was lower levels of aversive chemicals in the North Dakota leafy spurge.

Trial 3

The sheep ate similar (P ≥ .68) amounts of leafy spurge from the fertilized and non- fertilized sites on the first 2 days of the trial (Fig. 3). However, their consumption of spurge from the fertilized site was greater on the third (P = .06) and fourth (P = .01) days of the trial (Fig. 3). The feeding behavior of the sheep suggests that they gradually learned to reduce their consumption of the non-fertilized leafy spurge and increase their consumption of the fertilized leafy spurge. Their feeding behavior was consistent with the learning model of ruminant diet selection in respect to aversive phytochemicals (Provenza 1995).

Crude protein levels in leafy spurge from the fertilized and non-fertilized sites were 12.2 and 13.3%, respectively. Neutral detergent fiber levels were 42.5 and 37.3% for the fertilized and non-fertilized leafy spurge, respectively, and ADF levels were 35.6 and 31.3% for the fertilized and non-fertilized spurge, respectively. Thus, there is no evidence from these data that the

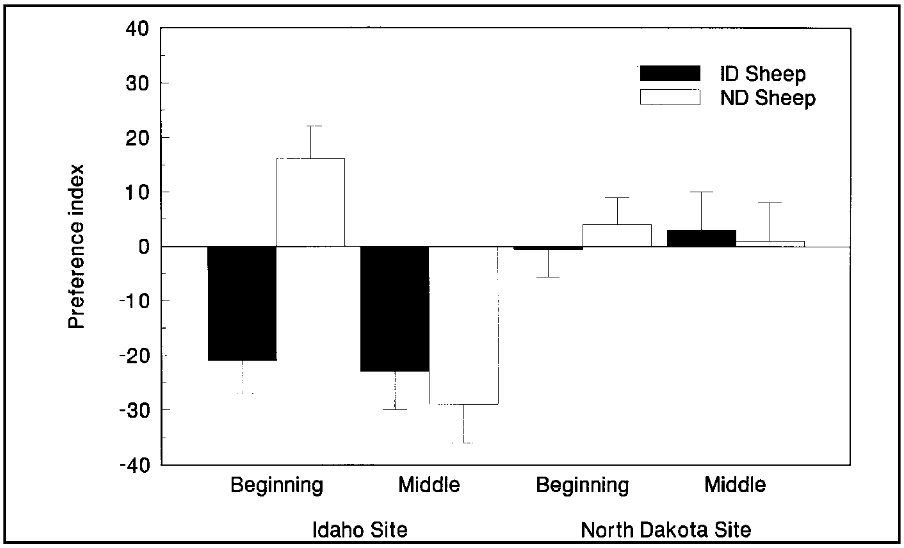

Fig. 2. Strauss' index of preference (% spurge in diet % spurge in standing crop) for leafy spurge at the beginning and middle of grazing trials in Idaho and North Dakota by sheep that originated from Idaho or North Dakota. Bars represent the standard error of the least squares mean.

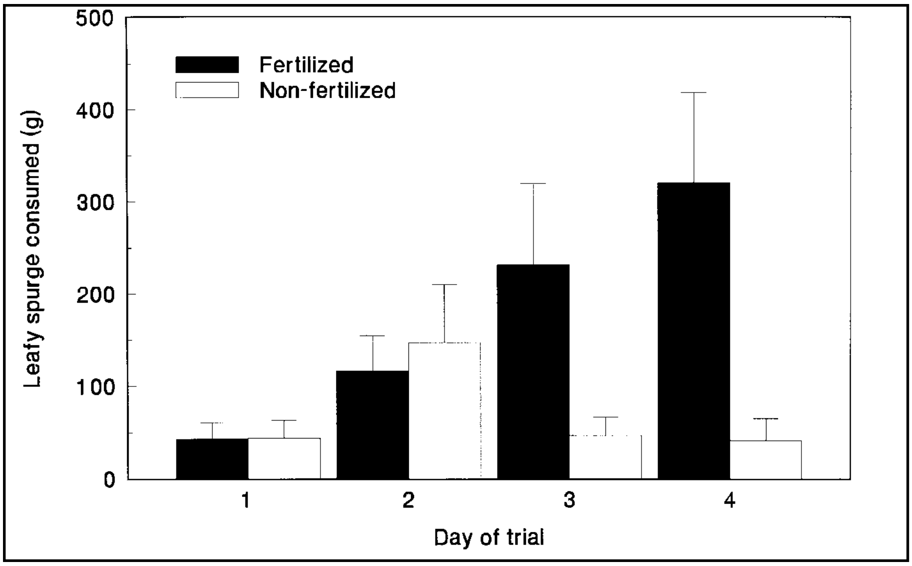

Fig. 3. Air-dried leafy spurge consumed by sheep on the 4 days of Trial 3. The leafy spurge was harvested from fertilized and non-fertilized sites near the Idaho pasture used in Trial 1. Bars represent the standard error of the mean.

sheep developed a preference for the fertilized spurge because it offered them greater levels of CP or lower levels of fiber.

There is considerable supporting evidence for the carbon-nutrient balance hypothesis, which suggests that carbon-based phytochemicals will accumulate in plant tissues when low nutrient uptake limits plant growth more so than does photosynthesis (Bryant et al. 1983, 1991, Mihaliak and Lincoln 1985, Mihaliak et al. 1987, Fajer et al. 1992, Ruohomki et al. 1996). We suspect that the leafy spurge collected from the non-fertilized site had higher levels of aversive carbon-based phytochemicals than did the leafy spurge collected from the fertilized site.

Conclusions

Different preferences of sheep for leafy spurge from sites in Idaho and North Dakota appears to result from differences in the leafy spurge growing on these sites rather than from differences in the sheep. We have 2 reasons to suspect that the differences in leafy spurge on these sites is more likely a function of differences in growing conditions than of genetic differences between colonies of leafy spurge. First, chloroplast DNA analysis of leafy spurge from the Idaho site indicated that this leafy spurge is genetically similar to leafy spurge collected in North and South Dakota and Nebraska (Nissen, personal communication). Second, results from the third trial indicate that soil fertility may affect the palatability of leafy spurge to sheep. Leafy spurge growing on soils with higher fertility was preferred by the sheep. With respect to Trial 1, the NO_3-N level in the Idaho soil was not only lower than that of the North Dakota soil, there was also much less soil at the Idaho site to hold nitrogen due to the high amount of rock fragments in this soil. These results indicate that the aversive compounds in leafy spurge are probably carbon-based rather than nitrogen-based compounds since nitrogen-based phytochemicals will accumulate in plants growing on soils with higher fertility (Bryant et al. 1983). This supports our previous results (Kronberg et al. 1995), which indicated that 1 or more carbon-based compounds likely affect consumption of leafy spurge through negative post-ingestive consequences.

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Spatial use of warm-season food plots by white-tailed deer

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Abstract

White-tailed deer (*Odocoileus virginianus* Zimm.) appear to concentrate foraging activity along the perimeters of warm-season food plots. Because of this, we tested the hypothesis that (1) providing travel lanes (i.e., rows not planted) free of vegetation within food plots will increase deer use of the plots and result in an equal spatial distribution of forage use within the plots, and (2) skip-row planting will result in increased yield and survival of lablab (*Dolichos lablab* L.), an annual legume. During 1994 and 1995, lablab was established by planting (1) every row spaced 0.9 m apart (solid), (2) 2 rows and not planting 1 row (skip 1), and (3) 2 rows and not planting 2 rows (skip 2) in two 5-ha food plots. Planting scheme did not affect spatial patterns of food plot use by deer. Utilization was concentrated at food plot perimeters on 9 of 15 sampling dates. Food plot utilization by deer was greater in skip 2 treatments only during August 1995, possibly as a result of greater forage availability resulting from greater plant survival than solid rows. Deer foraging in food plots apparently shifted foraging activities to an area of greater forage availability as the resource supply was depleted. Skip-row planting had lower overall planting costs/ha than solid planting but maintained similar forage production per hectare.

Key Words: *Dolichos lablab* L., edge, lablab, *Odocoileus virginianus* Zimm., skip-row planting, southern Texas

Resumen

El venado cola blanca (*Odocoileus virginianus* Zimm.) parece ser que concentra su actividad forrajera a lo largo de perimetros de parcelas alimenticias durante las estaciones de alta temperatura ambiental. Por lo cual, nosotros analisámos esta hipótesis (1) proporcionar lineas de recorrido (i.e., filas no plantadas) libres de vegetación adentro de las parcelas a su causa se aumentar en el uso con una misma distribución espacial del uso del forrage, y (2) sembrar lineas alternas teniendo como resultado un incremento en la cosecha y sobrevivencia de lablab (*Dolichos lablab* L.), una leguminosa anual. Durante 1994 y 1995, lablab fué establecida abase de plantación (1) con un espacio entre lineas de 0.9m (sólido), (2) plantando 2 lineas y no plantando 1 linea (saltando 1), y (3) plantando 2 lineas y no plantando 2 lineas (saltando 2) en dos parcelas alimenticias de 5-ha. El esquema de plantación no afectó a los venados en sus patrones espaciales en el uso de las parcelas alimenticias. La utilización dentro de los perímetros de las parcelas de alimentación se concentró en 9 de las 15 fechas de muestreo. La utilización adentro de las parcelas alimenticias por los venados fue mayor en el tratamiento saltando 2 líneas solamente durante agosto de 1995, posiblemente esto es el resultado de la gran sobrevivencia de plantas en estas lineas solidas. La actividad de forrajeo de venados en las parcelas alimenticias aparentemente cambió aáreas de mayor disponibilidad de forraje cuando el recurso fu agotado. Las plantaciones de lineas alternadas tuvieron un menor costo de plantación/ha que las plantaciones sólidas pero ambas mantuvieron una producción similar de forraje/ha.

Planting warm-season food plots is a common management practice to increase forage for white-tailed deer (*Odocoileus virginianus* Zimm.) throughout the southeastern United States. Adams et al. (1992) reported that 23% of landowners in Texas who lease hunting rights plant food plots as a management technique. In Mississippi, Vanderhoof and Jacobson (1989) found that maintaining 0.5% of an area in agronomic food plots year-round increased body mass, number of antler points, beam circumferences, and beam lengths of white-tailed deer. Additionally, Johnson et al. (1987) documented a 19% increase in live weights of yearling male white-tailed deer after establishment of cool-season food plots. Both of these studies were conducted in relatively mesic habitats. In semi-arid habitats, low rainfall could be a limiting factor to deer nutrition and food plot success.

The nutritional value of natural forage species in the southeastern United States varies seasonally and is often low during summer (Varner et al. 1977, Jacobson 1994). Meyer et al. (1984) proposed that reduced crude protein and energy levels in deer diets during summer may decrease fawn survival. Food plots could be a management tool to increase availability of nutritious forage for white-tailed deer during summer. Feather and Fulbright (1995) reported that warm-season forages did not persist through August in semi-arid southern Texas.

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Mozingo (1984) reported that skip-row planting produced greater yields on a planted hectare basis than did planting all rows (solid planting) because of more efficient use of moisture and light by the plants. Research on the effects of row width on yields of warm-season crop plants that are also grown in food plots for deer has focused on seed yield rather than forage yield (Mozingo 1984, Weaver et al. 1991).

In previous research on summer food plots planted in 'Rongai' lablab (*Dolichos lablab* L.), deer tended to forage at the perimeter of plots from April to June rather than foraging within the plots as they did from July to October (Hehman 1995). Vegetation was dense during early summer because lablab grew across rows, which possibly obstructed access to the interior of the plots. Uniform grazing in stands of cultivated forages is desirable because ungrazed plants become mature, fibrous, and less palatable, whereas plants that are too heavily grazed lose vigor or die (Vallentine 1990). Our first objective was to test the hypothesis that food plots which provide travel lanes free of vegetation will increase intensity of deer use and more equally distribute use within the plots. Based on this hypothesis, we predicted that (1) foraging will be greater in plots with skip-row planting schemes than in plots with solid planting schemes, and (2) if food plots are planted with skip-rows, deer will forage in the interior of the plots in equal proportion to the perimeter. An alternative hypothesis was forage use by deer should be greater at the perimeter of the plots regardless of planting scheme. A second objective was to test the hypothesis that skip-row planting results in greater plant survival and yield of lablab forage than solid planting.

Materials and Methods

Study Area

Research was conducted on El Tecomate Ranch in Starr County, Tex., (98˚48'N, 26˚42'W). The climate is warm-temperate, subtropical with mild winters and only a short humid period in summer when daily maximum temperature averages 38 C. Average (1931-1962) yearly precipitation is 440 mm with peaks in June and October (Soil Conserv. Serv. 1972) (Table 1).

The study sites had McAllen fine sandy loam (fine-loamy, mixed, hyperthermic Typic Ustochrept) and Ramadero loam (fine-loamy, mixed, hyperthermic Pachic Argiustoll) soils (Soil Conserv. Serv. 1972). Vegetation on the ranch is a honey mesquite (*Prosopis glandulosa* Torr.) mixed brush community forming a continuous shrubland. Primary woody species include honey mesquite, cenizo (*Leucophyllum frutescens* (Berl.) I. M. Johnst. C.), blackbrush acacia (*Acacia rigidula* Benth.), and granjeno (*Celtis pallida* Torr.) interspersed with prickly pear cactus (*Opuntia lindheimeri* Engelm.).

Deer densities within the study area were estimated as 11 adult deer km^{-2} in October 1994 and 9 adult deer km^{-2} in October 1995 by counts from a helicopter. Aerial counts of white-tailed deer in south Texas underestimate total numbers because dense brush limits visibility (DeYoung 1985).

Food Plot Establishment

Two 5-ha food plots about 1.6 km apart with dimensions of 250 x 210 m (plot 1) and 310 x 180 m (plot 2) were used. Each plot was surrounded by a 3.2-m high fence designed to exclude deer. Once plants reached about 25 cm tall, the upper 1.6 m of the fence was lowered to allow deer entry into the plots. In 1994, plots were planted on 5 March, and the high fence was not lowered until 8 weeks later on 29 April because of low rainfall (Table 1) and slow plant growth. In 1995, plots were planted on 12 March, and the high fence was lowered 5.5 weeks later on 19 April.

'Rongai' lablab was planted in a randomized, complete-block design. Lablab was planted because it is drought tolerant and palatable to white-tailed deer (Beals et al. 1993, Feather and Fulbright 1995). The 2 food plots each contained 3 blocks (replications). Each of the 6 blocks was partitioned into 3 experimental units (food plot 1: 210 $\times$ 27 m; food plot 2: 180 $\times$ 27 m). Three planting schemes were randomly assigned to the 3 experimental units, with each experimental unit receiving a different planting scheme. The 3 planting schemes were (1) plant every row; (2) plant 2 rows and skip (not plant) 1 row; and (3) plant 2 rows and skip 2 rows. Each planting scheme contained 30 rows spaced 0.9 m apart. Seeding rates were 17 kg ha^{-1}, 11 kg ha^{-1}, and 8.5 kg ha^{-1} for planting schemes 1, 2, and 3, respectively (1 seed every 15 cm of row). The plots were planted with a John Deere® Maxemerge 6-row planter pulled by a John Deere® 2955 tractor. Plots were treated with Treflan (DowElanco, Indianapolis, In.) in

Table 1. Monthly precipitation (mm) for 2 food plots on El Tecomate ranch, Starr County, Texas (Jan 1994–Oct 1995) and long-term (LT) (1931–62) monthly mean rainfall (mm) collected by the Soil Conservation Service (1972) at Rio Grande City, Starr County, Tex.

	1994		1995		LT
Date	Plot 1	Plot 2	Plot 1	Plot 2	Mean
	-mm-				
Jan.	36	30	15	15	17
Feb.	0	0	0	0	24
Mar.	13	15	66	64	20
Apr.	8	20	0	0	22
May	25	25	66	66	32
Jun.	17	168	41	38	53
Jul.	8	10	20	18	51
Aug.	28	20	25	25	35
Sep.	97	58	150	145	43
Oct.	33	38	10	10	80
Nov.	0	0	—	—	47
Dec.	2	22	—	—	15
Total	438	406	393	381	439

Table 2. Mean (± SE%, n = 6) grazed lablab plants within each of 3 planting schemes for 15 sampling dates on El Tecomate ranch, Starr County, Tex., 1994–95 (May–Aug).

	Solid	Skip 1	Skip 2
Date	X±SE	X±SE	X±SE
	(%)		
1994			
May 11	53±5.1a[1]	49±6.9a	49±5.4a
May 26	88±3.3a	89±2.8a	87±2.9a
Jul 14	12±5.1a	12±4.8a	12±4.0a
Jul 27	28±6.9a	27±6.5a	33±7.0a
Aug 10	47±5.9a	46±7.4a	54±6.2a
Aug 24	73±5.8a	72±7.1a	80±5.9a
1995			
May 5	13±3.7a	32±7.6a	22±5.1a
May 18	27±6.5a	50±11.4a	46±8.6a
Jun 1	44±7.7a	60±11.2a	60±8.8a
Jun 15	30±6.1a	39±9.2a	30±7.1a
Jun 29	30±7.0a	31±8.3a	25±5.7a
Jul 13	28±6.4a	34±8.4a	22±5.9a
Jul 27	33±6.7a	42±9.3a	31±6.6a
Aug 10	69±7.6a	74±7.6a	71±5.4a
Aug 24	89±3.2a	97±1.2b	96±1.6b

[1]Means within a row sharing the same letter were not significantly (Tukey's HSD, P > 0.05) different.

February at 1 liter ha^{-1} and periodically cultivated as necessary for weed control. Fertilizer (N-P-K at 5-34-4; Texag, Mission, Texas) was applied to the soil in a foliar spray in early May at 190 liters ha^{-1}.

Spatial Patterns of Food Plot Use

Spatial patterns of food plot use were determined by ocular estimation with a modification of the methods described by Andren and Angelstam (1993). Our methods differed from Andren and Angelstam (1993) in that we classed plants only as grazed or ungrazed rather than using 4 grazing intensity classes. This method was employed to test our predictions of greater foraging in skip-row plots and proportional use of perimeters and interiors in skip-row plots compared to solid-planted plots. Four of the 30 rows in each planting scheme were randomly selected. At 3-m intervals along each row, the nearest plant was recorded as grazed or ungrazed. If there was not a living plant at each 3-m interval, that interval was recorded as a mortality, which provided an estimate of plant survival. Therefore, in this paper, survival was defined as at least 1 living plant within each 1 m of row at each interval, and mortality was defined as no living plants for each 1 m of row at each interval. The proportion of grazed plants was calculated for food plot location (perimeter and interior) within each planting scheme/block combination. Perimeter was defined as the outer portion of each plot up to 1/4 of the plot length (0-53 and 0-45 m for plots 1 and 2, respectively), and interior was defined as the central half of the plots. Data were analyzed by comparing proportions of grazed plants in relation to location and planting scheme. Sampling was conducted at 2-week intervals from April through August. Three sampling dates during June and July 1994 were missed because plants were heavily defoliated by grazing, and the landowner raised the fence for 1 month to prevent deer access to the plots.

Forage Standing Crop

Forage standing crop within enclosures was estimated during 1994 and 1995 by centering three, 2.8-m diameter circular wire enclosures on 3 randomly selected rows within each planting scheme in each of the 6 blocks. Sample size adequacy was calculated with equations of Bonham (1989:67) to estimate standing crop means in a treatment within 20% of the population mean at the 95% confidence level. All plant material within a 0.9-m^2 quadrat inside each wire enclosure was clipped to ground level and dried at 40 C to a constant mass. Plots were harvested during late June and late August.

Forage standing crop in the presence of grazing (forage availability) was estimated concurrently with monitoring food plot use by double sampling (Bonham 1989:202–205). Eighteen, 0.9-m^2 quadrats were placed at 10- and 8-m intervals for food plots 1 and 2, respectively. A row within each planting scheme was randomly selected for sampling at each interval. Biomass of vegetation was ocularly estimated in 18 quadrats and clipped in 9. The 2:1 ratio of estimated to clipped plots was selected based on equations of Bonham (1989:204). Plant material was weighed in the field, and 3 subsamples per replication were dried at 40° C to adjust for plant water content. Sampling was conducted monthly from late May to late August.

Statistical Analyses

We used analysis of variance for a split-block experimental design (PROC ANOVA; SAS 1988) for each sampling date with planting scheme as the whole-plot treatment in a randomized, complete block design with 6 blocks (replications) and location (perimeter or interior) as the sub-plot treatment to detect significant ($\underline{P}$ < 0.05) differences in mean percentages of grazed plants. A split-block design is a variation of the split-plot design in which the levels of 1 treatment factor (in our case, planting scheme) are randomly assigned to plots in a randomized, complete block design (Kuehl 1984). Tukey's HSD test was used as a mean separation procedure ($\underline{P}$ < 0.05). Each sampling date was analyzed separately because of missing sampling dates during 1994.

We used repeated measures analysis of variance (PROC ANOVA; SAS 1988) for a randomized, complete-block design with forage standing crop within enclosures and $\log_{10}$ transformed monthly forage availability as dependent variables to test for significant ($\underline{P}$ < 0.05) planting scheme and sampling date main effects and interactions. Biomass data were $\log_{10}$ transformed because biomass data tend to follow a lognormal distribution

Table 3. Mean (± SE%, n = 6) (averaged across 3 planting schemes) grazed lablab plants relative to food plot perimeter and interior for each sampling date on El Tecomate ranch, Starr County, Tex., 1994–95 (May–Aug).

Date[1]	Perimeter X±SE	Interior X±SE
	(%)	
1994		
May 11	57±3.9a	43±5.0b
May 26	88±2.4a	88±2.5a
Jul 14	19±4.4a	6±1.9a
Jul 27	38±5.9a	21±4.1a
Aug 10	54±5.4a	44±4.9a
Aug 24	75±4.8a	75±5.4a
1995		
May 5	32±4.0a	12±4.6b
May 18	56±5.8a	26±7.5b
Jun 1	74±4.8a	36±7.5b
Jun 15	50±3.9a	16±5.3b
Jun 29	45±4.1a	11±3.9b
Jul 13	45±4.4a	11±3.5b
Jul 27	55±4.0a	16±4.4b
Aug 10	85±2.4a	58±5.9b
Aug 24	96±1.8a	92±1.9a

[1]Planting scheme X location interaction was not significant (P > 0.05) for each sampling date.
[2]Pairs of means within a row sharing the same letter were not significantly (P > 0.05) different.

(Zar 1984, Bonham 1989:84). The sampling date by planting scheme interaction for monthly forage availability was significant ($\underline{P}$ = 0.01); therefore, these data were analyzed by sampling date. Tukey's HSD test was used to separate significant ($\underline{P}$ < 0.05) main effect means. All differences discussed are statistically significant at the 5% level unless otherwise specified.

Results

Spatial Patterns and Intensity of Deer Foraging

The proportion of grazed plants was greater in skip 1 or skip 2 planting schemes than in solid row plantings on 24 August 1995 (Table 2). There were no significant differences in proportion of grazed plants among planting schemes on other sampling dates.

The planting scheme by location (perimeter vs. interior) interaction for percent grazed plants was not significant for any of the 15 sampling dates. Averaged across planting schemes, the proportion of grazed plants during 1994 was greater in plot perimeters than in interiors only during 11 May (Table 3). During 1995, the proportion grazed plants was greater in plot perimeters than in interiors during 8 of 9 sampling dates, indicating that deer concentrated foraging efforts at plot perimeters throughout most of the year.

Forage Standing Crop and Availability

Averaged across sampling dates, mean ($\underline{n}$ = 6) forage standing crop within enclosures did not differ among planting schemes with solid, skip 1, and skip 2 averaging 852 ± 111, 916 ± 114, and 815 ± 99 kg/ha (X ± SE). However, mean ($\underline{n}$ = 6) forage availability was greater in skip 2 than in solid plantings in August 1994 and was greater in both skip 1 and skip 2 than in solid plantings in August 1995 (Table 4).

The skip 2 planting scheme had greater plant survival than did solid rows from 27 July through 24 August 1994, and during 10 and 24 August 1995 (Table 5). The skip 1 planting scheme had greater plant survival than the skip 2 scheme on 13 July and the solid scheme during 27 July through 24 August 1995.

Discussion and Conclusions

Spatial Patterns of Deer Foraging

Planting in skip-rows did not increase foraging by deer compared to solid-rows, except during 24 August 1995. More foraging occurred in skip-row plantings during 24 August 1995 possibly because forage availability was greater in the skip-row planting schemes, resulting from greater plant survival. This is supported by the greater proportion of grazed plants in skip-row planting schemes than in solid rows on 24 August 1995. There were fewer surviving plants in solid rows, and if deer foraging was proportionately distributed among planting schemes, the proportion of grazed plants should have been lower in skip-row plantings because there were more plants from which to choose. Deer apparently fed in skip-rows during August 1995 because of greater forage availability and not as a result of travel lanes furnished by the skip-rows.

Skip-row planting did not result in even spatial distribution of deer foraging among food plot perimeters and interiors. The concentration of foraging efforts at plot perimeters throughout most of 1995 indicates an "edge effect" similar to that reported for black-tailed deer (*Odocoileus hemionus columbianus* Raf.) (Hanley 1983) and for medium and large ungulates feeding at the edge of 0.15- to 1.3-ha glades within Acacia bushland in Kenya (Young et al. 1995). However, in our study deer did not consistently restrict foraging activity to food plot edges, e.g., 26 May through 24 August 1994 and August 1995 when deer use did not differ between plot edges and interiors.

Deer utilized food plots in our study area primarily at night and spent diurnal hours in the adjacent, dense shrubland that surrounded each of the plots (Bonner 1996). Dense brush, which

Table 4. Mean (± SE kg/ha, n = 6) lablab forage availability within each of 3 planting schemes for each sampling date on El Tecomate ranch, Starr County, Texx, 1994–95 (May–Aug).

Date	Solid X±SE	Skip 1 X±SE	Skip 2 X±SE
		(kg/ha)	
1994			
May	147±14a[1]	96±110a	82±11a
Jun	475±41a	368±36a	275±31a
Jul	382±46a	323±41a	394±42a
Aug	211±38b	251±50ab	279±37a
1995			
May	772±60a	831±59a	841±59a
Jun	1,532±119a	1,457±94a	1,649±116a
Jul	743±57a	1,099±99a	1,018±76a
Aug	27±13b	190±35a	346±36a

[1]Means within a row sharing the same letter were not significantly (Tukey's HSD, P > 0.05) different.

Table 5. **Mean (± SE%, n = 6) lablab plant survival within each of 3 planting schemes for each sampling date on El Tecomate ranch, Starr County, Tex., 1994-95 (May–Aug).**

Date	Solid X±SE	Skip 1 X±SE	Skip 2 X±SE
	(%)		
1994			
May 11	91±1.9a[1]	96±0.7a	91±1.3a
May 26	90±2.0a	95±1.3a	90±1.6a
Jul 14	87±2.4a	91±1.7a	92±1.1a
Jul 27	78±2.2b	88±2.0ab	92±1.1a
Aug 10	60±3.2b	72±2.6ab	84±1.4a
Aug 24	53±3.5b	68±2.7ab	81±1.8a
1995			
May 5	100±0.3a	100±0.3a	100±0.5a
May 18	100±0.3a	100±0.4a	100±0.4a
Jun 1	100±0.2a	100±0.3a	100±0.3a
Jun 15	97±0.5a	97±0.6a	97±0.4a
Jun 29	96±0.6a	97±0.4a	98±0.4a
Jul 13	95±0.5ab	96±0.4a	94±0.7b
Jul 27	86±1.4b	92±0.8a	88±1.4ab
Aug 10	32±2.5b	66±2.3a	77±2.0a
Aug 24	21±2.0b	61±2.5a	71±2.1a

[1]Means in a row sharing the same letter were not significantly (Tukey's HSD, $P > 0.05$) different.

surrounded our food plots, is used for bedding by deer diurnally, whereas openings dominated by herbaceous vegetation are the center of crepuscular and nocturnal feeding activity (Inglis et al. 1986). During 1995, deer traveling from the shrubland into the plots were confronted with abundant forage at plot edges, and further travel into the plots to obtain forage was unnecessary during most of the summer. However, when forage supply was depleted in plot edges, deer began foraging in plot interiors. Williamson and Hirth (1985) found similar foraging strategies in that deer preferred to feed along clear-cut edges, but they foraged in clear-cut interiors when an abundance of preferred browse was present.

"Edge effects" were not evident during 1994 in which 11 May was the only date showing significant differences in proportion of grazed plants between edge and interior. Deer use of food plot perimeters and interiors was similar during 14 July 1994 possibly because few deer were using the food plots during this time. However, because forage availability during 1994 was low, compared to 1995, deer traveled further into the plots throughout the rest of the year.

When forage was abundant at the perimeter of the plots, deer were able to satisfy nutritional needs while remaining in close proximity to the dense brush outside the plots. Forages eaten by white-tailed deer in south Texas during summer are energy deficient (Meyer et al. 1984). Deer possibly restricted foraging activity to the perimeter of food plots during 1995 to minimize the energy expenditures resulting from travel into the plots.

Once forage in the perimeter of the plots was depleted, they foraged in the interior. Foragers remain in a patch until forage is depleted below some threshold and the time spent in a patch by a forager will be proportional to relative food availability (Senft et al. 1987). Possibly, when forage in the perimeter of the food plots was depleted below some critical threshold it was more energetically efficient for deer to begin feeding in the interior of the food plots. In August 1995, deer focused foraging activity on skip-row plantings possibly because forage availability and, subsequently, intake rate in the solid plantings had fallen below some critical threshold.

A second hypothesis is that deer foraged at the perimeter of the plots to remain near the "escape cover" provided by the dense brush adjacent to the plots (Stephens and Krebs 1986). Energy status and proximity to escape cover could interact to influence foraging patterns of deer in food plots. For example, yellow-eyed juncos (*Junco phaenotus* Wagler) with positive energy budgets were risk averse, whereas those with negative energy budgets were risk prone (Stephens and Krebs 1986). Designing food plots to maximize perimeter and minimize interior, e.g., rectangular-shaped plots rather than square ones, would minimize the amount of travel into the plots and provide greater proximity of escape cover to foraging areas.

Forage Standing Crop and Availability

Both skip 1 and 2 skip rows maintained similar standing crops compared to solid rows but, using seed costs from McBryde (1995), overall planting costs were 6% and 8% lower, respectively, because of reduced seeding rates/ha. Because skip 2 involves planting half of the food plot and allowing the other half to remain fallow, skip 2 planting schemes produced about 200% more forage than solid rows on a per hectare planted basis.

Differences in forage availability resulted from greater plant survival in the skip-row planting schemes, presumably the result of more efficient use of light and moisture in skip-rows (Mozingo 1984). Our conclusions are supported by the greater percentage of living plants in skip 2 schemes than in solid schemes on 24 August 1994 and the greater percentage of living plants in skip-row schemes than in solid schemes on 24 August 1995.

By incorporating a skip 2 planting scheme in a semi-arid environment that receives 15 to 21 cm of rainfall during the growing season: (1) overall planting cost was reduced 8% compared to solid planting while maintaining similar forage production; (2) percent plant survival throughout the summer was increased; and (3) availability of nutritious forage to deer during nutritionally-restricted periods was increased.

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A qualitative spatial model of hardwood rangeland state-and-transition dynamics

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Abstract

We present a method for computerizing the transition rules of a state-and-transition model and then linking this model to a geographic information system. The resulting simulation characterizes rangeland vegetation dynamics in space and time. The method makes use of an expert system, a computer program that forms logical chains of transition rules. Simulation using state-and-transition rules, sometimes called qualitative simulation, has the disadvantage that it is less precise than traditional numerical simulation. However, it may have the advantage of being able to generate more robust simulation of complex vegetation communities. We demonstrate the application of the method by constructing a model of hardwood rangeland in the western foothills of the Sierra Nevada. The model is tested by comparison with historic black-and-white aerial photographs. The model is found to agree generally with the observed data but to differ substantially in some locations. Implications of this difference are discussed.

Resumen

Presentamos un método para computarizar las reglas de transición de un modelo de estados y transición y enlazamos este modelo a un sistema de información geográfica. La simulación resultante caracteriza en espacio y tiempo la din mica de la vegetación del pastizal. El método utiliza un sistema experto, que es un programa de computación que forma cadenas lógicas de las reglas de transición. La simulación usando reglas de estado de transición, a veces llamada cualitativa, tiene la desventaja de que es menos precisa que la simulación númerica tradicional. Sin embargo, tiene la ventaja de ser capaz de generar una simulación mas sólida para comunidades vegetales complejas. Demostramos la aplicación del método construyendo un modelo del pastizal "hardwood" al pie de la montaña del lado oeste de la Sierra Nevada. El modelo es probado por comparación de fotografías aéreas históricas en blanco y negro. Se encontró que el modelo genealmente concuerda con los datos observados; sin embargo, difiere substancialmente en algunas localidades. Se discuten las implicaciones acerca de esta diferencia

Key Words: geographic information systems, simulation models, vegetation dynamics

The state-and-transition model, introduced to range science by Westoby et al. (1989), has potential to be useful in summarizing information about vegetation dynamics. State-and-transition models in range management have generally been implemented through simple printed flowcharts, but they can be directly implemented on a computer using expert system methodologies (Noble 1987). Expert systems are a type of computer program that forms logical chains of transition rules. Starfield and his collaborators (Starfield and Bleloch 1983 Starfield et al. 1989) have developed expert system-based ecosystem models comprised of discrete states together with rules to describe the transitions between states. These models are used to forecast the response of these ecosystems to various forms and magnitudes of disturbance.

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Computer implementation of state-and-transition models offers a number of advantages. One is that the exercise of writing the transition rules in precise logical form imposes a high level of rigor and precision on the model. A second is that using the computer to keep track of logical relationships opens the way for more complex qualitative models that include some degree of mechanism. A third is that it offers the potential for introducing explicit representation of spatial effects through the linkage with a geographic information system (GIS). This explicit representation of spatial variability is essential in an explanatory model that is to be used as a management tool (Grice and Macleod 1994). The use of GIS and cartographic modeling (Tomlin 1990) provides a natural linkage between spatial and temporal processes in the model. In this paper we introduce a methodology for implementing state-and-transition models as computer simulations and linking them with geographic information systems.

Materials and Methods

Simulation methodology

The simulation methodology is based on establishing a correspondence between the rules of a rule-based expert system (Noble 1987, Plant and Stone 1991) and the transition rules of a state-and-transition model. We use the QTIP (Qualitative Temporal Inference Program) expert system (Plant 1997) to encode the model's transition rules. The QTIP incorporates qualitative (i.e., non-numerical) simulation based on concepts originally developed for mechanical and electrical systems (de Kleer and Brown 1984, Kuipers 1986, Whitehead and Roach 1990). The most important aspect of qualitative simulation is that the variables take on ordinal rather than rational or interval values (Stevens 1946). The QTIP was originally developed for the qualitative modeling of crop production systems (Plant and Loomis 1991). The important feature of the program for application to state-and-transition modeling is that it combines an expert system with dynamic simulation of system behavior. The QTIP uses an event-based simulation (Langran 1992), which means that the time variable jumps in chronological sequence from one event to the next rather than changing in fixed steps. The state-and-transition model is linked with a GIS through an algorithm that alternates between spatial steps and dynamic steps. The spatial model is laid out as a grid of square cells in a raster-based GIS. Spatial steps are carried out in the Idrisi GIS (The Idrisi Project, Clark University, Worcester, Mass.). The specific GIS software is not critical, however. We used Idrisi because it is a simple raster-based system that functions very well and because a large data set of Idrisi files has been assembled for the study site. At each time step, for each cell the program calls on the GIS to determine the spatial relationships between that cell and the rest of the cells in the model (e.g., proximity to the nearest cell with a high level of shrubs). Following this GIS spatial analysis, the program uses the QTIP dynamic simulation to process state-transition rules, generating a prediction of the state of the cell at a later time. This process is repeated for every raster cell at each time step.

We demonstrate the algorithm by applying it to an existing state-and-transition model of the hardwood rangelands of the western foothills of the Sierra Nevada in California. The output of the model is compared with hardwood vegetation dynamics at a study site located at the University of California Sierra Foothill Research and Extension Center (SFREC) (latitude 39˚16'N, longitude 121˚16'W), at elevation approximately 1,000 meters. Soils are predominantly Auburn rocky loam, which is a member of the loamy, oxidic, thermic Ruptic-Lithic Xerochrepts, and Sobrante very rocky loam, which is a member of the fine-loamy, mixed, thermic Mollic Haploxeralfs. In this region the overstory is dominated by blue oak (*Quercus douglasii* H. and A.) in association with other oak species and with foothill pine (*Pinus sabiniana* Douglas). The understory includes a number of native shrub species, e.g., ceanothus (*Ceanothus* spp.) and poison oak (*Toxicodendron diversilobum* (Torrey & A. Gray) E. Greene). The groundcover, which formerly was dominated by native perennial bunchgrasses, now consists primarily of introduced Mediterranean annual grasses (e.g., wild oat, *Avena fatua* L., soft chess, *Bromus mollis* L.) and forbs (e.g., filaree, *Erodium* spp.). The region's climate is Mediterranean, with hot, dry summers and cool, wet winters but with little frost.

The purpose of this paper is to present the methodology rather than to develop a detailed simulation of a particular site or sites. We therefore use a model made by combining 2 existing state-and-transition models that have been independently constructed for hardwood rangelands in this region (George et al. 1992, Huntsinger and Bartolome 1992). These models are similar in their classification of states. The model of George et al. (1992) contains more detail in its description of groundcover and that of Huntsinger and Bartolome contains a more detailed description of the oak/shrub understory states. To test the model, we compare its output with a data set drawn from a sequence of 5 black-and-white aerial photographs taken between 1952 and 1993 of the study site.

The simulation methodology is presented in 2 stages. The first stage describes the dynamic component of the model. This involves the development of the state-and-transition model and the translation of its transition rules into a knowledge base for the qualitative simulation model. The second stage presents the spatial component of the model. This involves linking the transition rules of the QTIP knowledge base with the analysis modules of the Idrisi GIS.

The Dynamic Component

The qualitative simulation model is based on the principle that each of the model variables takes on categorical values that may be either ordinal or nominal (Stevens 1946). Ordinal values have an ordered relationship (e.g., *high, moderate,* and *low*). Nominal values have no such ordering (e.g., *sandy, rocky,* and *loamy*). The method replaces traditional dynamic equations with expert system rules phrased so that the direction of cause and effect parallels the direction of inference in the rule (Plant 1997). For example, if a moderate or high fire causes groundcover to be low due to burning then this would be phrased as

If *fire_level* ≥ *moderate*
Then *groundcover* = *low*.

Each step of the dynamic simulation process involves testing all the rules and implementing any that apply. This process is repeated cyclically until no new conclusions can be drawn (this is called *forward chaining*, cf. Plant and Stone 1991). For example, if the rule base contained a second rule stating

If *groundcover* = *low*
Then *seed_production* = *low*

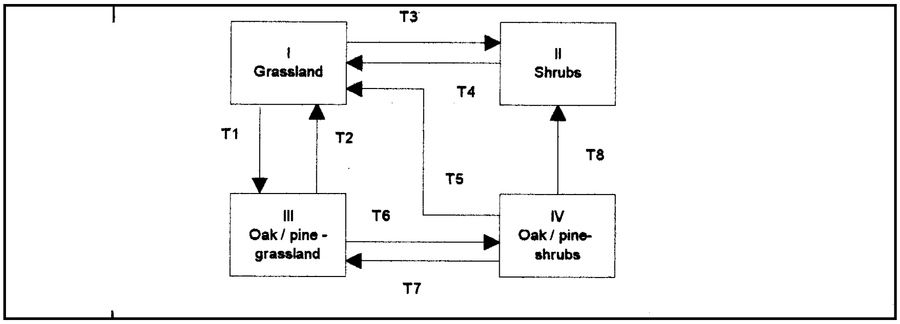
and if input data included a value of *moderate* for *fire_level*, then the forward chaining process would first use the first rule to generate the value *low* for *groundcover* and then use the second rule to generate the value *low* for *seed_production*. Dynamics are introduced into the model by incorporating the capability to alter values at a later time as described below.

Figure 1 shows the hardwood rangeland state-and-transition model with the catalog of transitions, expressed in the descriptive form proposed by Westoby et al. (1989). The transition descriptions have been slightly simplified from the original papers of George et al. (1992) and Huntsinger and Bartolome (1992) to facilitate translation into computer form. The model emphasizes the dynamics of the long-lived shrub and tree life forms that dominate these ecosystems.

The first step in converting this state-and-transition model into a qualitative simulation model is to establish the variables and their range of values. Table 1 lists the full set of variables in the model. The variables characterizing the vegetation are: (1) *groundcover*, the level of cover of the herbaceous groundcover, (2) *shrubs*, the understory shrub cover level, (3) *saplings*, the cover of immature trees, (4) *overstory*, the cover of mature trees, and (5) *litter_level*, characterizing the amount of herbaceous material left at the end of the growing season. There are 4 variables characterizing the 4 external inputs simulated in the model: *fire_level*, *grazing_level*, *herbicide_applied*, and *tree_cutting*. Finally, there are 2 fixed-value parameters, *soil_texture* and *soil_depth*.

Each of the variables describing vegetation may take on 1 of the values *high*, *moderate*, or *low*. The 3 variables *groundcover*, *shrubs*, and *overstory* play a special role in the qualitative model since they determine the location's state in the state-and-transition model. There are 8 possible combinations of *high* and *low* values among the 3 vegetation types. However, only 4 of these are possible in a real state since *groundcover* and *shrubs* are assumed to be mutually exclusive so that they cannot both remain *high* or *low* in the same cell. (A location that consisted of bare rock could have both values *low* at the same time in a stable state, but such a location would not take on any other values and so may be ignored in this discussion). Each of the 4 possible combinations of values is interpreted as one of the states in the state-and-transition model as shown in Table 2. The values of *litter_level*, *herbicide_applied*, *tree_cutting*, *grazing_level*, and *soil_depth* are also *high*, *moderate*, or *low*. The variable *soil_texture* may be either *rocky_loam* or *very_rocky*, reflecting the 2 soil textures found at the test site. The variable *fire_level* may take on 1 of the 4 values *none*, *grass_fire*, *shrub_fire*, and *crown_fire*.

The full QTIP knowledge base interpreting the state-and-transition model is available at the world wide web given at the end of the paper. The model is written in the QTIP knowledge base syntax, which is based on the computer language LISP (Winston and Horn 1981). A complete description of this syntax is given by Plant



Transition 1 (Grassland to oak/pine - grassland). This transition is sufficiently rare that it is not included in the catalog of Huntsinger and Bartolome (1992). Protection from grazing and fire facilitates overstory regrowth in situations where such regrowth is possible. Foothill pine establishes an overstory in about 20 years. Oak overstory, if it is established at all, takes about 50 years to mature. Herbaceous understory remains present. Overstory establishment is inhibited by dense litter mat that prevents seed contact with soil, and by shallow or infertile soil.

Transition 2. (Oak/pine-grassland to grassland). Drought, crown fire, herbicide application, or cutting remove overstory trees and leave herbaceous groundcover.

Transition 3 (Grassland to shrub). Protection from grazing and fire facilitates shrub invasion where conditions favor such invasion. Shrub establishment is favored by rocky soil, even in the presence of grazing. Therefore, this transition often takes place in regions that were previously dominated by shrubs but underwent transition to grassland (Transitions 4, 5, or 7). Shrubs become dominant in 10 to 20 years. Herbaceous understory declines as shrub cover increases.

Transition 4 (Shrub to grassland). Wildfire or controlled burning remove shrubs and groundcover. Groundcover is re-established in the succeeding year from residual and dispersed seed.

Transition 5 (Oak/pine - shrub to grassland). Drought or crown fire remove both trees and shrubs. Herbicide application or cutting remove overstory trees and, in combination with lower intensity fire, lead to establishment of herbaceous groundcover.

Transition 6 (Oak/pine - grassland to oak/pine - shrub). This transition occurs over a span of decades, if at all. Protection from fire and grazing facilitates this transition in areas where it is possible. As with Transition 3, this transition often takes place in regions where the understory was previously dominated by shrubs but underwent transition to grassland.

Transition 7. (Oak/pine -shrub to oak/pine - grassland). Shrub fire removes shrub understory and may kill pines. Herbaceous groundcover established in succeeding year from residual and dispersed seed.

Transition 8. (Oak/pine - shrub to shrub). Herbicide application or cutting removes trees. If shrub understory is left intact it will remain stable.

Fig. 1. State-and-transition description of vegetation dynamics of blue oak woodland in the western foothills of the Sierra Nev., based on a synthesis of existing state-and-transition models of George et al. (1992) and Huntsinger and Bartolome (1992).

Table 1. List of parameters and variables used in the state-and-transition model for hardwood rangeland.

Vegetation layers	External inputs	Fixed parameters
overstory	fire_level	soil_depth
saplings	grazing_level	soil_texture
shrubs	herbicide_applied	
groundcover	tree_cutting	
litter_level		

Table 2. Correspondence between values of variables in the model and states of the state-and-transition model for hardwood rangelands.

State	groundcover	shrubs	overstory
I. Grassland	*high*	*low*	*low*
II. Shrubs	*low*	*high*	*low*
III. Oak/pine- grassland	*high*	*low*	*high*
IV. Oak/pine- Shrubs	*low*	*high*	*high*

(1997), but the rules are self-explanatory. Each rule is numbered according to the transition it interprets. For example, rule T3&6.4 (i.e., the fourth rule used in transitions 3 and 6) has the following form:

(Rule T3&6.4
if(soil_type/=very_rocky)
shrubs = low)
(grazing_level=low)
(litter_level)=low)
(dist_shrubs=low)
then (predict shrubs moderate plus
time 5 prob 0.2))

Transitions 3 and 6 involve shrub invasion. The transition rule states that if the soil texture is not *very rocky*, and if the current grazing level is low but the litter level is also low (as would occur, for example, after a grass fire), and if the current shrub level is low but there are shrubs nearby, then there is a 20% chance that a moderate level of shrubs will be present on the site in 5 years. The value of 20% was determined by our own experience and observations from historical aerial photos at the SFREC. Other rules in the knowledge have a similar structure. Each rule is a statement of cause and effect in the sense that if the parameters have the values indicated in the "if" part of the rule, then this will cause the effect shown in the "then" part of the rule. The probabilistic component of the rule is implemented by selecting a random number on the interval 0 to 1. If the number is between 0 and 0.2, the transition is implemented, otherwise not.

A single time step of the model consists of successively running through the rules as described above. If the test of the "if" part of a rule is passed, the "then" part is implemented. If the implementation involves an event that occurs at a later time, as is the case with Rule T3&6.4 above, then this transition is placed in a chronologically ordered "event queue." All the rules in the knowledge base are cyclically tested until no new transitions are generated. At this point the time step is complete for that raster cell. If any events have been placed in the event queue, after all raster cells are processed the system updates its time to the value of the next occurring event and the transition is implemented. The spatial portion of the algorithm is carried out, and the process is then repeated with the new parameter values.

The Spatial Component

The spatial component of the simulation process links the state-and-transition model of the previous section to the geographic information system. Parameter and variable values for the model are stored in GIS layers (these are Idrisi files, called *image files* in Idrisi terminology), with 1 layer for each parameter or variable. Each image file contains data for the grid of cells that represents the site. Each cell in an image file contains a single number that represents the value in that cell of the quantity represented by the GIS layer. The raster cells in the hardwood rangeland model are squares representing a land surface 35 m on a side. This size was selected because it is small enough to characterize relatively uniform areas but large enough that a single cell will contain more than 1 tree.

At each time step the QTIP program proceeds on a cell-by-cell basis. For each cell it first reads from the Idrisi image files the values of all the model variables in that cell. It then runs a single dynamic step of the simulation for the cell. During this step, any time a transition rule is invoked to predict a future event, QTIP creates new Idrisi image files to store that event. After the time step has been carried out for all of the cells, QTIP calls Idrisi to perform GIS operations such as distance and area calculations using the newly-written image files.

In the present hardwood rangeland model there is only 1 spatial calculation. This involves the spread of shrubs. At the spatial and temporal scale of the model, shrubs are assumed to spread more rapidly to contiguous regions so that the probability that a site with herbaceous groundcover will be invaded by shrubs is increased if there are shrubs at a nearby site. This is reflected in Rule T3&6.4, given as an example in the previous section, in which the variable *dist_shrubs* must have the value *low* for the rule to be triggered. This variable represents the distance from the cell to the nearest cell in which the variable *shrubs* has the value *high*. Idrisi computes values of the variable *dist_shrubs* for each cell during the spatial part of the simulation algorithm. This is accomplished in a 3 step process. First, a layer is constructed in which each cell is assigned a value 0 or 1 depending on whether the variable *shrubs* has the value *high* in that cell. Next, the Idrisi Distance module is used to compute the distance of each cell from the nearest high-shrub cell. Finally, these distances are reclassified as *low* if they have a value of 175 m or less.

Idrisi image files are also used to characterize external inputs to the system. Disturbances (e.g., fire, tree cutting, herbicide application, and changes in the grazing regime) are defined in image files and read by QTIP during the spatial part of the algorithm. Each disturbance is treated as an event and placed in the "event queue." Conditions after the disturbance are re-evaluated during the dynamic time step, and a forecast consistent with these new conditions is generated. If a change in value takes place in any cell, then all changes of value of that variable in that cell predicted at a later time are eliminated from the event queue. For example, if the event queue contains a transition of the *shrub* variable to *moderate* in 5 years and a fire takes place in the meantime reducing shrubs to *low* in

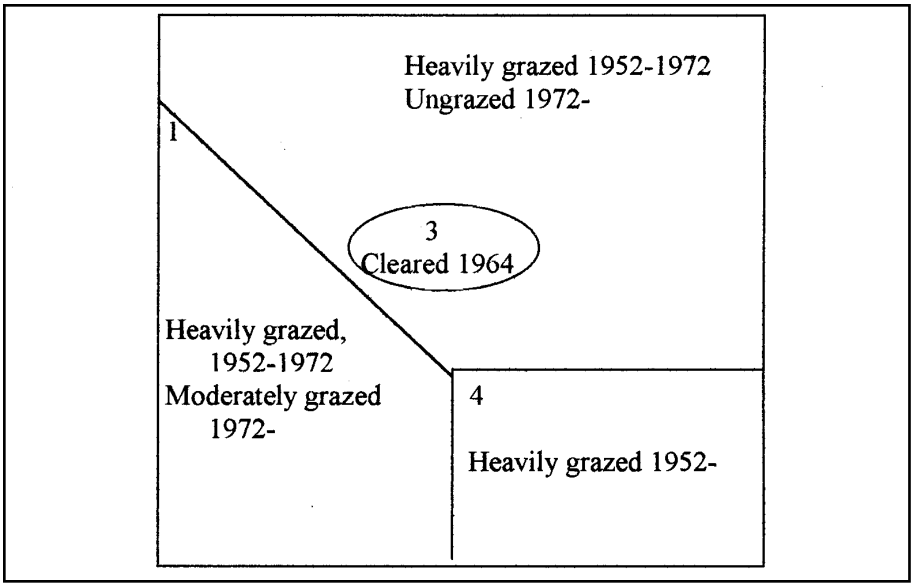


Fig. 2. Schematic map of the study site used to illustrate the state-and-transition model. Site is 700 m on a side and is located at the University of California Sierra Foothills Research and Extension Center. The site is divided into 4 areas based on grazing and clearing history.

that cell, then the shrub transition to *moderate* in that cell is removed from the queue of future events.

Comparison of model output with study site

The model was tested by comparing its simulation results with the vegetation dynamics in a 49 ha site on the Koch tract of the SFREC. The site is a square, 700 m on a side. Black and white aerial photographs including the site taken in 1952, 1972, 1984, 1989, and 1993 were obtained from the National Archives, USDA, and the WAC Corporation, Eugene, Ore. All photos were taken in May, June, July, or August. An orthophotograph of the site taken in 1978 was obtained from the US Geological Survey and was used as the base map. The photographs were georegistered to the base map using the Idrisi Resample module with approximately 20 landmarks in each photograph.

Figure 2 is a simple schematic map of the site. The southeast corner, denoted area 4 in Figure 2, is privately owned. The remainder of the site was incorporated into the SFREC in 1960. The northeast portion, denoted area 2 in Figure 2, was surrounded by an exclosure in 1972, and no domestic animal grazing has occurred in this area since that time although wild herbivores still have access. Area 1 in Figure 2 has been continuously grazed since the late nineteenth century (McClaran 1986). Detailed grazing records are not available, but the grazing intensity on the SFREC has been moderate (approximately 0.7 acres/AUM) for at least the last 20 years. Grazing intensity on the privately-owned area is generally heavier. An area in the ungrazed region, denoted area 3 in Figure 2, was cleared of oak trees in 1964. Parts of the grazed area of the SFREC have been cleared more recently in 1988 and 1989. The southwest portion of the site was part of an area in which McClaran (1986) examined fire scars in tree rings in order to establish the dates at which fires had occurred. McClaran concluded that the most recent fire on the site occurred in 1944.

Locations at the site containing each of the 4 vegetation states in the state-and-transition model of Figure 1 were identified and their position determined using a differentially corrected GPS (Trimble Pro-XL, Trimble Navigation, Sunnyvale, Calif.). The locations recorded with the GPS were identified in the most recent (1993) aerial photograph and used to guide photointerpretation. Each of the aerial photographs was interpreted after mounting the photograph on a light table. Our conclusions regarding our ability to accurately interpret black-and-white photos matched those of Davis et al. (1995). Different tree species could not be distinguished at all. Individual mature trees could easily be distinguished from shrubs, but clusters of immature trees were difficult to distinguish from shrubs. In general, mature trees appeared darker than other vegetation. Shrub understory could not be reliably distinguished from herbaceous understory.

Photointerpretation was partially carried out using image processing software Paint Shop Pro (JASC, Inc., Eden Prairie, Minn.) and Adobe Photoshop (Adobe Systems, Mountain View, Calif.). The georegistered aerial photographs were subdivided into 400 square cells, each having a side length of 35 m on the ground, corresponding to the raster cells in the GIS model. For each cell a histogram of the frequency of darkness of the gray tones was constructed. Amount of dark gray in the cell was correlated to canopy cover by comparing ground-based observations with the 1993 photo. Cover was classed as *high, moderate,* or *low* based on the cover classes defined by Pillsbury et al. (1991), with their “scattered” and “low” categories lumped together as *low*. Thus, 0–33% cover was classed as *low*, 34–75% cover was classed as *moderate*, and 76–100% cover was classed as *high*. The cover classes in each cell of the 1952 photo were then estimated based on their gray level.

The 1952 photograph did not appear to contain many areas high in shrubs. Therefore, shrub cover was assumed to be generally low at the start of the simulation except in 2 areas that appear to have been high in shrubs. Soil texture data was taken from the library of Idrisi image files maintained by the SFREC. The original files, which had been digitized from SCS soil survey maps, were resampled to the model grid of 35 m on a side. Soil depth was assumed to be moderate except in those areas where rocky outcroppings could be observed on the ground.

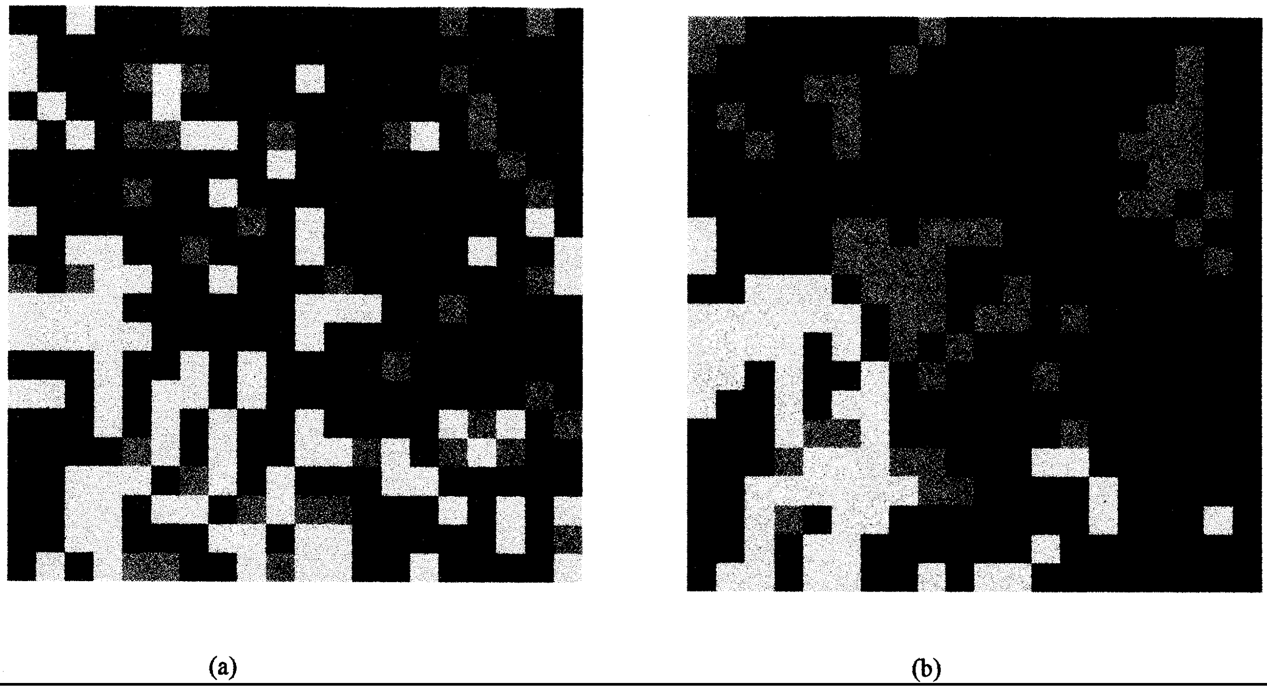


Fig. 3. (a) 1993 aerial photograph resampled to the same cell size as the model (35 m) and reclassified into categories of *low* (0–33% cover), *moderate* (34–75% cover), and *high* (76–100% cover). (b) Model output in year 41, corresponding to 1993. In both images the lightest shade corresponds to cover value of *low*, the medium shade corresponds to a cover value of *moderate*, and the darkest to shade corresponds to *high*.

The simulation process consisted of setting the model variables to values consistent with those in the 1952 photo and running the model for a simulated time of 41 years. Simulation output was compared quantitatively with the 1993 aerial photograph as follows. The photograph was resampled to the same 35 m grid as the model, so that each raster cell in the photo was assigned the gray scale value at the center of the cell. These values were then reclassified into 1 of 3 values, corresponding to *high*, *moderate,* and *low* cover. A GIS layer was then produced by subtracting the model output from the resampled, reclassified image. Cells in this resultant layer could take on one of 5 values between –2 and 2. A value of –2, for example, indicated that the photo was *low* and the model output was *high.* A value of 0 indicated no difference. The level of agreement of between the model and the 1993 photo was then indicated by the frequency histogram of the resultant GIS layer. The mean and standard deviation indicate the level of bias and the accuracy of the model, respectively. A mean and standard deviation of zero would indicate a perfect match of model output to the data.

Results

The first row of Table 3 shows the frequency histogram comparing the initial model with the data. Figure 3 shows the resampled, reclassified 1993 aerial photo and the model output of the variable *overstory* in year 1941. In all figures of model output, the light shade of gray represents cells in which *overstory* has the value *low*, the medium shade represents the value *moderate*, and the darkest shade of gray represents the value *high*.

The initial simulation results indicated fairly good general agreement. One subjectively substantial difference between the model output and the real data was that the site had several areas where tree establishment remained low over the entire simulation (these areas are also clearly visible in an earlier 1937 photo not used in this study because of its poor quality). The model had no provision to predict the existence of these areas. There are a number of possible reasons for the existence of these treeless areas including shallow soil, dense litter mats from medusahead (*Taeniatherum asperum* Nevskii) infestations, and subtle differences in soil properties such as acidity, water holding capacity, and drainage. In the absence of any evidence favoring one particular cause over another, we established a variable called *overstory_potential* and gave it the value *low* in those cells that did

Table 3. Frequency histograms of deviation of the simulation output from actual data. Histogram values indicate difference between data and model, where *high, moderate,* and *low* are valued at 2, 1, and 0 respectively. Mean and standard deviation respectively indicate level of bias and accuracy of model.

Difference	-2	-1	0	1	2	Mean	Std Dev
Original Model	0.105	0.0925	0.6675	0.0975	0.0375	-0.13	0.8631
Modified Model	0.0975	0.08	0.6625	0.1225	0.0375	-0.0775	0.8593

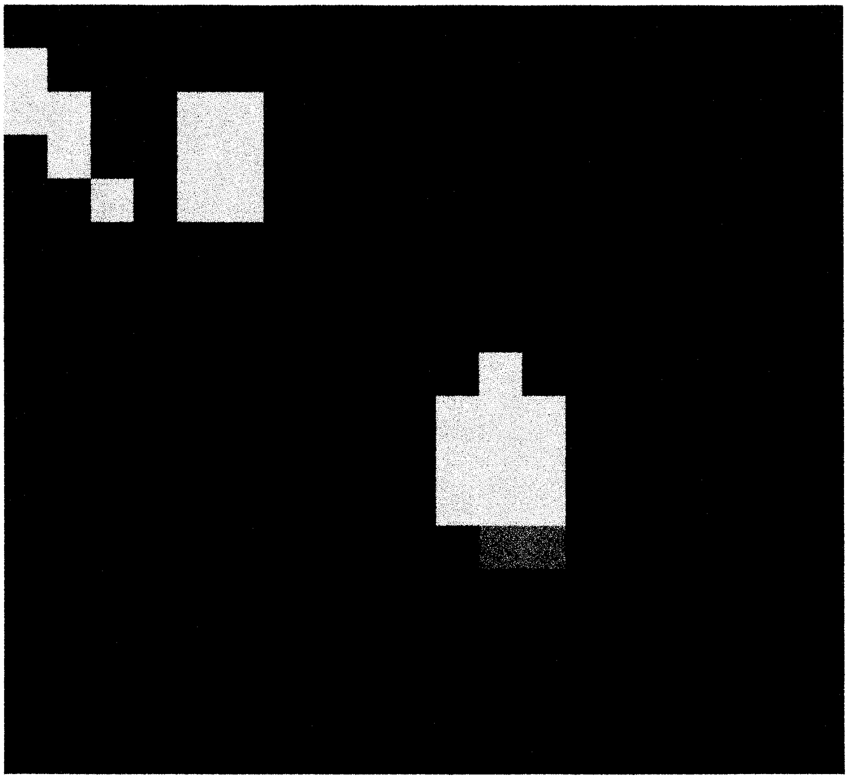


Fig. 4. Spatial distribution of the parameter *tree_potential*, introduced to induce the model output to display areas that remain treeless for at least 56 years.

not exhibit increase in canopy cover or sapling growth over the time span of the simulation. Figure 4 shows a representation of the *overstory_potential* layer used in the modified model.

Figure 5 shows the overstory component of the simulation of the model as finally constituted. Only in those cells in which the value of *overstory_potential* was *low* was there any difference between the simulation results with the original and the modified models. In the figure each aerial photograph is matched with the corresponding model output. In both the simulation output and the data, the general tendency of the site between years 1952 and 1972 was for canopy cover to increase. Cover remained roughly constant between the years 1972 and 1993 except in areas that were cleared. The second row of Table 3 shows the frequency histogram of comparison between the model output and the resampled, reclassified aerial photo. There is little quantitative improvement, although the modified model does (since it is forced to) accurately reflect the fact that some areas on the site remain treeless. It is important, however, to recognize that the reference data set of Figure 3a, although it is constructed according to objective criteria, may itself be criticized for its accuracy of representation.

Discussion and Conclusions

As shown in Figure 3 the simulation results generally reflect the vegetation dynamics observed on the test site as interpreted through analysis of historic aerial photographs. The vegetation trends on the site fall within the pattern of vegetation dynamics observed by Davis et al. (1995). They found that there has been little or no net statewide gain or loss of canopy cover in those areas of blue oak woodland not subject to artificial vegetation loss (e.g., through urban development or clearing). They found that some areas of blue oak woodland increased in canopy cover and some declined. It should be noted that on our study site much of the increase in canopy cover was due to the increase in size of mature trees. There is little indication of substantial growth of trees from recently germinated acorns.

The simulation results presented in this paper are not a true validation test of the model. This would require replication of the comparison between model and real site on a range of randomly selected sites. The object of this paper is not to present a properly validated spatial state-and-transition model but rather to demonstrate that the methodology introduced in this paper may be useful for developing spatially explicit state-and-transition models. This methodology consists of interpreting the catalog of transitions as a set of rules in the rule base of a qualitative simulation model and of linking this qualitative model to a GIS by alternating between dynamic and spatial updating of the model variables. The qualitative simulation model is used to provide the dynamic updating and the GIS is used to provide the spatial updating.

Since vegetation communities are highly stochastic, no simulation program can predict with certainty the future course of vegetation dynamics. Markov and semi-Markov transition models have been used to study vegetation dynamics in a probabilistic sense (Callaway and Davis 1993, Scanlan 1994, Scanlan and Archer 1991). The alternating spatial and temporal step algorithm used in this paper could be applied equally well to these models to add an explicit spatial component. Within the context of qualitative models such as that discussed in this paper, there are at least 2 ways to incorporate uncertainty about the outcome of the process. One is to include an explicit uncertainty calculus in the

Fig. 5a
1952

Fig. 5b
1952

Fig. 5c
1989

Fig. 5d
1993

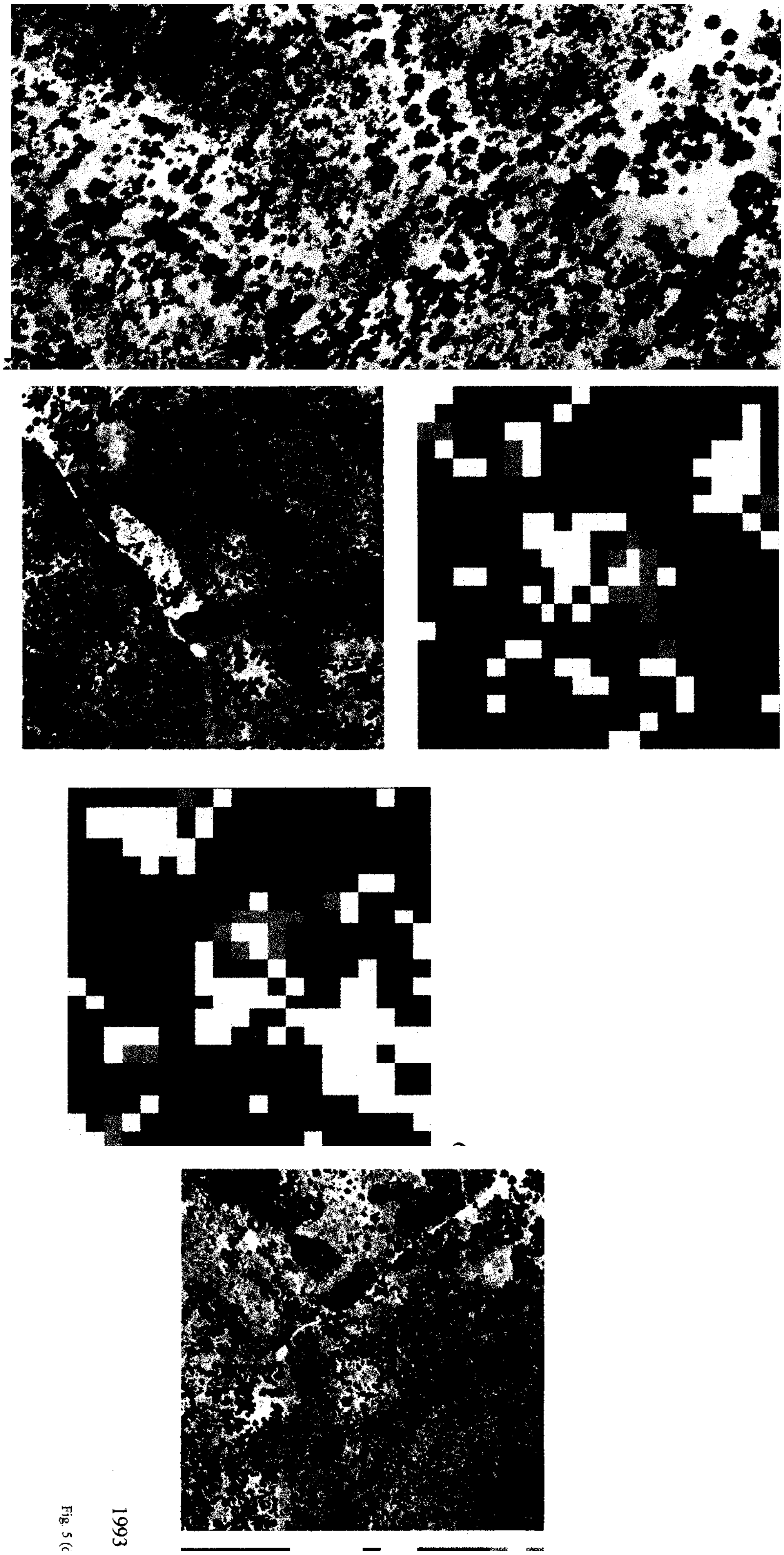


Fig. 5. Orthographically registered aerial photographs of the study site, shown next to the corresponding model output of the value of *overstory*. (a) Site in 1952, used as the initial state in the model. (b) Site in 1972. (c) Site in 1989. (d) Site in 1993. The 1993 photograph was used to calibrate the gray scale. In both images the lightest shade corresponds to cover value of *low*, the medium shade corresponds to a cover value of *moderate*, and the darkest shade corresponds to *high*.

program. This is common practice in expert system design (Plant and Stone 1991, chapter 3). In the present application the 2 most appropriate representations of uncertainty are Bayesian networks (Olson et al. 1990) and fuzzy logic (DuBois and Prade 1980). A second approach, which is taken in the QTIP program described in this paper, is to provide a framework for Monte Carlo simulation (Rubinstein 1981). In this approach, the result of an individual simulation is dependent on the value of 1 or more random variables. The simulation is run repeatedly, generating values of these random variables each time, and statistics are collected describing the distribution of the simulation results.

The methodology of qualitative simulation may be compared to more quantitative methods such as traditional simulation models (Shugart 1984) and individual-based models (Humphries et al. 1996). The qualitative simulation model has 2 primary advantages in this use over numerical population models. The first is that the qualitative model fits more naturally with the transition rules of the state-and-transition model. These transition rules are expressed in qualitative rather than quantitative terms. The forward-chaining algorithm of the dynamic step, in which rules are successively and repeatedly tested to determine whether the conditions of their "if" parts are satisfied, ensures that all rules will be invoked when it is appropriate to do so. Moreover, the QTIP program, like all rule-based expert systems, can provide a means for explaining its transitions (e.g., Plant and Stone 1991). In QTIP, each time a rule is invoked to change the value of a variable, a record of that transaction is added to a file. After a simulation run, this file can be used to assist in determining how the solution was generated.

The second advantage of qualitative simulation is that, to use the terms of Plant (1997), the qualitative model trades precision for robustness. That is, the solution of a qualitative model, since it is expressed in terms of a few discrete states rather than a continuum of numerical values, lacks the precision of a traditional numerical model. However, because each state represents a range of numerical values, and because the dynamics of the solution are controlled by a model with an inherently simpler structure, the qualitative model may be more robust than the numerical one. Traditional numerical models have been useful for deriving general principles in community ecology but have been less successful in accurately predicting the dynamics of particular ecological communities. The qualitative simulation methodology does have disadvantages. It cannot provide precise numerical estimates of observable quantities. Also, the relatively coarse, categorical description of states makes it difficult or impossible to describe some subtle processes in vegetation dynamics.

Qualitative simulation fits naturally with the state-and-transition model as a complement to GIS for spatial and dynamic simulation. This is illustrated by the ability of the simple model demonstrated here to detect spatial inconsistencies in the state-and-transition model such as the persistence of treeless areas. Westoby et al. (1989) emphasized that the primary use of the state-and-transition model is as a management tool. Grice and Macleod (1994) pointed out that most state-and-transition models have been descriptive with little or no explanatory component. If such a model is to contain an explanatory component, it must also be spatially explicit if it is to be truly useful as a management tool. Although Bellamy and Brown (1994) discussed the advantages of linkage between a state-and-transition model and a GIS, there have been few attempts to actually implement such a linkage.

The application of a computer-based, spatially explicit state-and-transition model depends on the spatial scale of the model. The model described in this paper is approximately at the scale of the individual paddock. At this scale, the model discussed in this paper would be useful to the individual ranch manager as a tool for evaluating alternative vegetation and animal management scenarios to estimate their effect on oak growth or regrowth. At a larger spatial scale, such models would be useful to policy makers as a means of estimating or visualizing the effect of alternative land use policies on vegetation dynamics. A primary value in both the small scale and the large-scale use is the possibility of enabling the manager to identify unintended consequences of management decisions.

Software Availability

The qualitative simulation model runs on any DOS-based computer with a 486 or Pentium processor. The source code is written in C and can be compiled using any common C compiler. This source code as well as the model itself is available on the Internet at

http://agronomy.ucdavis.edu/plant.

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Effects of management on species dynamics of Canadian aspen parkland pastures

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Abstract

The effects of grazing, fertilizing, and seeding on persistence of herbaceous species was monitored by point quadrat about every second year from 1975 to 1989 in a low-fertility pasture in the aspen parkland vegetation zone of east-central Saskatchewan, Canada. Ground cover response to continuous grazing was contrasted with that of 4- and 6-paddock rotationally-grazed areas fertilized in the fall of every other year with 90 kg N, 45 kg P_2O_5, 10 kg S ha^{-1}. The original vegetation in 2 paddocks of the 6-paddock system was replaced with Russian wildrye (*Psathyrostachys juncea* (Fisch.) Nevski) in 1976, and in 1 of the other 4 paddocks in turn with smooth brome (*Bromus inermis* Leyss.)-alfalfa (*Medicago sativa* L.) in 1979 and 1981, crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.) in 1983, and a meadow brome (*Bromus riparius* Rehm.)-alfalfa mix in 1985. Initially, smooth brome and creeping red fescue (*Festuca rubra* L.) dominated the vegetation with ground cover estimates of 10–20% and 40–60%, respectively. Alfalfa ground cover was less than 1%. With the changes in management, Kentucky bluegrass (*Poa pratensis* L.) replaced creeping red fescue. Alfalfa increased until 1980 and then declined to its original level, apparently in response to precipitation trends. Russian wildrye almost died out and was replaced by brome and Kentucky bluegrass. Reseeding with smooth bromegrass-alfalfa did not consistently increase brome ground cover beyond that obtained by rotational grazing and fertilization, and increased alfalfa only temporarily. Cultivation during the summer before spring seeding resulted in partial recovery of the old vegetation and invasion by Kentucky bluegrass. Total ground cover varied from year to year in response to spring precipitation. Forbs usually increased after reseeding, but declined to their original levels within 5 years.

Key Words: *Bromus inermis*, *Medicago sativa*, *Psathyrostachys juncea*, *Agropyron cristatum*, *Bromus riparius*, grazing system, seeding, fertilizing

Resumen

Los efectos de pastoreo, fertilización y siembra en la persistencia de especies herbáceas fue determinado desde 1975, por muestreo en cuadrículas aproximadramente cada dos años, en una pastura establecida en un suelo de baja fertilidad en la zona de los parques de álamo tremblón (chopo) en el centro este de Saskatchewan, Canadá. La respuesta de la cubierta vegetal al pastoreo continuo fue comparado con aquella observada bajo pastoreo rotativo en sistemas de 4- y 6- parcelas fertilizadas cada segundo año en el otoño con 90 kg N, 45 kg P_2O_5 y 10 kg S ha^{-1}. La vegetación original de dos parcelas del sistema de y-parcelas fue reemplazada con *Psathyrostachys juncea* (Fisch.) Nevski en 1976, dos parcelas fueron sembradas con un mezcla de *Bromus inermis* Leyss. y *Medicago sativa* L., una en 1979 y la otra en 1981, otra parcela fue sembrada con *Agropyrum cristatum* (L.) Gaertn. en 1983, y la parcela restante fue sembrada con una mescla de *Bromus riparius* Rehm. y *Medicago sativa* en 1985. Inicialmente, *Bromus inermis* y *Festuca rubra* L. dominaban L. dominaban la vegetación, cubriendo 10–20% y 40–60% de la superficie, respectivamente. *Medicago sativa* cubría menos del 1% de la superficie. Con los cambios introducidos en el manejo, *Poa pratensis* L. Reemplazó *Festuca rubra*. *Medicago sativa* incrementó el porcentaje de superficie cubierta hasta 1980, para luego disminuir hasta alcanzar sus niveles originales, aparentemente, esto fue en respuesta a variaciones pluviométricas durante el período del estudio. *Psathyrostachys juncea* desapareció casi completamente y fue reemplazada por *Bromus* sp. y *Poa pratensis*. Resembrando una mezcla de *Bromus inermis* y *Medicago sativa* no aumentó la proporción de la superficie cubierta por *Bromus inermis* mas allá de la obtenida por medio del pastoreo rotativo y fertilización, e incremento temporalmente el porcentaje de la superficie cubierta por *Medicago sativa*. Labranza del suelo en el verano anterior a la siembra de primavera produjo una recuperación parcial de la vegetación antigua y una invasión de *Poa pratensis*. El porcentaje de la superficie del suelo cubierta por vegetación vario de año en año, dependiendo del régimen pluviométrico en la primavera. Especies herbáceas de joja ancha normalmente aumentaron despuás de la resiembra, para luego disminuir hasta sus niveles originales dentro de cinco años.

In the grass-forest transition zone of western Canada, commonly called the aspen parkland, grazing areas have been developed from aspen-conifer forest, rough fescue (*Festuca hallii* (Vasey) Piper) grasslands, and abandoned farmland. Each pasture is a unique mixture of original vegetation, tree regrowth, moist meadows, ponds, lakes, and swamps. The unifying aspect is the dominance of the seeded forages: smooth bromegrass (*Bromus inermis* Leyss.), creeping red fescue (*Festuca rubra* L.), and alfalfa (*Medicago sativa* L.). Looman (1976) concluded that the

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seeded forages have established an equilibrium with the environment after about 20 years. Even though soil fertility has declined to low levels, smooth bromegrass remains a dominant component of the pastures because of the environmental similarity to its native Eurasia.

Recommendations for increasing pasture productivity in the aspen parkland (Tremblay 1995) include the use of alfalfa in spite of the risk of bloat (Beacom 1991), rotational grazing although evidence for its value is inconsistent (Cooke et al. 1965, Walton et al. 1981), and fertilization which has only a 1 to 2 year benefit (Nuttall et al. 1991). Above-ground dry matter measures of species productivity used in these reports have not shown clearly the effects of management on the relationships among several species in a pasture. Other reports show that management can affect biodiversity (de Vries and Kruijne 1960) and ground cover composition (Gifford and Hawkins 1976). Changes in plant associations following fertility changes (Looman 1980) or grazing strategies (Savory 1983) may have productivity implications.

In this study we measure species ground cover to detect: 1) Changes in resident vegetation of an aspen parkland pasture when fertilizer is applied and cattle management is changed from continuous to rotational or time-restricted grazing. 2) The permanence of changes in vegetation resulting from changes in fertility, grazing management, and species replacement.

Materials and Methods

Study Site

The 375 ha experimental area is part of the 5,000 ha Pathlow Community Pasture in east-central Saskatchewan (52° 41'N, 104° 58'W). Topography is undulating to varying degrees, with most soils being textural variants of luvisolic soils (Cryoboralfs, USDA-SCS 1975). By the mid-1960's, small areas totalling about 40% of the study site had been farmed for about 30 years, with the remainder in poplar (*Populus* spp.) forest. At that time, the woody growth was burned, and the entire area cultivated and seeded to a mixture of grasses and legumes, primarily smooth bromegrass, creeping red fescue, and alfalfa. In 1975, when this study began, smooth bromegrass comprised 10–30%, and creeping red fescue about 50% of the herbaceous ground cover. Kentucky bluegrass (*Poa pratensis* L.) was a minor constituent of the understory with < 5% ground cover. Alfalfa was unevenly distributed and had a ground cover < 2%. Broad-leaved, mostly native species (forbs), were present in small numbers. Season-long grazing and no additional fertilizer since seeding had led to deterioration and reduced grazing capacity.

Summaries of weather records from the Environment Canada site 3 km north of Pathlow pasture are presented in Table 1. Growing-season degree-days are summed between 1 April and 30 September: rarely are temperatures outside this period warm enough for growth. For the period from 1 September to 31 May, which supplies the water affecting growth at the time of the surveys, precipitation during the period 1975 to 1979 was average to above average from 1980 to 1983 was mostly below average, was above average in 1984 and 1985, and was below average from 1986 to 1989. Growing season degree-days tended to be the inverse of the precipitation.

Table 1. Weather summaries for 1975–1989 at a site 3 km north of the experimental area in east-central Saskatchewan (52°41'N, 104°58'W).

Year	Precipitation: Prev. Summer (1 Jun–31 Aug prev yr.)	Precipitation: Winter (1 Sept prev. yr —31 Mar)	Precipitation: Spring (1 Apr—31 May)	Growing Season Degree-Days above 5°C
	(mm)	(mm)	(mm)	(°C)
1975	232	132	102	1,434
1976	233	112	48	1,706
1977	235	90	153	1,627
1978	144	178	72	1,556
1979	242	227	47	1,491
1980	169	168	10	1,705
1981	210	89	44	1,720
1982	146	207	91	1,453
1983	149	100	64	1,591
1984	245	157	153	1,656
1985	139	221	104	1.305
1986	168	127	68	1,548
1987	173	130	46	1,716
1988	187	154	16	1,867
1989	131	131	66	1,676
Average	187	148	72	1,603

Treatments

The grazing systems consisted of 4-paddock, and 6-paddock rotations, each replicated 4 times, and a continuously-grazed paddock replicated twice. Each paddock in the rotations was about 8 ha (400 × 200 m), and each continuously-grazed area was about 16 ha (400 × 400 m). The 40 paddocks in the rotations were fertilized with 90 kg nitrogen, 45 kg phosphate and 10 kg sulphur ha^{-1} in fall 1975. Thereafter, half the paddocks were fertilized at the same rates in the fall in 1977, 1979, 1981, 1983, and 1985, and the other half were fertilized in fall 1978, 1980, 1982, and spring 1985. All paddocks were fertilized each fall thereafter at half the initial rate.

In 1976, 2 paddocks of the 6-paddock system in each replicate were seeded with 5.6 kg ha^{-1} 'Swift' Russian wildrye [*Psathyrostachys juncea* (Fisch.) Nevski] and 19 kg ha^{-1} oats (*Avena sativa* L.). In 1979 and 1981, a paddock in each replicate was reseeded with 9 kg ha^{-1}, 'Carlton' smooth bromegrass and 2.2 kg ha^{-1} 'Rambler' alfalfa. In 1983, one paddock per replicate was seeded with 9 kg ha^{-1} 'Parkway' crested wheatgrass [*Agropyron cristatum* (L.) Gaertn.], and in 1985, one was seeded with 9 kg ha^{-1} 'Regar' meadow bromegrass (*Bromus riparius* Rehm.) and 2.2 kg ha^{-1} 'Rambler' alfalfa. In each case, the paddocks were cultivated to destroy resident vegetation the summer prior to reseeding.

Each year, starting in 1976, grazing commenced when the grass reached 10–15 cm, usually during the last week of May. Cow-calf units grazed in a paddock for 1–3 weeks and were moved to the next paddock when most of the forage had been consumed. Each paddock was grazed once or twice during the grazing season depending on forage production. Specifics on livestock numbers and grazing duration are presented in McCartney et al. (1999).

Botanical survey methodology

In fall 1974, prior to fencing, the experimental area was divided into rectangles, each 305 × 152 m. In spring 1975, basal ground cover was estimated in every second rectangle in a checkerboard pattern. In each sampled rectangle, 10 sites were selected randomly. Basal cover of all herbaceous species was estimated using an 18-pin vertical point frame with pins spaced 5 cm apart. Six frames about 2 m apart were read per site (i.e. 108 pins). Following subdivision into paddocks, 10 sites were selected at random in each paddock, and visited in 1976, 1978, 1980, 1982, 1984, 1988, and 1989 using the same procedure as in 1975, with the exception that 12 frames (i.e. 216 points) were read per site. The continuously-grazed paddocks were surveyed only in 1975, 1984, 1988, and 1989. The paddocks seeded to Russian wildrye were not included in the 1976 survey because of the recent disturbance. The sampling was started in late May and usually completed by the end of June.

Data summarization and statistical analyses

Data were analyzed: 1) For differences between grazing systems in total vegetation ground cover; and 2) For composition by species/species groups (smooth bromegrass, creeping red fescue, bluegrasses (mostly *Poa pratensis* L.), alfalfa, annual plus biennial forbs, and perennial forbs (Table 2). As paddocks were seeded, 3 species–Russian wildrye, crested wheatgrass, and meadow bromegrass, were added. These data were analyzed for effects of the various rejuvenation treatments (fertilizer, breaking and seeding) on the relative proportions of the species and species groups within grazing systems.

Ground cover data, i.e. the number of basal hits with respect to the number of pins dropped per site, and number of basal hits by species/species group with respect to total number of hits, are expected to exhibit a binomial distribution. These data were analyzed using a generalized linear model using a logit link, fitted by maximum likelihood, and summarized by an analysis of deviance. These procedures, which include the ordinary linear model and the analysis of variance for identically distributed normal data as special cases, are described in detail by McCullagh and Nelder (1989).

Because of the non-constant variance associated with the binomial distribution, terms in fitting of the generalized linear model were included sequentially according to the following rules:

Subject to the actual experimental protocol,

1. Block factors are fitted before treatments and interactions:
2. Treatment main effects and interactions having lesser importance are included before those of primary interest;

Table 2. The most frequently occuring annual, biennial, and perennial forbs found between 1975 and 1989 at the study site, Pathlow pasture, east-central Saskatchewan.

Annual and biennial Forbs	Perennial Forbs
Androsace septentrionalis L.	*Antennaria aprica* Greene
Axyris amaranthoides L.	*Antennaria neglecta* Greene
Capsella bursa-pastoris (L.) Medic.	*Antennaria rosea* Greene
Chenopodium album L.	*Aster ciliolatus* Lindl.
Crepis tectorum L.	*Erigeron philadelphicus* L.
Descurainia sophia (L.) Webb	*Fragaria virginiana* Dcne.
Draba nemorosa L.	*Galium boreale* L.
Lappula echinata Gilib.	*Maianthemum canadense* Desf.
Lepidium densiflorum Schrad.	*Plantago major* L.
Monolepis nuttalliana (R&S) Greene	*Solidago canadensis* L.
Potentilla norvegica L.	*Taraxacum officinale* Weber
Thlaspi arvense L.	*Thalictrum venulosum* Trel.
	Viola cucullata Ait.
	Viola rugulosa Greene

Table 3. Analyses of Deviance: total plant counts (basal cover) in relation to the number of sampled points, assuming binomial data distribution, Pathlow pasture, east-central Saskatchewan.

Year	Source of Deviance						
	Replicates (R)	Grazing System (GS)	R x GS	Fertility (F)	GS x F	Paddocks within R x GS x F	Residual Degrees of Freedom
1975	23.9	3.4	19.0	0.5	0.4	49.4	254
1976	147.2	0.6	21.9	0.3	0.0	46.2	289
1978	35.2	6.2	15.9	49.6	0.5	99.2	363
1980	25.3	10.4	9.1	27.1	7.9	123.4	361
1982	11.0	4.3	3.2	76.9	0.1	200.2	362
1984	28.1	14.3	2.1	0.0	7.4	298.9	363
1988	2.8	15.6	5.4	0.8	9.4	97.4	366
1989	9.9	6.9	15.0	1.3	1.0	57.6	363
D.F.	3	1	3	1	1	27+	
Chi^2 5%	7.8	3.8	7.8	3.8	3.8	40.1+	

Degrees of freedom 18 in 1975, 19 in 1976, Chi^2 28.9 in 1975, 30.1 in 1976.

Table 4. Mean basal ground cover % (standard error) by grazing system between 1975 and 1989, Pathlow pasture, east-central Saskatchewan.

Year	4-Field rotation fertilizer		6-Field rotation fertilizer reseeding		Continuously grazed		Significance Level
	(%)						
1975	20	(0.3)	22	(0.4)	21	(0.7)	NS
1976	28	(0.2)	27	(0.2)	-	-	NS
1978	20	(0.2)	19	(0.2)	-	-	5%
1980	14	(0.2)	12	(0.1)	-	-	1%
1982	21	(0.2)	19	(0.2)	-	-	5%
1984	27	(0.2)	24	(0.2)	35	(0.7)	1%
1988	13	(0.2)	15	(0.2)	27	(0.7)	1%
1989	30	(0.3)	28	(0.2)	34	(0.7)	1%

NS, 5%, 1%: not significantly different, different for $P < 0.05$, $P < 0.01$

3. Marginality constraints are obeyed, i.e. higher-order interactions are not included before those of lower order included in (marginal to) them.

The sequential fitting allows estimates of the changes in deviance (interpretable as goodness of fit) to be determined as each term is included. Changes in deviance are referred to the chi-squared distribution for testing significance; a probability of less than 5% is considered to be significant. From the fitted model, estimates of expected values, which in the ordinary analysis of variance are called "least square means", and approximate standard errors are obtained. Further details on theory and applications can be found in McCullagh and Nelder (1989). Genstat 5, Release 2.1, (Lawes Agricultural Trust 1987) was used for all statistical computations.

Results

Total vegetation cover

Interaction among paddocks, replicates, grazing systems, and fertility was significant in 1975 before treatments were applied, demonstrating the variability of the vegetation in the pasture (Table 3). Adding fertilizer to half the paddocks in alternate years had significant effects on vegetation cover between 1978 and 1982, but not in 1984. The analyses reflect the uniform fertilizer additions across the pasture in 1988 and 1989.

Imposition of rotational grazing systems also caused significant differences in vegetation cover (Table 3). By 1984, the continuously-grazed paddocks had greater vegetation cover than the rotationally-grazed paddocks, and the 4-field paddocks had more cover than the 6-field paddocks (Table 4). With rotational grazing, the cover varied by 100% between the years with greatest (1989) and least (1980) cover. The increase between 1975 and 1976 was probably in response to the fertilizer application in fall 1975. In later years, changes appeared to be in response to spring moisture. Year-to-year cover changes were much less in continuously-grazed paddocks.

Species responses to continuous grazing

The proportion of smooth bromegrass in the vegetation changed little between 1975 and 1989, remaining at about 11% (Table 5). Creeping red fescue declined significantly from 49% to 19% in the same period and Kentucky bluegrass increased slightly from 2% to 8%. Alfalfa and annual-biennial forbs almost disappeared. There was a major increase in perennial forbs from 7% in 1975 to over 50% in 1989, caused mainly by the spread of mat-forming *Antennaria* species.

Species responses in the 4-field rotation

For most of the 13-year period of the surveys, there was significantly more bromegrass and creeping red fescue cover in paddocks fertilized the fall before each survey than in the paddocks fertilized 18 months previously (Table 6). During this time the proportion of bromegrass cover in the paddocks increased by about 50%, and that of the fescue declined about 5-fold. There was no consistent effect of fertilizer application timing on Kentucky bluegrass cover although it increased in proportion from < 3% to 40% of the ground cover between 1976 and 1989. The proportion of alfalfa in the vegetation cover quadrupled between 1975 and 1982, and then declined to its original level by 1989 with no significant differences due to the differential fertilizer application times. Cover of annual and biennial forbs was consistently < 1% after 1975. Perennial forbs also varied little among years, averaging about 3% cover the year after fertilizing and about 5% the second year after fertilizing.

Species responses in the 6-field rotation

<u>Paddocks seeded to Russian wildrye with an oat companion in 1976</u> By 1978, Russian wildrye contributed

Table 5. Mean ground cover % (standard error) of major species in continuously grazed unfertilized pastures, Pathlow, east-central Saskatchewan.

Year	Smooth Bromegrass		Creeping Red Fescue		Kentucky Bluegrass		Alfala		Annual + Biennial Forbs		Perennial Forbs	
	(%)											
1975	10.3	(1.2)	48.9	(1.9)	2.4	(0.6)	1.1	(0.4)	3.2	(0.7)	6.7	(1.0)
1984	10.8	(0.9)	35.1	(1.3)	7.6	(0.7)	0.6	(0.2)	0.1	(0.1)	35.2	(1.1)
1988	12.7	(1.0)	28.3	(1.3)	8.0	(0.8)	0.1	(0.1)	0.1	(0.1)	41.6	(1.4)
1989	11.5	(0.8)	18.6	(1.0)	7.4	(0.7)	0.1	(0.1)	0.1	(0.1)	51.8	(1.3)

Table 6. Mean ground cover % (standard error) of major species in fertilized 4-field rotational grazing system, Pathlow pasture, east-central Saskatchewan.

Year	Smooth Bromegrass		Creeping Red Fescue		Kentucky Bluegrass		Alfala		Annual+ Biennial Forbs		Perennial Forbs	
	(%)											
Paddock fertilized fall previous to the year of survey[1]												
1975	20.6	(1.1)	55.6	(1.3)	0.6	(0.2)	0.7	(0.2)	0.9	(0.3)	1.4	(0.3)
1976	17.4	(0.5)	62.0	(0.7)	3.0	(0.3)	0.3	(0.1)	0.1	(0.0)	3.5	(0.3)
1978	15.3	(0.6)	60.3	(0.7)	5.1	(0.4)	1.7	(0.2)	0.1	(0.1)	3.3	(0.3)
1980	22.5	(0.8)	52.8	(1.0)	7.4	(0.5)	2.8	(0.3)	0.0	(0.0)	2.9	(0.3)
1982	29.6	(0.7)	29.7	(0.7)	15.7	(0.5)	2.8	(0.2)	0.4	(0.1)	2.9	(0.3)
1984	24.3	(0.6)	29.1	(0.6)	16.4	(0.5)	1.2	(0.2)	0.2	(0.1)	4.4	(0.3)
1988	31.8	(1.0)	9.8	(0.6)	35.7	(1.0)	1.4	(0.2)	0.0	(0.0)	3.3	(0.4)
1989	31.5	(0.6)	11.2	(0.4)	40.0	(0.6)	0.5	(0.1)	0.1	(0.0)	3.7	(0.3)
Paddocks fertilized in fall 18 mos. previous to the survey[1]												
1975	19.4	(1.1)	44.8	(1.4)	1.4	(0.3)	0.6	(0.2)	1.6	(0.4)	4.0	(0.6)
1976	14.8	(0.5)	53.6	(0.7)	2.7	(0.2)	0.3	(0.1)	0.1	(0.0)	6.8	(0.4)
1978	16.8	(0.7)	49.1	(0.9)	5.0	(0.4)	1.2	(0.2)	0.1	(0.1)	5.0	(0.4)
1980	18.7	(0.8)	40.8	(1.0)	5.6	(0.5)	2.0	(0.3)	0.0	(0.0)	5.3	(0.5)
1982	29.6	(0.7)	31.4	(0.8)	12.8	(0.6)	1.9	(0.2)	0.2	(0.1)	5.3	(0.4)
1984	21.1	(0.6)	7.5	(0.7)	19.3	(0.6)	0.9	(0.1)	0.2	(0.1)	3.9	(0.3)
1988	27.1	(0.9)	4.7	(0.4)	36.1	(0.9)	1.7	(0.3)	0.0	(0.0)	6.3	(0.5)
1989	26.9	(0.6)	9.2	(0.4)	41.5	(0.7)	0.4	(0.1)	0.1	(0.0)	5.3	(0.3)

[1]Paddocks fertilized each fall, 1988–1989.

Table 7. Mean ground cover % (standard error) of major species before and after seeding Russian wildrye in 1976, Pathlow pasture, east-central Saskatchewan.

Year	Smooth Bromegrass		Creeping Red Fescue		Kentucky Bluegrass		Russian wildrye		Annual+ Biennial Forbs		Perennial Forbs	
	(%)											
Paddock fertilized fall previous to the year of survey[1]												
1975	29.3	(6.0)	58.6	(6.5)	0.0	(0.1)	-	-	0.0	(0.0)	1.7	(1.7)
1978	12.3	(0.8)	12.4	(0.8)	19.3	(1.0)	25.1	(1.0)	0.1	(0.1)	13.9	(0.8)
1980	15.1	(1.07)	12.5	(0.9)	27.5	(1.2)	21.4	(1.1)	0.7	(0.2)	7.7	(0.7)
1982	18.8	(0.8)	6.9	(0.5)	28.7	(1.0)	16.3	(0.8)	0.7	(0.2)	7.3	(0.6)
1984	17.5	(0.7)	10.2	(0.6)	37.5	(0.9)	4.8	(0.4)	0.0	(0.0)	6.7	(0.5)
1988	23.0	(1.2)	3.9	(0.6)	47.3	(1.4)	2.3	(0.4)	0.0	(0.0)	4.1	(0.6)
1989	20.4	(0.8)	1.7	(0.3)	46.6	(1.0)	4.6	(0.4)	0.0	(0.0)	0.9	(0.2)
Paddocks fertilized 18 mos. prior to the survey[1]												
1975	14.8	(4.5)	50.8	(6.4)	0.0	(0.1)	-	-	0.0	(0.0)	0.0	(0.1)
1978	8.7	(0.7)	17.5	(0.9)	17.2	(0.9)	23.7	(1.0)	0.2	(0.1)	19.9	(1.0)
1980	11.5	(1.0)	17.8	(1.1)	27.1	(1.3)	21.3	(1.2)	0.1	(0.1)	7.6	(0.8)
1982	13.3	(0.7)	9.0	(0.6)	35.8	(1.1)	15.5	(0.8)	0.1	(0.1)	3.2	(0.4)
1984	11.7	(0.6)	9.3	(0.6)	41.0	(1.0)	5.7	(0.4)	0.2	(0.0)	8.0	(0.5)
1988	15.7	(1.0)	1.8	(0.4)	53.9	(1.3)	5.6	(0.6)	0.2	(0.1)	4.1	(0.5)
1989	15.5	(0.7)	4.4	(0.4)	57.2	(1.0)	3.1	(0.3)	0.0	(0.0)	2.1	(0.3)

[1]Paddocks fertilized each fall, 1988-1989.

only 25% to the total ground cover, and continually declined thereafter (Table 7). Bromegrass re-established after cultivation, and increased to 15–20% of the ground cover by 1989. Paddocks fertilized the fall previous to the surveys had more bromegrass cover than paddocks fertilized earlier, and this difference was significant after 1980. Creeping red fescue did not recover fully after cultivation, with significantly poorer recovery where fertilized the fall previous to the surveys. Its cover declined further over time. Kentucky bluegrass cover increased from near zero in 1975 to over 46% by 1989. Alfalfa was absent from these paddocks.

Paddocks seeded to Bromegrass-Alfalfa in 1979 Reseeding tripled bromegrass ground cover in the vegetation (Table 8), and it remained significantly above its initial level. Creeping red fescue declined slowly in the period before reseeding, and dropped to a low level as bromegrass re-established. Kentucky bluegrass cover increased rapidly after 1984. Reseeding increased the proportion of alfalfa in the ground cover from 3% in 1978 to 11% by 1982. Thereafter, alfalfa steadily declined to its pre-rejuvenation level. Forbs were a major component of the ground cover the year after seeding, but had declined to low levels by 1984.

Paddocks seeded to bromegrass-alfalfa in 1981 Reseeding increased bromegrass ground cover 50% above

Table 8. Mean ground cover % (standard error) of major species before and after reseeding with smooth bromegrass-alfalfa, paddocks fertilized in fall 18 mos prior to survey[1], Pathlow pasture, east-central Saskatchewan.

Year	Smooth Bromegrass		Creeping Red Fescue		Kentucky Bluegrass		Alfala		Annual+ Biennial Forbs		Perennial Forbs	
	(%)											
Reseeding in 1979												
1975	12.4	(1.2)	57.2	(1.8)	0.6	(0.3)	1.1	(0.4)	0.7	(0.3)	3.2	(0.6)
1976	14.0	(0.7)	51.5	(1.0)	4.1	(0.4)	0.8	(0.2)	0.1	(0.1)	4.6	(0.5)
1978	14.4	(1.0)	48.3	(1.3)	4.5	(0.6)	2.8	(0.5)	0.3	(0.1)	9.1	(0.8)
1980	23.2	(1.9)	19.7	(1.5)	3.2	(0.8)	8.7	(1.3)	14.0	(1.4)	11.8	(1.5)
1982	47.8	(1.5)	2.6	(0.5)	7.3	(0.8)	10.6	(1.0)	8.5	(0.9)	6.9	(0.7)
1984	38.7	(1.1)	6.3	(0.6)	8.3	(0.7)	9.5	(0.7)	0.2	(0.1)	2.9	(0.4)
1988	34.4	(1.4)	1.1	(0.3)	30.1	(1.4)	6.9	(0.8)	0.0	(0.0)	3.2	(0.5)
1989	36.3	(1.0)	7.9	(0.6)	35.3	(1.0)	2.3	(0.3)	0.1	(0.1)	2.7	(0.3)
Reseeding in 1981												
1975	13.4	(1.2)	54.5	(1.8)	2.3	(0.6)	0.6	(0.3)	1.1	(0.4)	2.6	(0.6)
1976	18.3	(0.8)	54.7	(1.0)	8.3	(0.6)	0.7	(0.2)	0.1	(0.1)	2.9	(0.4)
1978	12.2	(0.8)	46.7	(1.3)	8.7	(0.7)	2.0	(0.4)	0.0	(0.0)	5.9	(0.6)
1980	22.2	(1.5)	22.8	(1.4)	15.5	(1.3)	3.6	(0.7)	1.7	(0.6)	4.0	(0.7)
1982	34.4	(1.3)	2.4	(0.5)	5.1	(0.7)	3.7	(0.5)	14.1	(0.9)	12.0	(1.0)
1984	37.7	(1.1)	7.3	(0.6)	12.5	(0.7)	3.7	(0.4)	0.9	(0.2)	4.1	(0.5)
1988	32.1	(1.3)	4.5	(0.6)	33.9	(1.3)	4.3	(0.6)	0.2	(0.1)	7.1	(0.8)
1989	30.7	(1.0)	2.7	(0.3)	37.3	(1.0)	1.7	(0.3)	0.2	(0.1)	3.0	(0.4)

[1]Paddocks fertilized each fall, 1988-1989.

its pre-seeding values and reduced creeping red fescue cover to a minor constituent, where it remained with some fluctuations through 1989 (Table 8). Kentucky bluegrass cover was increasing prior to reseeding, and after a reduction in response to cultivation, increased steadily to 37% by 1989. Reseeding alfalfa in 1981 did not result in increased cover, but apparently delayed the decline that occurred in other treatments. Forbs were a major component of the ground cover the year after seeding, but had declined to low levels 2 years later.

<u>Paddocks seeded to crested wheatgrass in 1983</u> Crested wheatgrass established well and was 62% of the total ground cover in 1984 (Table 9). Its cover declined to 41% by 1989. Cultivation reduced bromegrass cover to 4% and creeping red fescue and alfalfa to very low levels. Kentucky bluegrass increased between 1975 and 1989 from 1% to 34% of total ground cover, and was not noticeably affected by the establishment of the crested wheatgrass. Forbs cover increased significantly the year after seeding, but had declined to their previous levels by 1988.

<u>Paddocks seeded to meadow bromegrass-alfalfa in 1985</u> Meadow bromegrass established poorly, and formed only 27% of ground cover in 1989 (Table 10). Smooth bromegrass remained a major constituent through the reseeding period and Kentucky bluegrass increased its cover. Creeping red fescue cover was reduced to 8%. Seeding alfalfa increased its cover to 4% in 1988, but this was followed by a decline to 1% in 1989. Forbs showed no response to reseeding.

Discussion

There are 4 basic influences on the relative proportions of species in pasture: weather patterns and trends, the timing and intensity of grazing, the application of fertilizer, and reseeding. The latter 3 are aspects of pasture management, and in the order given, represent an increasing degree of intervention in the ecosystem. Of the species originally present, smooth bromegrass and alfalfa are considered desirable components from an animal productivity viewpoint. Creeping red fescue and Kentucky bluegrass are usually considered less desirable because of low productivity, although red fescue was included in the original seeding because it can produce higher quality forage late in the growing season (Elliott and Baenziger) 1977).

Table 9. Mean ground cover % (standard error) of major species before and after seeding crested wheatgrass in 1983, and fertilizing in fall previous to measurement, Pathlow pasture, east-central Saskatchewan.

Year	Smooth Bromegrass		Creeping Red Fescue		Kentucky Bluegrass		Crested Wheatgrass		Annual+ Biennial Forbs		Perennial Forbs	
	(%)											
1982	40.6	(1.2)	17.3	(0.9)	13.0	(0.8)	-	-	0.0	(0.0)	2.8	(0.4)
1984	4.0	(0.5)	0.3	(0.1)	12.3	(0.9)	62.2	(1.3)	2.8	(0.5)	6.8	(0.7)
1988	14.2	(0.9)	0.2	(0.1)	24.2	(1.1)	40.2	(1.2)	0.4	(0.2)	1.2	(0.3)
1989	12.2	(0.6)	0.1	(0.1)	33.9	(0.9)	41.7	(1.0)	0.1	(0.1)	1.6	(0.2)

Table 10 Mean ground cover % (standard error) of major species before and after seeding meadow bromegrass in 1985 and fertilizing in fall previous to measurement, Pathlow pasture, east-central Saskatchewan.

Species	Year					
	1984		1988		1989	
	(%)					
Smooth bromegrass	33.9	(1.1)	27.9	(1.4)	22.4	(0.8)
Creeping red fescue	21.0	(0.9)	7.7	(0.8)	7.1	(0.5)
Kentucky bluegrass	14.7	(0.8)	19.4	(1.2)	25.5	(0.9)
Alfalfa	2.6	(0.4)	3.6	(0.6)	1.2	(0.2)
Meadow bromegrass	—	—	20.0	(1.1)	26.7	(0.9)
Annual + biennial forbs	0.1	(0.1)	1.0	(0.3)	0.2	(0.1)
Perennial forbs	4.3	(0.5)	3.8	(0.6)	2.8	(0.3)

Species responses to continuous grazing

The greatest change in these paddocks was the major increase in perennials, mainly low-growing *Antennaria* spp. Perhaps the vegetation was on the edge of a "threshold" to a lower stability point as alluded to by Looman (1980). Although bromegrass ground cover remained the same as at the start, decline of creeping red fescue and alfalfa, and increase in unproductive perennials suggests that the areas were overgrazed (Looman 1976). However, McCartney et al. (1999) reported that dry matter yields in the continuously grazed paddocks averaged over the 13-year period, were comparable to those in an adjacent field in the community pasture, grazed in some years only in late summer.

Species responses in the fertilized 4-field rotation

The increase of smooth bromegrass ground cover was probably a result of improved fertility more than rotational grazing. Fertilizing smooth bromegrass increases both the proportion of leafy tillers and their size (Waddington 1968).

Alfalfa ground cover increased during a period of average to above average precipitation. Its later reduction shows that rotational grazing does not guarantee its continued presence, contrary to the report of Walton et al. (1981). Perhaps competitive success of alfalfa depends on a water supply at depth which is replenished at intervals by higher than normal precipitation or by ground water infiltration from elsewhere, similar to many rangeland shrubs (Looman 1983). Also, previous work in the same climate zone (Cooke et al. 1965, Walton et al. 1981) was conducted on better-quality soils. The apparent response of alfalfa to weather- or soil- related factors rather than management changes suggests that problems in retaining it in pastures lie as much in its characteristics as in the treatments applied.

The most striking feature of change was the replacement of creeping red fescue by Kentucky bluegrass as the principal understory grass. This replacement was likely caused by the improved fertility conditions which are more favourable to Kentucky bluegrass than to creeping red fescue (Elliott and Baenziger 1977). Kentucky bluegrass is a major component of many pastures in the central and northern parts of the prairie provinces (Looman 1976). Its minor status initially in the present case is probably due to the inclusion of creeping red fescue when seeded in the mid-1960s, followed by a rapid decline in fertility. It has also been observed that creeping red fescue growth is poorer with low light levels (Dobb and Elliott 1964) which it would have received after 1975 because of the increased vigour of bromegrass.

Species responses in the 6-field rotation

The choice of Russian wildrye to extend the grazing season in both spring and fall was based on the success of Cooke et al (1973). Russian wildrye seedlings are small, slow-growing, and difficult to establish (Smoliak et al 1970). Shading by the oat companion crop during the establishment year probably increased the difficulty. All the species previously present except for alfalfa re-established along with the wildrye, and the progression to dominance by smooth bromegrass with a Kentucky bluegrass understory proceeded perhaps slightly faster than in the other paddocks. Russian wildrye survived only on the dry knolls, probably because of greater drought tolerance than bromegrass and bluegrass. It was also observed to be growing successfully in paddocks where it was not seeded, on soil heaps formed from the remnants of trees, roots, and soil piled and burned during pasture establishment in the mid-sixties. It was able to establish when these heaps of rich, relatively dry topsoil had bare patches due to the activities of bulls. It appears that Russian wildrye is not adapted to low-fertility soils in the parkland zone, in contrast to its success in the same region on a fertile deep black soil after establishment on fallow (Cooke et al. 1973).

The use of cultivation and reseeding of smooth bromegrass and alfalfa to increase their contribution to the vegetation worked well in 1979, but less so in 1981 following a winter of low precipitation. In general, the effects merely accelerated or accentuated changes in the grasses that were already taking place, and delayed the decline in alfalfa that was evident in other paddocks.

Crested wheatgrass is a competitive caespitose grass that is easily established (Smoliak et al. 1970) and can be grazed earlier in spring than smooth bromegrass (Cooke et al. 1973). Although in the year following seeding it dominated the vegetation in our study, by 1989, the pre-seeding vegetation had re-established dominance in ground cover. This suggests that crested wheatgrass pastures in northeastern Saskatchewan are unlikely to be as stable as those observed by Looman and Heinrichs (1973) in the southwest of the province.

Meadow bromegrass has better regrowth potential than smooth brome (Beacom 1991), and was intended to replace creeping red fescue for late summer grazing. It did not establish well in 1985, nor did the alfalfa seeded with it, in spite of precipitation during the establishment period being well above the long-term average. Competition from inadequately-controlled resident vegetation is the probable reason.

Cultivating in summer did not rid a paddock of all resident vegetation prior to seeding new species the following spring. Although alfalfa and creeping red fescue were effectively removed, bromegrass was not. The concurrent invasion by Kentucky bluegrass has parallels in the invasions of crested wheatgrass into Russian wildrye and meadow bromegrass pastures in a semi-arid location at Swift Current (Holt, pers. commun.), about 500 km southwest of the experimental site.

Differences between paddocks in proportions of the various plant species remained throughout the experimental period and are considered a result of the uniqueness of each paddock. The rapid response to changes in management, particularly of the rhizomatous grasses, suggests that changes in the relative proportions of pasture species are permanent only so long as the management changes are permanent. Pastures used for extensive grazing, and intended to be truly permanent, not part of a rotation with annual crops, should be managed by considering ecological principles rather than agronomic practices, even though the desired species are introduced rather than native. In particular, it seems unnecessary to cultivate and reseed to improve the proportion of smooth brome and alfalfa, because there was little benefit beyond that achieved by applying fertilizer and grazing rotationally. It seems probable that the use of caespitose grasses such as crested wheatgrass and Russian wildrye, and even of less aggressively-spreading rhizomatous grasses such as meadow bromegrass will require their reseeding from time to time if they are to be used to lengthen the grazing season in the parkland area of western Canada.

Conclusions

1) Increasing pasture fertility and changing from continuous to rotational grazing increased smooth bromegrass ground cover, replaced creeping red fescue with Kentucky bluegrass as the principal understory grass, and had little effect on the minor components alfalfa and other broadleaved species.

2) Cutlivation in summer and seeding with different species the following spring did not allow enough time to fully control all species in the resident vegetation. Smooth bromegrass and Kentucky bluegrass reestablished and sometimes replaced the seeded species within a few years. Forbs in quantity were ephemeral, and declined to low levels without specific control measures.

3) The rapid responses of the pasture components to changes in management and weather demonstrate the dynamic nature of their interrelationships. Permanent changes in vegetation require permanent changes in management and the use of species which are adapted to soil, climate and the pasture management used.

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Enhancing intermediate wheatgrass establishment in spotted knapweed infested rangeland

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Abstract

The objective of this study was to compare intermediate wheatgrass establishment at 4 seeding rates, in combination with tillage and/or glyphosate (n-phosphomethyl glyine), in spotted knapweed infested rangeland. We hypothesized that the establishment of intermediate wheatgrass seedlings would be greatest at high seeding rates, while spotted knapweed density and biomass would be negatively impacted by intermediate wheatgrass densities. Glyphosate (1.16 liters a.i./ha; with and without), tillage (200 mm depth; with and without), and 4 seeding rates (0, 500, 2,500, 12,500 m^{-2}) of intermediate wheatgrass seeds were factorially arranged in a randomized-complete-block design with 4 blocks at each of 2 sites in Montana. Treatments were applied in the fall of 1995. By the second growing season, intermediate wheatgrass failed to established in plots seeded with 500 seeds m^{-2}, the currently recommended seeding rate. Increasing the seeding rate to 2,500 and 12,500 m^{-2} increased intermediate wheatgrass tiller density by 80 and 140 plants m^{-2}, respectively, at Hamilton and 158 and 710 plants m^{-2}, respectively, at Bozeman. At the highest seeding rate, combining tillage with glyphosate increased tiller density over 3 times more than other treatments where intermediate wheatgrass successfully established at Hamilton. However, neither tillage nor glyphosate affected intermediate wheatgrass density at Bozeman by the second growing season. In the first season, seeding rates of 0, 500, 2,500, 12,500 m^{-2} produced 214, 208, 176, and 114 knapweed plants m^{-2}, respectively ($LSD_{0.05}$=36.1) at Bozeman, but had no effect at Hamilton. Our revegetation study suggests that increasing intermediate wheatgrass seeding rates can facilitate their establishment in spotted knapweed infested rangeland. Using high seeding rates to control spotted knapweed and increase seedling establishment may enhance our ability to use revegetation as an effective weed management strategy.

Key Words: *Centaurea maculosa*, *Bromus tectorum*, *Elytriga intermedia*, revegetation, tillage, glyphosate, seedling establishment.

Spotted knapweed (*Centaurea maculosa* Lam.), a deep-taprooted perennial weed of Eurasian origin, has been

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Resumen

El objetivo de este estudio fue comparar el establecimiento dé intermediate wheatgrass (*Elytriga intermedia (Host) Nevski*) en 4 dósis de siembra, en combinación con preparación de suelo y/o glyphosate (n-phosphomethyl glyine), en praderas infestadas con spotted knapweed (*Centaurea maculosa* Lam.) Formulamos una hipótesis, la cual suponía que el establecimiento de plántulas de intermediate wheatgrass alcanzarían sus niveles más altos a niveles altos de siembra, mientras la densidad y biomasa de spotted knapweed mostrarían un impacto negativo según las densidades de intermediate wheatgrass. Glyphosate (1.16 litros a.i./ha; con y sin), preparadión de suelo (a 200 mm de profundidad, con y sin y 4 dósis de siembra (0, 500, 2,500 y 12,500 m^2) de semillas de intermediate wheatgrass fueron arreglados factorialmente en un diseño de bloques completamente al azar, con 4 bloques ubicados en cada uno de los dos sitios en Montana. Se aplicaron los tratamientos en el otoño de 1995. Para la segunda temporada de cultivo, intermediate wheatgrass no pudo establecerse en las parcelas sembradas con 500 semillas m^{-2}, el nivel de siembra que se recomienda actualmente. Aumentando el nivel de la siembra a 2,500 y a 12,500 m^{-2} aumentó la densidad de rebrotes de intermediate wheatgrass en 80 y 140 plantas m^{-2} respectivamente, en Hamilton y en 158 y 710 plantas m^{-2} respectivamente, en Bozeman. Al nivel más alto de dósis de siembra, la combinación de preparación de suelo con glyphosate aumentó la densidad de rebrotes en exceso de 3 veces más que en otros tratamientos y en los cuales intermediate wheatgrass tuvo Èxito en establecerse en Hamilton. Sin embargo, para la segunda temporada de cultivo, ni la preparación de suelo ni glyphosate afectaron la densidad de intermediate wheatgrass en Bozeman. Durante la primera temporada de cultivo, dósis de siembra de 0, 500, 2,500 y 12,500 m^{-2} produjeron 214, 208, 176, 114 plantas m^{-2} de spotted knapweed, respectivamente (LSD = 36.1) en Bozeman, pero no causaron ningún efecto en Hamilton. Nuestro estudio de revegetación sugiere que al aumentar las dósis de siembra de intermediate wheatgrass, se puede facilitar su establecimento en praderas infestadas con spotted knapweed. Es posible que el uso de niveles altos de siembra para controlar spotted knapweed e incrementar el establecimiento de plántulas pueda mejorar nuestra capacidad de utilizar la regegetación como estrategia eficaz en el control de malezas.

expanding its range throughout the northwestern United States and Canada since the late-1800s (Watson and Renney 1974, Harris and Cranston 1979, Strang et al. 1979, Roché and Talbott 1986). This invasive weed has been spreading at about 27% per year since 1920 (Chicoine et al. 1985). It is estimated that spotted knapweed infests about 2.2 million hectares of grassland in Montana (Lacey et al. 1989) and about 10,000 hectares in both eastern Washington (Roché 1988) and British Columbia (Cranston 1988). Spotted knapweed reduces forage production (Watson and Renney 1974, Harris and Cranston 1979), species richness (Tyser and Key 1988), and wildlife habitat (Bedunah and Carpenter 1989). Increases in bare-ground (Tyser and Key 1988), surface water runoff and stream sedimentation (Lacey et al. 1989), and management costs are also associated with knapweed *(Centaurea* spp.) infestations.

Spotted knapweed control is often short-term if desirable species are not available to occupy safe sites opened by the control procedure (James 1992, Sheley et al. 1996). In these areas, introducing and establishing competitive plants is essential for successful management of spotted knapweed and the restoration of desirable plant communities (Hubbard 1975, Larson and McInnis 1989, Borman et al. 1991). Seedling establishment appears associated with the availability of safe sites (Harper et al. 1965, Wright et al. 1978) and the availability of seeds (Pickett et al. 1987). Rehabilitating knapweed infested rangeland with desirable grasses typically fails, however, because of competition with weeds for safe sites during the initial stages of establishment (Borman et al. 1991, James 1992). In addition, density-dependent (competition) and density independent factors interact to determine seedling survival during intermediate wheatgrass (*Elytriga intermedia* (Host) Nevski) establishment in spotted knapweed infested rangeland (Velagala et al. 1997).

Density of desired plants may influence weed competition during the initial stages of establishment. In a growth chamber, Jacobs et al. (1996) found that bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh.) Löve) was 4 times more competitive than spotted knapweed seedlings at densities (1,000–5,000 plants m^{-2}) higher than normal for rangeland revegetation. Similarly, Velagala et al. (1997) found that increasing intermediate wheatgrass from <1,000 plants m^{-2} to >1,000 plants m^{-2} removed the competitive effect of spotted knapweed on intermediate wheatgrass biomass where interspecific interference occurred.

The objective of this study was to determine whether extraordinarily high seeding rates could be used to facilitate the initial establishment of intermediate wheatgrass in spotted knapweed infested rangeland. We compared intermediate wheatgrass density and biomass at 4 seeding rates in combination with tillage and glyphosate (n-phosphomethyl glyine). We hypothesized that the establishment of intermediate wheatgrass seedlings would be greatest at high seeding rates, control procedures that increase the availability of safe sites would increase wheatgrass establishment, and spotted knapweed density and biomass would be negatively impacted by wheatgrass densities.

Materials and Methods

Study Sites

The study was conducted during 1995, 1996, and 1997 about 11 km east-northeast of Hamilton, Mont. (46° 17' N, 114° 1' W) at an elevation of 1,341 m and about 15 km southwest of Bozeman, Mont. (45° 36' N, 111° 11' W) at an elevation of 1,524 m. The Hamilton site is a *Festuca scabrella/ Pseudoroegneria spicata* habitat type and the Bozeman site is a *Festuca idahoensis/Pseudoroegneria spicata* habitat type (Mueggler and Stewart 1980). Both sites were dominated by spotted knapweed and cheatgrass (*Bromus tectorum* L.), with very few other species present. Hamilton soils were Stecum stony loamy coarse sand (mixed typic Cryorthenths) and were moderately deep. Bozeman soils were loamy-skeletal over sandy or sandy skeletal (mixed typic Argiboroll). Annual precipitation at both sites ranges from 406 to 457 mm with a bimodal distribution with peaks in the winter and spring. The mean annual temperature at Hamilton is 6.6°C and 6.1°C at Bozeman. Precipitation and temperature were monitored within 6.5 km of each site. During the period of the study, precipitation and temperature were near the long-term average (Table 1).

Table 1. Seasonal summary of precipitation and temperature at Hamilton and Bozeman Montana during the period of the study.

Site	Year	Period	Total precipitation	Mean temperature Max	Min
			(mm)	------------- (˚C)	---------
Hamilton	1995	Fall	84	5.2	-3.5
	1996	Winter	63	4.4	-6.8
	1996	Spring	141	18.3	4.1
	1996	Summer	69	26.9	7.3
	1996	Fall	121	6.8	-7.1
	1997	Winter	65	4.5	-8.5
	1997	Spring	194	18.0	3.1
	1997	Summer	96	26.5	9.2
Bozeman	1995	Fall	46	6.3	2.8
	1996	Winter	50	2.7	-10.1
	1996	Spring	167	18.2	3.1
	1996	Summer	59	26.4	8.9
	1996	Fall	1215	7.8	-1.1
	1997	Winter	59	5.3	-5.0
	1997	Spring	133	16.6	4.2
	1997	Summer	34	27.9	9.5

Environmental conditions were monitored daily. Precipitation amounts are monthly cumulative values. Maximum and minimum temperatures are means for the designated period.

Procedures

Glyphosate (with and without), tillage (with and without), and 4 seeding rates (0, 500, 2,500, 12,500 m^{-2}) of intermediate wheatgrass seeds were factorially applied in a randomized-complete-block design with 4 blocks (replications) at each site (128 total plots). Glyphosate, a non-selective herbicide, which is rapidly deactivated by binding to soil particles, was applied at 1.16 liters a.i./ha using a CO_2 pressurized backpack sprayer calibrated to deliver a total volume of 410 liter ha^{-1}. Tillage was accomplished using a tractor mounted rototiller that mixed the soil to a depth of about 200 mm. Seeds of 'Oahe' intermediate wheatgrass were broadcast on the soil surface of each plot (1.82 m^2) immediately after application and were covered with a small amount of soil (< 2 mm). Intermediate wheatgrass seeds were purchased from Circle S Seeds Inc., Three Forks, Mont. in October 1995. Intermediate wheatgrass is an important grass species used for revegetating spotted knapweed infested rangeland on these habitat types (Holzworth and Lacey 1991). Ninety-four percent of the seeds germinated in a standard test (Wiesner 1991). Treatments were applied during November 4 through 8 November 1995 at Bozeman, and 11 November through 14 November 1995 at Hamilton.

Sampling

The study was sampled at peak standing crop (July) in 1996 and 1997. Density of intermediate wheatgrass, spotted knapweed, and cheatgrass were determined by counting the number of plants in a randomly placed 0.44 m^2 circular hoop in each plot. Biomass was determined by clipping plants to ground level. Plants were separated by species, dried (60°C, 48 hr) to a constant weight, and weighed.

Analysis

Analysis of variance was used to determine the effects of intermediate wheatgrass seeding rate, tillage, and glyphosate on density and biomass of intermediate wheatgrass, spotted knapweed, and cheatgrass. Initial analysis of variance included site, year, seeding rate, tillage, glyphosate, and their factorial combinations in the model. This analysis indicated the presence of 4- and 5-way interactions. Therefore, sites and years were analyzed separately. Seeding rate, tillage, glyphosate, seeding rate*tillage, seeding rate*glyphosate, tillage*glyphosate, and seeding rate*tillage*glyphosate were included in the model. Pr ≤ F values are presented to separate significant ($\alpha = 0.05$) main effect means for tillage and glyphosate. Mean separations for significant seeding rate and interactions were achieved using Fisher's protected LSD ($P \leq 0.05$) comparisons (Peterson 1985).

Results

Intermediate wheatgrass

Hamilton

Analysis of variance indicated seeding rate*tillage (1996) and seeding rate*tillage*glyphosate (1997) interacted to affect intermediate wheatgrass tiller density at Hamilton (Table 2). In 1996, unseeded plots and those seeded at rates of 500 m^{-2} yielded similar wheatgrass density, regardless of tillage (Fig. 1). Seeding at 2,500 m^{-2} did not increase wheatgrass density without tillage. At that seeding rate, tillage increased wheatgrass tiller numbers 3-fold. Increasing seeding rate to 12,500 m^{-2} increased wheatgrass density over all other seeding rates. Plots tilled and seeded at 12,500 m^{-2} had the highest wheatgrass density (250 tillers m^{-2}) in 1996 at Hamilton.

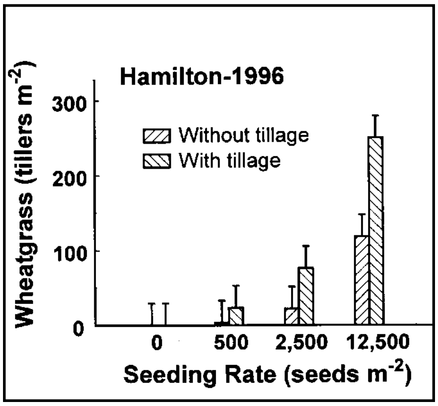

Fig. 1. Effect of tillage*seed rate on intermediate wheatgrass density at Hamilton in 1996. Error bars represent least significant differences ($\alpha = 0.05$).

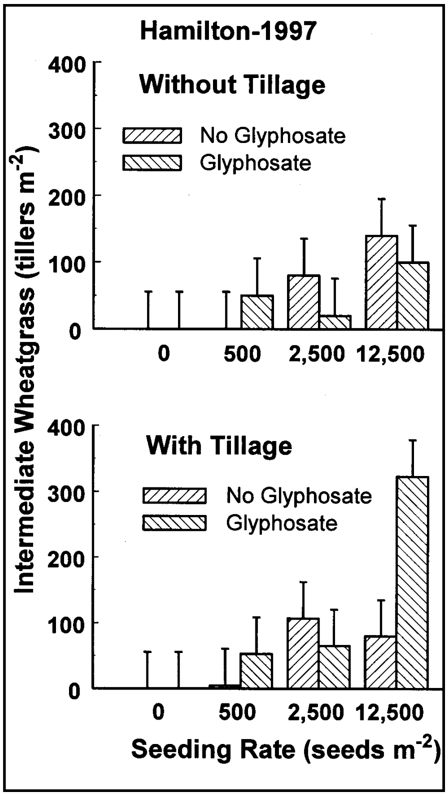

Fig. 2. Effect of tillage*glyphosate*seed rate on intermediate wheatgrass density at Hamilton in 1997. Error bars represent least significant differences ($\alpha = 0.05$).

By 1997, intermediate wheatgrass was not present in plots seeded at a rate of 500 m^{-2} when broadcast without tillage or glyphosate at Hamilton (Fig. 2). Increasing the seeding rate to 2,500 and 12,500 m^{-2} increased tiller density to about 80 and 140 m^{-2}, respectively. Neither tillage nor glyphosate increased wheatgrass tiller density, and glyphosate actually lowered tiller density when applied at the 2,500 m^{-2} seeding rate. At the highest seeding rate, combining tillage with glyphosate increased tiller density over 3 times more than other treatments where wheatgrass successfully established at Hamilton.

In 1996, only seeding rate affected intermediate wheatgrass biomass at Hamilton (Table 2). Seeding rates of 0, 500, 2,500, and 12,500 m^{-2} yielded 0.0, 0.3, 1.4, and 3.8 g m^{-2} ($LSD_{0.05}$ = 0.67) of biomass the first year after seeding. In 1997, seeding rate and tillage affected wheatgrass biomass at

Table 2. Pr ≤ F values generated from analysis of variance of density and biomass of intermediate wheatgrass, spotted knapweed and cheatgrass collected at Hamilton, Montana in 1996 and 1997.

Year	Treatment	df	Intermediate Density	Intermediate Biomass	Spotted knapweed Density	Spotted knapweed Biomass	Cheatgrass Density	Cheatgrass Biomass
			(plants m^{-2})	(g m^{-2})	(plants m^{-2})	(g m^{-2})	(plants m^{-2})	(g m^{-2})
1996	Block	3	0.79	0.64	0.01	0.13	0.01	0.47
	Tillage	1	0.01	0.08	0.76	0.01	0.62	0.12
	Glyphosate	1	0.30	0.64	0.62	0.02	0.11	0.23
	Seeding rate	3	0.01	0.01	0.54	0.15	0.48	0.35
	Tillage*Glyphosate	1	0.05	0.11	0.90	0.35	0.23	0.47
	Tillage*Seeding rate	3	0.04	0.53	0.77	0.39	0.30	0.51
	Glyphosate*Seeding	3	0.47	0.11	0.82	0.67	0.53	0.45
	Till*Gly*Seeding rate	3	0.11	0.22	0.12	0.82	0.38	0.09
1997	Block	3	0.72	0.07	0.56	0.34	0.05	0.10
	Tillage	1	0.11	0.02	0.08	0.17	0.70	0.02
	Glyphosate	1	0.26	0.77	0.01	0.08	0.63	0.70
	Seeding rate	3	0.01	0.02	0.16	0.19	0.47	0.68
	Tillage*Glyphosate	1	0.08	0.31	0.19	0.75	0.57	0.42
	Tillage*Seeding rate	3	0.49	0.09	0.39	0.69	0.17	0.31
	Glyphosate*Seeding	3	0.05	0.43	0.29	0.27	0.77	0.31
	Till*Gly*Seeding rate	3	0.03	0.83	0.84	0.83	0.61	1.00

this site. Seeding rates of 0, 500, 2,500, and 12,500 m^{-2} yielded 0.0, 3.1, 3.8, and 4.0 g m^{-2}, ($LSD_{0.05}$ = 1.48), respectively indicating all nonzero seeding rates were similar 2 years after seeding. Tillage increased wheatgrass biomass from 1.56 to 3.85 g m^{-2} (P = 0.0242), regardless of seeding rate in 1997 at Hamilton.

Bozeman

In 1996, seeding rate*tillage and seeding rate*glyphosate interacted to affect intermediate wheatgrass tiller density at Bozeman (Table 3). Seeding at 500 or 2,500 m^{-2} without tillage did not increase wheatgrass tiller density over unseeded plots (Fig. 3a). Seeding at 12,500 m^{-2} increased wheatgrass density to about 64 tillers m^{-2}. As seeding rate increased, tillage increased wheatgrass density.

At Bozeman, seeding at 500 m^{-2} without glyphosate did not increase wheatgrass tiller density in 1996 (Fig. 3b). At that seeding rate, applying glyphosate increased wheatgrass density to 14 plants m^{-2}. Seeding at 2,500 m^{-2} produced about 22 tillers m^{-2}. Glyphosate had no effect on wheatgrass density at this seeding rate. Seeding rate of 12,500 m^{-2} without glyphosate increased wheatgrass density about 7 times those treatments with lower seeding rates. Application of glyphosate at this seeding rate nearly doubled wheatgrass density.

By 1997, only seeding rate determined the density of intermediate

Table 3. Pr ≤ F values generated from analysis of variance of density and biomass of intermediate wheatgrass, spotted knapweed and cheatgrass collected at Bozeman, Montana in 1996 and 1997.

Year	Treatment	df	Intermediate Density	Intermediate Biomass	Spotted knapweed Density	Spotted knapweed Biomass	Cheatgrass Density	Cheatgrass Biomass
			(plants m^{-2})	(g m^{-2})	(plants m^{-2})	(g m^{-2})	(plants m^{-2})	(g m^{-2})
1996	Block	3	0.11	0.12	0.64	0.77	0.02	0.02
	Tillage	1	0.01	0.01	0.01	0.01	0.58	0.18
	Glyphosate	1	0.05	0.28	0.32	0.01	0.01	0.01
	Seeding rate	3	0.01	0.01	0.02	0.01	0.92	0.36
	Tillage*Glyphosate	1	0.10	0.11	0.90	0.35	0.23	0.47
	Tillage*Seeding rate	3	0.01	0.01	0.17	0.01	0.93	0.83
	Glyphosate*Seeding	3	0.02	0.59	0.24	0.14	0.95	0.54
	Till*Gly*Seeding rate	3	N/S	0.92	0.11	0.04	0.84	0.80
1997	Block	3	0.07	0.35	0.02	0.54	0.02	0.03
	Tillage	1	0.98	0.22	0.77	0.09	0.07	0.01
	Glyphosate	1	0.95	0.04	0.37	0.20	.017	0.57
	Seeding rate	3	0.01	0.01	0.13	0.32	0.65	0.68
	Tillage*Glyphosate	1	0.98	0.72	0.24	0.14	0.37	0.50
	Tillage*Seeding rate	3	0.91	0.03	0.89	0.64	0.63	0.98
	Glyphosate*Seeding	3	0.62	0.01	0.22	0.78	0.01	0.43
	Till*Gly*Seeding rate	3	0.90	1.00	0.98	0.68	0.60	0.80

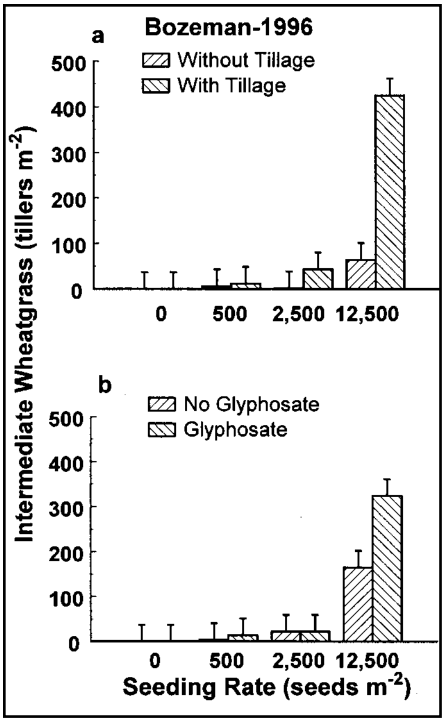

Fig. 3. Effect of tillage*seed rate (a) and glyphosate*seed rate (b) on wheatgrass density at Bozeman in 1996. Error bars represent least significant differences (α = 0.05).

wheatgrass tillers at Bozeman (Table 3). Increasing seeding rate from 0, 500, 2,500, and 12,500 m^{-2} increased wheatgrass density to 0.0, 67.3, 158.3, and 710.6 tillers m^{-2} respectively ($LSD_{0.05}$ = 87.0).

In 1996 and 1997, seeding rate*tillage interacted to affect intermediate wheatgrass biomass at Bozeman (Table 3). In 1996, the only treatment that increased the biomass of intermediate wheatgrass was the highest seeding rate combined with tillage (Fig. 4a). In 1997, seeding at a rate of 500 m^{-2} yield similar wheatgrass biomass as the unseeded plots (Fig. 4b). Wheatgrass biomass at this seeding rate was similar to that seeded with 2,500 m^{-2} and tilled. Seeding at 2,500 m^{-2} without tillage increased wheatgrass biomass over unseeded plots, but was similar to other treatments seeded with 500 or 2,500 seeds m^{-2}. Seeding with 12,500 m^{-2} without tilling doubled wheatgrass biomass over those plots seeded with 2,500 m^{-2} without tillage. Combining the highest seeding rate with tillage yielded the most wheatgrass biomass (28 g m^{-2}) of the seeding rate*tillage treatments in 1997.

Seeding rate also interacted with glyphosate to affect intermediate wheatgrass biomass in 1997 at Bozeman (Table 3). Of those plots seeded with 500 or 2,500 seeds m^{-2}, only those seeded at 2,500 combined with glyphosate yielded higher biomass than unseeded plots (Fig. 5). Seeding at 12,500 seeds m^{-2} without glyphosate yielded similar wheatgrass biomass as the latter treatment. However, combining the highest seeding rate with glyphosate yielded over 4 times the wheatgrass biomass of any other seeding rate*glyphosate treatment in 1997 at this site.

Spotted knapweed

Hamilton

In 1996, no treatment affected spotted knapweed density at Hamilton, but in 1997 glyphosate increased knapweed density from 305 to 419 plants m^{-2} ($P_{(0.05)}$ = 0.0068). However, tillage (P = 0.0015) and glyphosate (P = 0.0192) decreased knapweed biomass

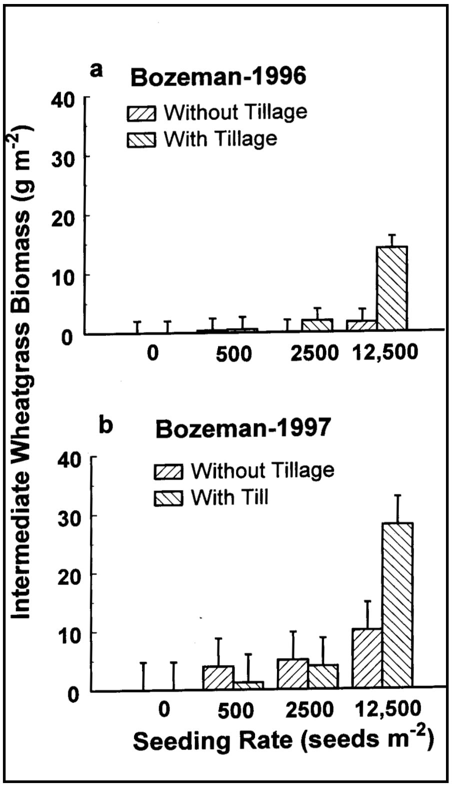

Fig. 4. Effect of tillage*seed rate on intermediate wheatgrass biomass at Bozeman in 1996 (a) and 1997 (b). Error bars represent least significant differences (α = 0.05).

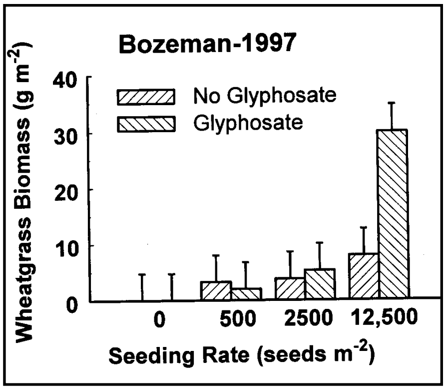

Fig. 5. Effect of glyphosate*seeding rate on intermediate wheatgrass biomass at Bozeman in 1997. Error bars represent least significant differences (α = 0.05).

from about 107 to 73 and 103 to 78 g m^{-2}, respectively, in 1996. By 1997, all treatment effects on spotted knapweed biomass were removed at Hamilton (Table 2).

Bozeman

In 1996, seeding rate (main effect) and tillage (main effect) affected spotted knapweed density (Table 3). Seeding rates of 0, 500, 2,500, and 12,500 m^{-2} produced 214, 208, 176, and 114 spotted knapweed plants m^{-2} ($LSD_{0.05}$ = 36.1) that year. At that time, tillage increased spotted knapweed density from 136 to 220 plants m^{-2} (P = 0.0008). By 1997, all treatment effects on spotted knapweed density were removed (Table 3).

In 1996, seeding rate, tillage, and glyphosate interacted to affect spotted knapweed biomass at Bozeman (Table 3). Without tillage or glyphosate, increasing seeding rate lowered spotted knapweed biomass (Fig. 6). Glyphosate lowered knapweed biomass in unseeded plots when applied without tillage. In plots without tillage those seeded and sprayed with glyphosate yielded lowest knapweed biomass. Tillage yielded similarly low spotted knapweed biomass, regardless of seeding rate or the application of glyphosate. However, by 1997 all treatment effects on spotted knapweed biomass were removed at Bozeman (Table 3).

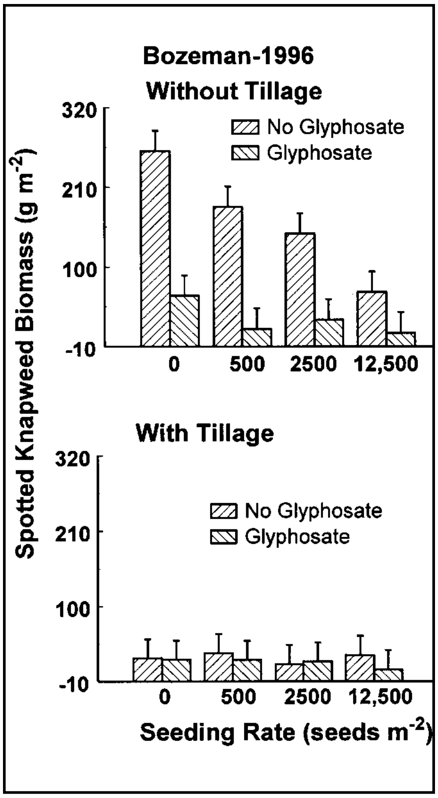

Fig. 6. Effect of tillage*glyphosate*seeding rate on spotted knapweed biomass at Bozeman in 1996. Error bars represent least significant differences ($\alpha = 0.05$).

Cheatgrass

Hamilton

Tillage was the only treatment that affected cheatgrass at Hamilton (Table 2). Tillage increased cheatgrass biomass from 6.0 to 15.0 g m^{-2} (P = 0.0236) in 1997 at this site.

Bozeman

In 1996, glyphosate increased cheatgrass density from 54 to 126 (P = 0.0080) tillers m^{-2} at Bozeman. In 1997, seeding rate*glyphosate interacted to affect cheatgrass density (Table 3). At seeding rates of 0, 500, and 2,500 m^{-2} applying glyphosate decreased cheatgrass density, but at the 12,500 m^{-2} seeding rate glyphosate increased cheatgrass density at Bozeman (Fig. 7). In 1996, glyphosate increased cheatgrass biomass from 2.2 to 8.4 g m^{-2} (P = 0.0080) at Bozeman. Tillage increased cheatgrass biomass from 27.6 to 62.2 g m^{-2} (P = 0.0023) in 1997 at this site.

Discussion

Most revegetation studies of weed infested rangeland examine methods using agronomic seeding rates that are designed to optimize crop yield (Zimdall 1980). The recommended seeding rate of intermediate wheatgrass ranges from 170 (Granite Seed Co. Lehi, Utah) to 430 seeds m^{-2} (Sheley and Larson 1994). In this study, intermediate wheatgrass establishment did not occur at 500 seeds m^{-2} under any treatment or treatment combinations by the second growing season. This helps explain the high rate of failure in revegetating weed infested rangeland.

Our revegetation study suggests that increasing intermediate wheatgrass seeding rate will facilitate its establishment in spotted knapweed-cheatgrass infested rangeland. In many cases, increasing seeding rate increased intermediate wheatgrass density. We believe increasing the number of available seeds increased their probability of reaching safe sites (Harper et al. 1965, Wright et al. 1978).

In the first season after seeding, spotted knapweed density and biomass was reduced at high seeding rates at Bozeman. Establishment of intermediate wheatgrass may have reduced safe site availability for spotted knapweed, similar to that found by Larson and McInnis (1989) for yellow starthistle (*Centaurea solstitialis* L.). Weed competition may have been reduced at high wheatgrass densities (Jacobs et al. 1996, Velagala et al. 1997).

Tillage tended to enhance establishment of intermediate wheatgrass, especially at the highest seeding rate. Tillage may have created safe sites (Kocher and Stubbendieck 1986), while high seeding rates may have provided enough seeds to fill a majority of those safe sites (Young 1988, Call and Roundy 1991). In addition, improved soil conditions may have enhanced growth (Donahue et al. 1977). Although tillage prior to seeding can increase seedling establishment, many rangeland sites are unsuitable for tillage.

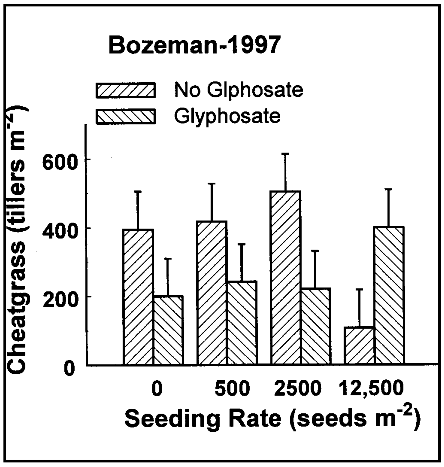

Fig. 7. Effect of tillage*seeding rate on cheatgrass density at Bozeman in 1997. Error bars represent least significant differences ($\alpha = 0.05$).

Glyphosate increased spotted knapweed density, but reduced its biomass at Hamilton. In this case, we believe that the herbicide controlled a majority of mature spotted knapweed plants, but created safe sites available to knapweed, and in some cases, wheatgrass seedlings. Glyphosate reduced knapweed biomass when applied in conjunction with seeding at Bozeman. The effect of glyphosate on controlling cheatgrass was variable between sites and years. Variations in the effects of glyphosate may be dependant on weather and plant phenology (Dewey et al. 1997).

Implications for Management

It has been proposed that an appropriate goal for rangeland weed management would be to develop an ecologically-healthy plant community that is relatively weed-resistant, while meeting other land-use objectives (Sheley et al. 1996). Promoting or establishing competitive desirable grasses is essential for sustainable management of spotted knapweed. Land managers are reluctant to attempt revegetation because of the high costs and probability of failure. Our study showed that currently recommended seeding rates may account for the high failure of many rangeland seedings. We believe that revegetation success can be enhanced by increasing seeding rates.

It is generally accepted that herbicides are required to control weeds during the establishment of grasses. However, Velagala et al. (1997) indicated that weed competition only accounted for a small portion of the variation associated with seedling establishment in many situations, and density independent factors determine establishment success. Our study suggests that high seeding rates can help overcome the effect of weed competition and increase the probability of desirable seeds reaching safe sites. Using high seeding rates to control spotted knapweed and enhance seedling establishment may increase the effectiveness of broadcast seedings on steep or inaccessible rangeland, where many weed infestations exist. Although the seeding rates used in this study are extraordinarily high, strip or patch seeding may ensure seedling establishment, after which, natural dispersal may occur. In addition, this may allow the inclusion of broad leaved species that may contribute to the health of the plant community and increase its resistance to invasion (Tilman 1996).

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Yield and feeding of prairie grasses in east-central Alberta

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Abstract

Information on the yield of grasses as the plants mature is useful to optimize grazing potential and quality hay production. The objectives of this study were to compare the yield and feeding value of 11 common prairie grasses over 2 yearly cycles of growth and determine which of the grasses may require supplementation to meet nutrient requirements of grazing cattle. Dry matter yield (DM), crude protein (CP), acid detergent fiber (ADF), calcium (Ca), and phosphorus (P) values were obtained for brome (*Bromus inermis* [L.]), creeping red fescue (*Festuca rubra* [L.]), crested wheatgrass (*Agropyron cristatum* [L.] *Gaertn*), intermediate wheatgrass (*Agropyron intermedium* (host) Beauv), meadow foxtail (*Alopecurus pratensis* [L.]), orchardgrass (*Dactylis glomerata* [L.]), pubescent wheatgrass (*Agropyron trichophorum* Link. richt), streambank wheatgrass (*Agropyron riparium* Scriba & Smith), slender wheatgrass (*Agropyron trachycaulum* Link Malte), tall fescue (*Festuca arundinacea* Schreb), and timothy (*Phleum pratense* [L.]) at weekly intervals from June to September, in 1992 and 1993. Most grasses reached maximum yields at week 8 in 1992 (drought year) and week 12 in 1993 (normal year). Herbage mass yields (g/0.25m^2) at week 8 in 1992 (highest to lowest yielding) were crested wheatgrass (235), intermediate wheatgrass(210), pubescent wheatgrass(173), brome(161), slender wheatgrass(152), meadow foxtail(114), Tall fescue(110), timothy(101), orchardgrass(83), creeping red fescue(56), and streambank wheatgrass(50). Herbage mass yields pattern of the grasses in 1993 was similar to that in 1992 except for crested wheatgrass and brome which ranked first and fourth in 1992 but ranked fifth and second, in 1993, respectively. Quality declined in all grasses as they matured. The average CP content of grasses declined from 24% to 13% in 1992 and from 21.5% to 12.1% in 1993 but were adequate to meet crude protein requirements of growing, pregnant or lactating grazing cattle. The Ca levels in all grasses were adequate for all classes of cattle on pasture but the low P levels of 0.11% in both years indicate that growing, pregnant or lactating cattle grazing on these pastures would require P supplementation.

Key Words: yield, feeding value, prairie grasses, nutrient composition

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Resumen

La información sobre el rendimiento de los pastos conforme las plantas maduran es útil para optimizar el potencial de pastoreo y la producción de heno de calidad. Los objetivos de este estudio fueron comparar el rendimiento y valor nutritivo de 11 pastos comunes de la pradera durante 2 ciclos de crecimiento y determinar cuál de los pastos puede requerir suplementación para satisfacer los requerimientos nutricionales del ganado en pastoreo. Los valores de rendimiento de materia seca (DM), proteína cruda (CP), fibra ácido detergente, calcio y fósforo fueron determinados semanalmente de junio a septiembre de 1992 y 1993 en los pastos "brome" (*Bromus inermis* [L.]), "creeping red fescue" (*Festuca ruba* [L.]), "crested wheatgrass" (*Agropyron cristatum* [L.] Gaertn), "intermediate wheatgrass" (*Agropyron intermedium* (Host) Beauv), "meadow foxtail" (*Alopecurus pratensis* [L.]), "orchardgrass" (*Dactylis glomerata* [L.]), "pubescent wheatgrass" (*Agropyron trichophorum* Link. richt), "streambank wheatgrass" (*Agropyron riparium* Scriba y Smith), "slender wheatgrass" (*Agropyron trachycaulum* Link Malte), "Tall fescue" (*Festuca arundinacea* Schreb) "timothy" (*Phleum pratense* [L.]). En 1992 (año seco) la mayoría de los pastos alcanzó su máximo rendimiento en la semana 8 y en 1993 (año normal) en la semana 12. En 1992 el rendimiento de forraje (g/0.25m^2) en la semana 8 (ordenados de mayor a menor) fue 235, 210, 173, 161, 152, 114, 110, 101, 83, 56 y 50 g para "crested wheatgrass", "intermediate wheatgrass", "pubescent wheatgrass", "brome", "slender wheatgrass", "meadow foxtail", "tall fescue", "timothy"," orchardgrass", "creeping red fescue", y " streambank wheatgrass" respectivamente. En 1993 el patrón de rendimiento de forraje fue similar al de 1992 excepto para "crested wheatgrass" y "brome" los cuales clasificaron en primero y cuarto lugar en 1992 y en quinto y segundo lugar en 1993; respectivamente. La calidad de todos los pastos declinó conforme maduraron. El promedio de proteína cruda disminuyó de 24% a 13% en 1992 y de 21.5% a 12.1% en 1993; sin embargo, el contenido de proteína cruda fue suficiente para satisfacer los requerimientos del ganado en pastoreo en las etapas de crecimento, lactancia y preñez. Los niveles de calcio de todos los pastos fueron adecuados para todas las clases de ganado en pastoreo. Los bajos niveles de fósforo (0.11%) en ambos años indican que ganado en crecimiento, lactancia y preñez que pastore estas praderas requerira suplementación de fósforo.

Traditional methods of open range grazing are being replaced with high intensity rotational grazing systems because of economic constraints such as the cost of land (Smith 1981). Thus, cattle producers continue to modify management practices such as cutting and grazing to optimize productivity and profitability from limited land bases. In addition, rates of gain of cattle in some grazing trials have been comparable to those achieved in feedlots in Alberta but at a much lower cost per kilogram of gain (McCaughey and Cliplef 1996). However, little information is available comparing grass species for high intensity range hay production in Alberta. Information on yields of herbage mass and changes in quality as the plant matures would help evaluate the potential of grass species for hay or grazing over an extended grazing season. The parkland area of the prairies cuts across Central Alberta which is also an area where beef enterprises are highly concentrated (Baron and Knowles 1984).

Increasingly, near infrared reflectance spectroscopy (NIRS) is being used to determine composition of feedstuffs including the determination of several proximate analysis parameters that usually are obtained by wet chemistry methods. Information on the applicability of NIRS in the analysis of growing forages would be useful since it would permit obtaining nutrient profiles of pastures. This technology has been shown to be reliable in proximate analysis (Shenk and Westerhaus 1994, Shenk 1989, Redshaw et al. 1986).

The objectives of this study were to compare the yield and quality of common prairie grasses over 2 years and to determine which grasses are adequate to meet nutrient requirements of all classes of grazing cattle. A second objective of the study was to evaluate the use of NIRS technology to predict nutrient composition of these grasses and test the accuracy of the calibrations developed.

Materials and Methods

Eleven pure cultivated stands of prairie grasses, brome (*Bromus inermis* [L.]), creeping red fescue (*Festuca rubra* [L.]), crested wheatgrass (*Agropyron cristatum* [L.] *Gaertn*.), intermediate wheatgrass (*Agropyron intermedium* (host) *Beauv*), meadow foxtail (*Alopecurus pratensis* [L.]), orchardgrass (*Dactylis glomerata* [L.]), pubescent wheatgrass (*Agropyron trichophorum* Link. richt), streambank wheatgrass (*Agropyron riparium* Scriba & Smith), slender wheatgrass (*Agropyron trachycaulum* Link *Malte*), tall fescue (*Festuca arundinacea* Schreb), and timothy (*Phleum pratense* [L.]) were used in 1992 in three, 16 × 12 m^2 replicated plots at the Alberta Agriculture, Tree Nursery and Horticulture Centre, Edmonton, Alberta, Canada. Each grass was randomly replicated in 3 different blocks. The plots were located in the Black soil zone in east-central Alberta. The soil was a Ponoka Light Loam (lacustrine, medium textured) (Bowser et al. 1962). The topography is level to undulating and the soil is found on the edge of basin-like areas, that is, on the edge of lacustrine basins. Based on soil fertility tests, only nitrogen was applied across the plots in the spring of 1992 at a rate of 34 kg ha^{-1}.

Samples consisted of weekly clippings from the 3 plots. The treatments were arranged in a multiway randomized block design with 3 replicates. Once randomized, the plot area remained unchanged. Subsamples were clipped to a stubble height of 3 cm with hand-held sheep shears from three 0.25 m^2 areas of each plot per week. Adjacent 0.25 m^2 areas of grass stands were sampled at each clipping to obtain cumulative herbage mass. In 1992, first clippings were taken on 15 June. After the last samples were taken in second week of August all plots were clipped to a stubble height of 7.5 cm using a gas-powered garden mower. The study was repeated in 1993, however, the first samples were taken on 21 June and the last samples in early September.

All individual forage subsamples were weighed prior to drying and were then oven dried at 60° C for 24 hours, re-weighed, and ground through a 1-mm screen (Wiley mill, Standard model 3, Arthur H. Thomas Co., Philadelphia, Penn). Crude protein (CP), calcium (Ca) and phosphorus (P) were measured colorimetrically with a Technicon Auto Analyzer II method in which samples had been prepared using the Kjeldahl digestion (method no. 7.022) according to standard procedures (AOAC 1990) and acid detergent fiber (ADF) was determined by the method of Goering and Van Soest (1970). The wet chemistry values obtained on 1992 pasture samples, corrected for dry matter (DM) content at 104°C (method no. 7.003, AOAC 1990), were used to develop NIRS regression equations to predict DM, CP, ADF, Ca, and P in the grasses.

Samples obtained in 1993 were scanned by the NIR system model 6500 instrument (NIR System, Inc., Silver Spring, Md), and the spectra

Table 1. Regression statistics for NIRS calibrations for predicting dry matter, protein, calcium, phosphorus, and acid detergent fiber for samples in 1992, 1993 and 1992 and 1993 combined.

	1992				1993				1992 and 1993 combined			
Nutrient	N	r^2	SEC	Slope	N	r^2	SEC	Slope	N	r^2	SEC	Slope
DM	176	0.99	0.06	0.98	206	0.95	0.13	0.95	386	1.00	0.08	1.00
CP	173	0.99	0.37	0.99	203	0.99	0.44	0.99	387	0.99	0.46	0.99
Ca	177	0.60	0.05	0.44	207	0.72	0.04	0.59	389	0.59	0.05	0.53
P	181	0.93	0.01	0.90	204	0.94	0.02	0.90	389	0.90	0.02	0.88
ADF	176	0.98	0.69	0.98	176	0.98	0.60	0.95	392	0.98	0.61	0.98

SEC= standard error of calibration.
N= number of samples in the calibration.

Table 2. Average herbage mass[1] of pasture species at different weeks in 1992 .

Pasture[2]	Week of Cut Herbage mass 2	4	5	6	7	8	10
	(g/0.25 m^2)						
BR	18.5^{bc}	44.9^{cde}	76.1^{ab}	100.3^{abc}	116.8^{abc}	161.2^{b}	148.5^{bc}
CRF	9.1^{c}	23.1^{f}	35.5^{c}	53.4^{bc}	60.9^{c}	56.2^{d}	47.5^{f}
CRWG	38.4^{a}	81.7^{a}	105.1^{a}	129.2^{a}	112.0^{abc}	235.4^{a}	118.7^{cde}
IWG	26.9^{b}	54.8^{c}	89.9^{ab}	109.1^{abc}	122.4^{abc}	210.7^{a}	196.0^{a}
MFT	40.7^{a}	67.7^{b}	83.5^{ab}	89.0^{abc}	101.4^{abc}	114.4^{c}	60.1^{f}
OCHG	15.4^{bc}	32.7^{ef}	52.1^{bc}	68.8^{abc}	127.5^{abc}	83.2^{cd}	69.9^{f}
PWG	19.2^{bc}	41.9^{cde}	79.3^{ab}	125.3^{ab}	175.5^{a}	173.3^{b}	170.0^{ab}
STWG	11.4^{c}	26.7^{f}	28.8^{c}	43.1^{c}	54.4^{c}	50.0^{d}	50.3^{f}
SWG	21.7^{bc}	48.4^{cd}	75.4^{ab}	105.0^{abc}	144.9^{ab}	152.1^{b}	132.2^{bcd}
TF	16.7^{bc}	30.9^{ef}	54.0^{bc}	80.2^{abc}	80.2^{bc}	109.8^{c}	93.5^{def}
TIM	12.7^{c}	34.7^{def}	59.1^{bc}	77.8^{abc}	86.5^{bc}	101.4^{c}	85.7^{ef}
SEM	2.9	3.6	8.3	14.9	16.1	11.6	10.8

[1]Herbage mass (DM yield).
[2] BR = brome; CRF = creeping red fescue; CRWG = crested wheatgrass; IWG = intermediate wheatgrass; MFT = meadow foxtail; OCHG = orchardgrass; PWG = pubescent wheatgrass; STWG = streambank wheatgrass; SWG = slender wheatgrass; TF = tall fescue; TIM = timothy. Column values with different superscripts are significantly different, $p < 0.05$.

collected as log (1/R) from 400 nm to 2,498 nm. All 1993 samples were scanned and samples that differed spectrally (from 1992 samples) were added to the 1992 calibration set. The combined sample spectra were used to develop new calibration regressions. Four hundred and two samples (Table 1) from the 2 year combined total of 1,782 samples, across different stages of growth, were selected using the Center, Select and Cal programs developed by Intrasoft International NIRS2 software, version 3.0 (NIRSystem, Inc., Silver Spring, Md., Shenk and Westerhaus 1991a) for calibration and validation. The total of 402 samples was made up of 187 samples selected from 693 samples in 1992 and 215 samples selected from 1,089 samples in 1993 (Table 1). The NIRS calibrations were obtained using 4 cross validation groups with modified partial least squares analysis using every eighth wavelength between 400 and 2,498 nm. The critical math treatment was 3, 5, 5, 1 calculated with a difference of 5 data points followed by a 5 point smooth. Detrend (NIRSystem, Inc., Silver Spring, Md., Shenk and Westerhaus 1991b) was used to reduce the interference of light scatter and particle size of sample in the spectra. Downweight was used to remove samples with large T or H values. Spectral distance calculations, selection of samples and calibration regressions were carried out by the Center, Select and Cal programs developed by Intrasoft International NIRS2 software, version 3.0 (NIRSystem, Inc., Silver Spring, Md., Shenk and Westerhaus 1991c). The Center program was used to order all samples according to H Mahalanobis distance and to remove or discriminate outlier samples with a cut-off distance of global H > 3.0 (Shenk and Westerhaus 1994). Accuracy of the new regression equations to predict the nutrient content of grasses was evaluated by comparing the predicted nutrient values with wet chemistry values of the samples in the calibration set.

The data were analyzed using General Linear Model (GLM) procedure of SAS (1990). Experimental design was a randomized block with 3 replicates per treatment. The data of each grass from the blocks were compared for quantity and quality of dry matter. Means when significant were separated by a student Newman Keul's test (SAS 1990). Significance was declared at $P \leq 0.05$ unless specified otherwise.

Table 3. Average herbage mass[1] of pasture species at different weeks in 1993.

PASTURE[2]	Week of cut 3	5	6	7	8	9	10	11	12	13	14
	(g/0.25 m^2)										
BR	53.9^{bc}	103.8^{a}	135.5^{a}	191.8^{a}	216.0^{a}	259.7^{a}	225.7^{abc}	302.4^{abc}	416.2^{ab}	331.0^{ab}	282.6^{abc}
CRF	24.6^{e}	54.5^{a}	77.1^{ab}	87.2^{c}	97.0^{c}	129.1^{ab}	134.5^{bc}	183.7^{def}	259.8^{cd}	209.2^{ab}	188.9^{cd}
CRWG	57.9^{b}	111.5^{a}	146.7^{a}	199.9^{a}	207.5^{a}	224.4^{ab}	229.0^{abc}	269.1^{abcd}	341.1^{bc}	249.8^{ab}	243.2^{bc}
IWG	35.1^{cde}	93.4^{a}	135.4^{ab}	215.6^{a}	222.4^{a}	257.9^{a}	253.7ab	357.9^{a}	469.5^{a}	393.2^{a}	359.3^{a}
MFT	82.8^{a}	104.2^{a}	119.1^{ab}	126.8^{bc}	102.9^{c}	107.4^{b}	109.3^{c}	164.0^{ef}	218.5^{d}	167.3^{ab}	140.1^{d}
OCHG	30.5^{de}	68.9^{a}	107.0^{a}	110.8^{c}	107.5^{c}	147.2^{ab}	138.7^{bc}	207.3^{cdef}	255.3^{cd}	194.3^{ab}	187.1^{cd}
PW	48.6^{bcd}	101.8^{a}	121.1^{ab}	156.7^{b}	190.3^{abc}	204.2^{ab}	288.9^{a}	342.7^{ab}	400.7^{ab}	318.0^{ab}	342.2^{ab}
STWG	41.8^{bcde}	71.4^{a}	68.9^{b}	83.8^{c}	103.2^{c}	113.8^{b}	147.9^{bc}	173.2^{def}	272.2^{cd}	197.2^{ab}	231.1^{bcd}
SWG	32.7^{de}	71.4^{a}	92.1^{ab}	121.4^{bc}	159.0^{abc}	171.0^{ab}	241.3^{abc}	290.0^{abc}	372.3^{b}	293.2^{ab}	332.1^{ab}
TF	30.6^{de}	65.5^{a}	86.5^{ab}	96.0^{c}	95.1^{c}	171.8^{ab}	214.9^{abc}	257.1^{bcde}	323.7^{bc}	253.9^{ab}	321.2^{ab}
TIM	41.0^{bcde}	84.2^{a}	82.0^{ab}	103.9^{c}	112.4^{c}	107.0^{b}	132.0^{bc}	147.7^{f}	221.9^{d}	180.3^{ab}	167.3^{d}
SEM	4.828	11.490	14.941	10.390	20.740	28.091	26.925	21.866	20.776	44.974	25.586

[1] Herbage mass (DM yield).
[2] BR = brome, CRF = creeping red fescue, CRWG = crested wheatgrass, IWG = intermediate wheatgrass, MFT = meadow foxtail, OCHG = orchardgrass, PWG = pubescent wheatgrass, STWG = streambank wheatgrass, SWG = slender wheatgrass , TF = tall fescue, TIM = timothy.
Column values with different superscripts are significantly different, $p < 0.05$.

Table 4. Mean daily temperature and total monthly precipitation at Oliver Tree Nursery, Edmonton, Alberta, during 1992 and 1993.

Month	Mean Daily Temperature 1992	1993	23 Year Average*	Monthly Precipitation 1992	1993	23 Year Average*
	(˚C)			(mm)		
May	9.8	12.3	11.1	33.3	51.2	49.2
June	16.0	13.9	14.9	21.8	77.3	93.6
July	15.3	15.3	16.7	40.7	61.9	91.7
August	14.2	15.1	15.6	35.4	78.5	68.2

Source: Environment Canada.
* Prepared/calculated by: Conservation and Development Branch, AAFRD, Edmonton, AB.

Results and Discussion

Dry Matter Yield

Tables 2 and 3 show the pattern of average herbage mass yield of grasses by pasture type and week of cut. The general growth pattern of all grasses, as indicated by herbage mass yield at each weekly cut, were similar. The cumulative herbage mass yields generally increased steadily until a maximum level was reached except for crested wheatgrass in 1992 and brome in 1993, both of which showed a decrease in yield of 13% before attaining a maximum. This may be due to a transient adverse effect of low precipitation (Table 1) on growth of crested wheatgrass in 1992. The reasons for the decreased herbage mass yield for brome are not readily apparent. All grasses in 1992 reached maximum yields at week 8 with the exception of creeping red fescue, orchardgrass and streambank wheatgrass which appeared to mature or peak earlier at week 7. Early maturity or low yield exhibited by these 3 grasses may be due to sensitivity of creeping red fescue and orchardgrass to lack of adequate moisture and the naturally low forage yield of streambank wheatgrass, considered the lowest yielding cultivated wheatgrass (Smoliak and Bjorge 1981). The longer, more normal, growing season with adequate precipitation in 1993 (Table 4), produced maximum herbage mass yields much later, at week 12, for all grasses (Table 3).

Based on data from both years, the 5 highest yielding grasses were intermediate wheatgrass, brome, crested wheatgrass, pubescent wheatgrass and slender wheatgrass. The 1993 herbage mass yields (in tons per hectare) of 18.8 for intermediate wheatgrass, 16.6 for brome, 13.6 for crested wheatgrass, 16.0 for pubescent wheatgrass, and 14.9 for slender wheatgrass, all being higher than the yields of the previous year. Dry matter (herbage mass) yields reported by Lakeland Agricultural Research Association (LARA) for some grasses in Alberta are much lower than those obtained in this study being: between 5.6 and 7.2 (tons ha^{-1}) for brome, between 3.7 and 4.8 for intermediate wheatgrass, between 1.8 and 2.5 for meadow foxtail (LARA 1994, 1995), between 4.3 and 7.2 (LARA 1995) and 3.2 and 3.7 for timothy (LARA 1993). The differ-

Table 5. Crude protein and acid detergent fiber levels of pasture species at different weeks in 1992.

Pasture[1]	Week of Cut 2	4	5	6	7	8	10
Crude protein				(%)			
BR	26.2[a]	23.4[abc]	20.3[ab]	17.8[a]	15.4[a]	12.3[a]	12.4[ab]
CRF	20.3[a]	20.9[bc]	17.6[b]	16.9[a]	16.3[a]	16.6[a]	11.3[ab]
CRWG	22.8[a]	20.7[bc]	18.0[b]	15.6[a]	14.0[a]	11.4[a]	12.7[ab]
IWG	26.0[a]	21.7[abc]	20.2[ab]	17.9[a]	15.8[a]	12.8[a]	12.1[ab]
MFT	23.9[a]	19.5[c]	18.5[b]	16.3[a]	15.9[a]	13.2[a]	14.1[ab]
OCHG	24.5[a]	26.0[ab]	21.5[ab]	18.7[a]	17.3[a]	15.8[a]	15.0[a]
PWG	26.5[a]	22.6[abc]	20.2[ab]	17.6[a]	15.7[a]	13.6[a]	12.6[ab]
STWG	23.4[a]	20.0[bc]	16.6[b]	16.2[a]	14.9[a]	12.6[a]	12.3[ab]
SWG	25.1[a]	21.2[bc]	18.4[b]	17.1[a]	14.3[a]	11.4[a]	10.8[ab]
TF	22.6[a]	23.1[abc]	19.8[ab]	17.1[a]	15.8[a]	11.9[a]	12.3[ab]
TIM	22.4[a]	22.5[abc]	19.3[ab]	17.4[a]	14.8[a]	12.6[a]	9.9[b]
SEM	0.39	0.36	0.40	0.47	0.48	0.48	0.33
Acid detergent fiber				(%)			
BR	18.2[a]	20.4[c]	25.6[c]	28.3[abc]	31.6[a]	32.5[abc]	31.3[cd]
CRF	17.3[a]	23.2[b]	25.4[c]	27.3[abc]	28.0[b]	29.0[c]	27.5[c]
CRWG	19.6[a]	22.6[b]	27.0[ab]	29.9[a]	32.3[a]	34.9[a]	32.5[abc]
IWG	19.8[a]	23.3[b]	27.5[a]	28.7[ab]	31.5[a]	35.0[a]	33.9[a]
MFT	22.0[a]	24.8[a]	27.7[a]	28.4[abc]	28.8[b]	30.8[bc]	27.3[e]
OCHG	16.1[a]	22.5[b]	25.7[c]	27.7[abc]	29.3[b]	29.0[c]	27.5[e]
PWG	19.9[a]	23.2[b]	27.8[a]	29.6[a]	31.1[a]	33.6[ab]	32.1[abc]
STWG	16.0[a]	24.1[ab]	28.6[a]	29.9[a]	31.5[a]	32.8[ab]	31.8[bcd]
SWG	21.4[a]	24.1[ab]	27.7[a]	29.6[ab]	31.5[a]	33.9[a]	33.6[ab]
TF	16.3[a]	21.2[c]	24.3[d]	26.1[c]	27.5[b]	30.3[bc]	26.8[e]
TIM	12.5[a]	23.1[b]	26.3[bc]	27.1[bc]	29.2[b]	31.4[abc]	30.2[d]
SEM	2.81	0.350	0.351	0.542	0.460	0.472	0.33

[1]BR = brome, CRF = creeping red fescue, CRWG = crested wheatgrass, IWG = intermediate wheatgrass, MFT = meadow foxtail, OCHG = orchardgrass, PWG = pubescent wheatgrass, STWG = streambank wheatgrass, SWG = slender wheatgrass, TF = tall fescue, TIM = timothy.
Column values with different superscripts are significantly different, $p < 0.05$.

Table 6. NIR estimated values of crude protein levels of pasture species at different weeks in 1993

	Week of cut										
PASTURE[1]	3	5	6	7	8	9	10	11	12	13	14
	(%)										
BR	22.1^{abc}	21.3^{a}	17.3^{ab}	11.9^{ab}	12.9^{bcd}	12.8^{c}	13.3^{dc}	11.9^{ab}	11.2^{a}	11.2^{ab}	10.3^{bcd}
CRF	19.7^{c}	20.9^{a}	19.4^{a}	14.4^{a}	15.8^{a}	16.2^{a}	17.5^{a}	14.5^{a}	14.1^{a}	13.5^{ab}	12.5^{abc}
CRWG	20.0^{c}	18.5^{a}	16.6^{ab}	10.9^{b}	11.5^{d}	13.2^{bc}	12.4^{d}	10.9^{b}	10.8^{a}	12.8^{ab}	10.3^{bcd}
IWG	24.1^{ab}	20.9^{a}	18.1^{ab}	11.7^{ab}	13.1^{bcd}	13.0^{bc}	12.7^{d}	11.7^{ab}	10.4^{a}	9.1^{b}	9.1^{d}
MFT	19.0^{c}	18.5^{a}	16.5^{ab}	13.5^{ab}	13.3^{bc}	15.1^{abc}	16.5^{ab}	13.5^{ab}	12.6^{a}	13.6^{ab}	10.8^{bcd}
OCHG	22.0^{abc}	19.2^{a}	15.9^{b}	12.5^{ab}	14.0^{b}	14.7^{abc}	14.7^{bcd}	12.5^{ab}	12.7^{a}	12.7^{ab}	11.7^{abcd}
PWG	23.1^{abc}	20.9^{a}	16.9^{ab}	12.6^{ab}	13.0^{bcd}	13.7^{abc}	13.8^{cd}	12.6^{a}	12.0^{a}	10.7^{b}	9.7^{dc}
STWG	20.2^{bc}	19.0^{a}	16.3^{b}	14.4^{a}	13.3^{bc}	15.5^{ab}	15.6^{abc}	14.4^{a}	13.0^{a}	13.9^{ab}	13.5^{ab}
SWG	22.2^{abc}	20.3^{a}	16.3^{b}	11.6^{ab}	11.7^{cd}	13.6^{bc}	13.3^{cd}	11.6^{ab}	11.9^{a}	10.4^{b}	10.4^{bcd}
TF	22.6^{abc}	20.6^{a}	17.9^{ab}	12.0^{ab}	14.6^{ab}	14.3^{abc}	14.4^{bcd}	12.0^{ab}	11.6^{a}	11.3^{ab}	11.7^{abcd}
TIM	18.9^{c}	18.9^{a}	18.3^{ab}	14.3^{a}	14.8^{ab}	15.5^{abc}	17.3^{bcd}	14.3^{a}	13.3^{a}	13.5^{ab}	10.3^{bcd}
SEM	0.840	0.805	0.572	0.656	0.393	0.525	0.556	0.656	0.719	0.993	0.650

[1]BR = brome, CRF = creeping red fescue, CRWG = crested wheatgrass, IWG = intermediate wheatgrass, MF = meadow fescue, MFT = meadow foxtail, OCHG = orchardgrass, PWG = pubescent wheatgrass, STWG = streambank wheatgrass, SWG = slender wheatgrass, TF = tall fescue, TIM = timothy.
Column values with different superscripts are significantly different , $p < 0.05$

ence in yields may be related to harvest methods. Our yields were higher than some reported yield values because our subsamples were clipped (from 0.25 m^2 areas) to a stubble height of 3 cm compared to stubble height of about 5 cm described elsewhere for Tall wheatgrass (Undersander and Naylor 1987). Also, in our study, by the end of July (week 9) in 1993 (Table 3), brome, crested wheatgrass and intermediate wheatgrass had, respectively, produced 62%, 66%, and 55% of their maximum herbage mass yield. In contrast, slender wheatgrass and pubescent wheatgrass produced a significant proportion of herbage mass (49% and 54%, respectively), during the latter third of the growing season. This implies that any adverse weather effects during the latter third of the growth period, such as low precipitation, would reduce expected yields in slender wheatgrass and pubescent wheatgrass pastures. Pastures which contain brome as a major component have been shown to result in inadequate forage supplies to meet the growing requirements of the cow and calf (Baron and Knowles 1984).

These results place creeping red fescue as one of the lowest yielding grasses (Table 2) and show streambank wheatgrass to be the lowest yielding wheatgrass in this study, in agreement with an earlier view that it was the lowest yielding cultivated wheatgrass (Smoliak and Bjorge 1981). As well, yields of each crop declined after reaching a maximum (Tables 2 and 3). The declines in growth or die back that occurred in 1992, shown by herbage mass yield data at week 10, could be attributed to the severe effects of drought or senescence caused by self-shading or advanced maturity that apparently ended the growth cycle earlier. The normal growth cycle has been reported to be considerably longer for grasses on the Canadian prairies (Kilcher and Troelsen 1973).

Crude Protein and ADF

Nutrient composition data of grasses are shown in Tables 5, and 6. As expected, nitrogen content (CP) of the grasses declined as the plant matured (Van Soest 1982). Quality, indicated by CP and ADF, was highest at first cut, at week 2 (1992) and generally declined in all grasses as the plants matured; and there was an inverse relationship between CP and ADF until the yields approached or reached maximum levels (Table 5). Crude protein content of the pastures in 1992, were initially high but generally decreased or reached a constant level for all grasses as time progressed. The average CP content of grasses declined from 24% to 13%, the latter value being much higher than 9% observed elsewhere for brome (Kilcher and Troelsen 1973), indicating an earlier maturing or earlier termination of the growth cycle in this study. The CP content of grasses of between 13 and 24% falls well within the NRC (1984,1989) range of values considered adequate to meet protein requirement of all classes of grazing cattle (NRC 1984, 1989). However, the ADF content, as is expected with a maturing plant, followed a general pattern of increasing in all grasses with age (Table 5) and, thus, the grasses in this study, as expected, declined in quality as they matured (Van Soest 1982, Kilchner and Troelsen 1973).

The pattern of CP declines as estimated by the NIR procedure in pastures as the plants matured in 1993 was not much different from 1992. From the highest levels initially at week 3, CP content declined in all grasses until week 7 or 8 (Table 6). Thereafter, all forages showed an increase in CP content to week 9 or 10 and followed by, as expected, a pattern of decline in quality, which is a characteristic of maturing plants.

Available information on forages pertains to harvests of pastures or stands that consist of grass mixtures for normal or physiological time frames. Forage composition data in this study were obtained from cumulative harvests at approximately weekly intervals in the growing season (Tables 5–10). This information enhances greater understanding of the effects of maturity on herbage yield and herbage composition of single forage species of cool season grasses in Alberta. Feeding value of the grasses, based on evaluation of the protein and

Table 7. NIR estimated acid detergent fiber levels of pasture species in 1993.

PASTURE [1]	Week of cut 3	5	6	7	8	9	10	11	12	13	14
	(%)										
BR	24.3^{ef}	27.7^{abcd}	31.4^{a}	31.7^{d}	34.2^{a}	32.9^{cdef}	32.5^{c}	31.7^{d}	33.2^{d}	33.5^{d}	33.5^{ef}
CRF	24.3^{bcd}	25.7^{bcde}	27.6^{cd}	31.5^{d}	26.6^{d}	29.5^{g}	30.4^{d}	31.5^{d}	33.3^{d}	33.5^{d}	34.4^{def}
CRWG	24.9^{cdef}	28.1^{abc}	30.6^{ab}	32.9^{cd}	34.0^{a}	32.9^{cdef}	33.5^{c}	32.9^{cd}	33.5^{d}	33.6^{d}	32.5^{f}
IWG	24.6^{efd}	26.7^{abcde}	29.4^{abc}	36.0^{a}	33.1^{a}	35.7^{ab}	37.2^{a}	36.0^{a}	36.9^{abc}	37.1^{abc}	35.5^{cde}
MFT	27.0^{b}	28.2^{ab}	30.1^{abc}	33.7^{bc}	31.1^{ab}	32.6^{def}	33.9^{c}	33.7^{bc}	37.3^{abc}	35.8^{bcd}	37.5^{abc}
OCHG	24.4^{def}	26.5^{abcde}	30.2^{abc}	30.1^{cd}	29.0^{bcd}	30.7^{fg}	32.3^{c}	33.1^{cd}	35.5^{cd}	35.5^{bcd}	36.0^{bcd}
PWG	25.7^{bcde}	26.3^{abcde}	28.5^{bcd}	35.2^{ab}	32.9^{a}	35.2^{abc}	36.2^{ab}	35.2^{ab}	35.8^{bcd}	36.1^{abcd}	35.4^{cde}
STWG	28.4^{a}	29.3^{a}	31.5^{a}	36.3^{a}	34.0^{a}	35.4^{ab}	35.8^{ab}	36.3^{a}	38.6^{a}	37.7^{ab}	38.3^{ab}
SWG	26.1^{bc}	27.2^{abcde}	30.0^{abc}	36.6^{6}	33.5^{a}	36.1^{a}	36.9^{a}	36.6^{a}	37.4^{abc}	39.0^{a}	38.2^{ab}
TF	23.5^{fg}	24.9^{de}	27.1^{d}	32.8^{cd}	29.7^{bc}	33.5^{bcde}	33.2^{c}	32.8^{cd}	33.2^{d}	34.3^{cd}	33.6^{ef}
TIM	24.0^{f}	25.1^{cde}	26.2^{d}	34.0^{bc}	27.8^{cd}	32.2^{ef}	33.2^{c}	34.0^{bc}	37.1^{abc}	36.4^{abcd}	37.1^{abc}
SEM	0.840	0.805	0.572	0.656	0.393	0.525	0.556	0.656	0.719	0.993	0.650

[1]BR = brome, CRF = creeping red fescue, CRWG = crested wheatgrass, IWG = intermediate wheatgrass, MF = meadow fescue, MFT = meadow foxtail, OCHG = orchardgrass, PWG = pubescent wheatgrass, STWG = streambank wheatgrass, SWG = slender wheatgrass, TF = tall fescue, TIM = timothy.
Column values with different superscripts are significantly different, $p < 0.05$

digestible energy content, derived from ADF values (Mathison et al 1982), indicate that the grasses in this study (Tables 5–7), remained, *qualitatively*, at an 'equivalent' of between the vegetative (grasses at 63%TDN and 15% protein content) and boot or bud stage of growth (grasses at 57%TDN and 11% protein content) for much of the growing cycle (Smoliak and Bjorge 1981). Such information can be useful in decisions to move cattle into or out of pasture species to extend the grazing season.

Mineral Composition

Changes in Ca and P contents of grasses with increasing maturity in 1992 and 1993 are shown in Tables 8, 9, and 10. All grasses in 1992 reached high Ca levels of between 0.38 and 0.56% at week 4 or 5. Five of the grasses, brome, meadow foxtail, pubescent wheatgrass, streambank wheatgrass, and slender wheatgrass attained 0.38% Ca level at the lower end while the 6 remaining grasses reached levels above 0.38% up to high end level of 0.56%. The Ca levels in 1992, as the grasses matured, remained adequate for cattle on pasture (NRC 1984,1989). However, the highest Ca levels of between 0.32–0.44% (Table 9) were attained much later in the growth cycle of grasses in 1993 (at week 9/10) compared to the grasses in 1992. The maximum levels in 1993 were generally lower than values for 1992 as a result of the comparatively higher forage yields (Table 2 and 3). Calcium levels in all grasses as they matured in 1993 (Table 9), were adequate for cattle on pasture (NRC 1984, 1989).

Phosphorus content of grasses in 1992 varied, from levels of between 0.15 and 0.24% initially, to between 0.10–0.16% levels at maximum yield (week 8). The latter levels were low enough to warrant supplementation to meet beef cattle requirement for P for all grasses with the exception of timothy. Initial P levels, generally higher in 1993 (Table 10) than in 1992, were highest in 1993 for 10 of the 11 grasses (between 0.28 and 0.35% P) (Table

Table 8. Mineral composition of various prairie grasses at different stages of growth in 1992.

Pasture[1]	Week of Cut 2	5	7	10
Calcium	(%)			
BR	0.34^{a}	0.38^{a}	0.29^{e}	0.32^{d}
CRF	0.40^{a}	0.49^{a}	0.47^{a}	0.47^{a}
CRWG	0.39^{a}	0.42^{a}	0.33^{cde}	0.35^{bcd}
IWG	0.39^{a}	0.45^{a}	0.35^{cd}	0.35^{bcd}
MFT	0.27^{b}	0.38^{a}	0.35^{cd}	0.40^{bc}
OCHG	0.33^{ab}	0.38^{a}	0.35^{cd}	0.36^{bcd}
PWG	0.32^{ab}	0.38^{a}	0.31^{de}	0.30^{d}
STWG	0.38^{a}	0.38^{a}	0.31^{bc}	0.32^{b}
SWG	0.34^{ab}	0.38^{a}	0.31^{de}	0.32^{d}
TF	0.38^{a}	0.46^{a}	0.41^{b}	0.42^{b}
TIM	0.33^{ab}	0.46^{a}	0.31^{cde}	0.34^{cd}
SEM	0.016	0.027	0.13	.016
Phosphorus	(%)			
BR	0.19^{cd}	0.17^{bc}	$0.14b^{c}$	0.09^{c}
CRF	0.21^{bc}	0.16^{bc}	$0.14b^{c}$	0.10^{c}
CRWG	0.15^{e}	0.14^{cd}	0.11^{c}	0.10^{c}
IWG	0.20^{bcd}	0.17^{bc}	0.15^{b}	0.10^{c}
MFT	0.24^{a}	0.19^{ab}	0.15^{b}	0.12^{b}
OCHG	0.22^{b}	0.17^{bc}	0.14^{bc}	0.11^{bc}
PWG	0.19^{bcd}	0.17^{bc}	0.14^{bc}	0.10^{c}
STWG	0.17^{de}	0.13^{d}	0.12^{bc}	0.08^{d}
SWG	0.19^{bcd}	0.17^{bc}	0.13^{bc}	0.10^{c}
TF	0.20^{bcd}	0.17^{bc}	0.14^{bc}	0.10^{c}
TIM	0.24^{a}	0.21	0.18^{a}	0.14^{a}
SEM	0.007	0.008	0.006	0.004

[1]BR = brome, CRF= creeping red fescue, CRWG = crested wheatgrass, IWG = intermediate wheatgrass, MFT = meadow foxtail, OCHG = orchardgrass, PWG = pubescent wheatgrass, STWG = streambank wheatgrass, SWG = slender wheatgrass, TF = tall fescue, TIM = timothy.
Column values with different superscripts are significantly different, $p < 0.05$.

Table 9. NIR estimated calcium levels of various prairie grasses at different stages of growth in 1993.

PASTURE[1]	Week of cut 3	7	10	14
	(%)			
BR	0.32^{cde}	0.31^{b}	0.32^{de}	0.30^{c}
CRF	0.39^{a}	0.43^{a}	0.43^{a}	0.39^{a}
CRWG	0.30^{e}	0.29^{b}	0.32^{e}	0.27^{c}
IWG	0.35^{bc}	0.33^{b}	0.33^{de}	0.28^{c}
MFT	0.30^{e}	0.36^{b}	0.37^{cd}	0.35^{b}
OCHG	0.34^{bcd}	0.31^{b}	0.32^{de}	0.34^{b}
PWG	0.34^{bcd}	0.33^{b}	0.36^{cde}	0.29^{c}
STWG	0.32^{cde}	0.34^{b}	0.40^{b}	0.34^{b}
SWG	0.32^{cde}	0.28^{b}	0.31^{e}	0.28^{c}
TF	0.34^{bc}	0.35^{b}	0.37^{c}	0.35^{b}
TIM	0.30^{e}	0.31^{b}	0.35^{cde}	0.27^{c}
SEM	0.006	0.015	0.011	0.01

[1]BR = brome, CRF = creeping red fescue, CRWG = crested wheatgrass, IWG = intermediate wheatgrass, MFT = meadow foxtail, OCHG = orchardgrass, PWG = pubescent wheatgrass, STWG = streambank wheatgrass, SWG = slender wheatgrass, TF = tall fescue, TIM = timothy.
Column values with different superscripts are significantly different, $p < 0.05$.

10), while 4 grasses (creeping red fescue, meadow foxtail, streambank wheatgrass and timothy) had maximum P levels at week 10. Phosphorus levels decreased in all grasses to between 0.12 and 0.31% at maximum yield (week 12). In 1993, P levels in brome, crested wheatgrass, intermediate wheatgrass, and pubescent wheatgrass were low enough to require supplementation to meet the requirements of beef cattle (Table 10).

Application of NIRS Technology to Predict Composition of Grasses

Values of standard error of calibration (SEC), the slope and r^2 obtained on calibration samples for each nutrient for the years 1992 and 1993 and 1992 & 1993 combined are shown in Table 10. Accuracy of prediction of chemical composition of grasses in this study compares favourably with other researchers. Our SEC value of 0.46% for CP compares closely with 1.0, 1.07, 0.95, 0.90 and 0.7 to 1.1% SE values obtained with scanning instruments by Norris et al. (1976), Shenk et al. (1979) and Marten et al. (1983) Redshaw et al. (1986), respectively. Similarly, SE of 0.61% for ADF prediction is lower than the value of 1% SE's obtained by Norris et al. (1976), Shenk et al. (1979 , 1981) and Marten et al. (1983) and is a third the 2.0% SE value obtained by Redshaw et al. (1986). The improvements in SE values in the current study is largely the result of improved software used. The SE for Ca at 0.05% compares favourably with a range of Ca determinations from 0.14 to 0.22% (Redshaw et al. 1986, Shenk et al.1979, 1981). Similarly, SE for P was 0.02% compared to between 0.02 and 0.04% in the other papers. In addition, the validation statistics of the regressions, such as the high r^2 values of 0.90 and slope of 0.88 or higher for CP, P, ADF and DM for 1992, 1993 and 1992 and 1993 combined indicate that the grass calibrations developed are excellent (Hsu et al. 1997, Shenk and Westerhaus 1991a, 1991b, 1991c; Shenk et al.1993). Except for Ca, the r^2 values obtained between actual and predicted for the grasses in 1992 and combined validation sets were 0.99 vs 1.00 (DM), 1.01 vs 0.99 (CP), 0.55 vs 0.59 (Ca), 0.88 vs 0.90 (P) and 0.97 vs 0.98 (ADF). The SEC's were 0.09(DM), 0.56(CP), 0.91(ADF), 0.06(Ca), and 0.03 (P) on data from the first year. Combining data from the 2 years improved the fit (Table 1). Overall mean values from NIRS prediction compared to wet chemistry analyses were 94.28, 94.28 for DM, 16.78, 16.80 for CP, 29.83, 29.84 for ADF, 0.35, 0.35 for Ca and 0.19, 0.19 for P, respectively. These data suggest a great potential for the application of NIRS calibrations in the analysis of nutrient composition of grasses, regardless of the stage of growth at harvest, because the procedure is capable of generating reliable results quickly.

Conclusions

Yield information on grasses as the plant matures is considered useful in optimizing grazing potential and quality hay production. Herbage mass yields (g/0.25m^2) of selected prairie grasses were similar for the grass species for both years, except for crested wheatgrass in 1992 and brome in 1993. Most grasses reached maximum yields at week 8 in 1992 (drought year) and week 12 in 1993 (a more normal year). Quality declined

Table 10. NIR estimated phosphorus levels of various prairie grasses at different stages of growth in 1993.

PASTURE [1]	Week of cut 3	7	10	14
	(%)			
BR	0.28^{ab}	0.17^{ef}	0.20^{efg}	0.13^{ef}
CRF	0.28^{ab}	0.30^{ab}	0.35^{ab}	0.24^{ab}
CRWG	0.23^{c}	0.13^{f}	0.15^{g}	0.13^{ef}
IWG	0.28^{ab}	0.16^{ef}	0.18^{fg}	0.10^{f}
MFT	0.31^{a}	0.31^{ab}	0.37^{a}	0.23^{ab}
OCHG	0.31^{a}	0.36^{a}	0.28^{cd}	0.26^{a}
PWG	0.28^{ab}	0.18^{def}	0.22^{def}	0.10^{f}
STWG	0.26^{b}	0.23^{bcde}	0.27^{cd}	0.23^{ab}
SWG	0.31^{a}	0.17^{ef}	0.24^{def}	0.17^{cd}
TF	0.31^{a}	0.21^{cdef}	0.25^{cde}	0.22^{b}
TIM	0.31^{a}	0.27^{bcd}	0.35^{ab}	0.20^{bc}
SEM	0.009	0.02	0.015	0.01

[1]BR = brome, CRF = creeping red fescue, CRWG = crested wheatgrass, IWG = intermediate wheatgrass, MFT = meadow foxtail, OCHG = orchardgrass, PWG = pubescent wheatgrass, STWG = streambank wheatgrass, SWG = slender wheatgrass, TF = tall fescue, TIM = timothy.
Column values with different superscripts are significantly different, $p < 0.05$.

in all grasses as they matured. There was an inverse relationship between CP and ADF until the yields approached maximum levels. The average CP content of grasses declined from 24% to 13% in 1992 and from 21.5% to 12.1% in 1993; however, these levels were adequate to meet protein requirements of grazing cattle. Based on both years' data, the 5 high yielding grasses identified were intermediate wheatgrass, brome, crested wheatgrass, pubescent wheatgrass, and slender wheatgrass. The Ca levels in all grasses were adequate for cattle on pasture but the low P levels near 0.10% (at week 8) in 1992 and 0.12% (at week 12) in 1993, indicate that cattle on such pastures would require P supplementation. With the exception of Ca, NIRS regression statistics obtained on all grasses yielded low values of standard error of calibration, r^2 values higher than 0.90 and slopes of actual vs predicted at 0.88 or higher for CP, P, ADF, and DM determinations.

These results strongly show that the calibrations developed for grasses in Alberta are acceptable. Thus, NIRS technology can be used to rapidly and accurately analyse for dry matter, crude protein, acid detergent fiber, calcium, and phosphorus in grasses at different stages of growth in Alberta. Addition of more data into the calibrations can only result in improved analysis and application of this technology in forage systems in Alberta.

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Predicting variable-temperature response of non-dormant seeds from constant-temperature germination data

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Abstract

The objective of many laboratory-germination experiments is to develop insight into the process of field establishment. It is relatively difficult, however, to infer potential field response from laboratory data given the enormous spatial and temporal variability in seedbed microclimate. Previous studies have attempted to survey large numbers of alternating day/night temperature regimes in order to estimate germination response to potential conditions of field microclimate. The objectives of this study were to estimate the errors associated with prediction of variable-temperature germination response from fewer, constant-temperature germination data. Non-dormant seeds of thickspike wheatgrass [*Elymus lanceolatus* (Scribn. and J.G. Smith) Gould], bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) Löve], Sandberg bluegrass (*Poa sandbergii* Vasey), and bottlebrush squirreltail [*Elymus elymoides* (Raf.) Swezey] were germinated under constant, alternating-constant and sine-wave temperature regimes. Predicted and measured cumulative-germination response generally coincided to within a day for most temperature treatments except for the most slowly germinating subpopulations of seeds. Thermal response models can be parameterized from relatively few experimental data but provide predictive inferences relevant to a wide number of variable-temperature conditions.

Key Words: seed, model, rate

Resumen

El objetivo de muchos estudios de germinación conducidos en laboratorio es desarrollar una visión del proceso de establecimiento en el campo. Sin embargo, debido a la gran variabilidad espacial y temporal del microclíma de la cama de siembra, es relativamente díficil predicir la respuesta potencial en campo a partir de información de laboratorio. Estudios previos han intentado investigar un gran número de rgimenes de temperaturas alternantes, día noche, para estimar la respuesta de germinación a las condiciones potenciales del microclíma en el campo. Los objetivos del presente estudio fueron estimar los errores asociados con la predicción de la respuesta de la germinación a temperaturas variables a partir de unos pocos datos de germinación a temperatura constante. Semillas no dormantes de Thickspike wheatgrass [*Elymus lanceolatus* (Scrinbn. and J.G. Smith)Gould], bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) Löve], sandberg bluegrass (*Poa sandbergii* Vasey.), y bottlebrush squirreltail [E*lymus elymoides* (Raf) Swezey] fueron germinadas bajo régimenes de temperatura constante, constante-alternante y seno-onda. La respuesta predicha y medida de germinación acumulativa generalmente coinciden dentro de un dia para la mayoría de tratamientos de temperatura, excepto para la mayoría de subpoblaciones de semillas de muy lenta germinación. Los par metros para desarrollar los modelos de respuesta a la temperatura pueden ser obtenidos a partir de relativamente poca información experimental y pueden proveer inferencias predictivas relevantes de un amplio nmero de condiciones variables de temperatura.

Most research concerning germination response of cool-season range grasses has been conducted under either constant or alternating-constant temperature conditions (Wester 1991). Alternating-constant temperature experiments can mimic diurnal temperature fluctuation in the seedbed but a comprehensive survey of potential germination response requires that a large number of treatment combinations be tested (Young and Evans 1982). An alternative approach is to develop predictive models for estimating variable-temperature germination response (Garcia-Huidobro et al. 1982b, Benech Arnold et al. 1990, Roundy and Biedenbender 1996). Such models can be developed from constant-temperature germination data if it is assumed that instantaneous germination rate is independent of diurnal temperature pattern (Garcia-Huidobro et al. 1982b, Benech Arnold et al. 1990). This assumption may not be correct for species that require fluctuating-temperature conditions to release dormancy (Thompson 1974, Thompson and Grime 1983, Murdoch et al. 1989, Benech Arnold et al. 1990). Application of thermal response mod-

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els to rangeland grass species has received relatively little attention in the literature (Jordan and Haferkamp 1989, Roundy and Biedenbender 1996). Roundy and Biedenbender (1996) used constant-temperature germination data to predict median germination response of 8 warm-season grasses under 3 variable-temperature regimes. Predicted and measured median germination times in their study averaged within 0.6, 1.3, and 3.6 days for thermal regimes representative of summer, spring, and winter, respectively.

The purpose of this study was to evaluate variable-temperature effects on the cumulative-germination response of 4 cool-season range grasses. We hypothesized that cumulative-germination response under alternating-constant and sine-wave temperature patterns could be predicted from constant-temperature germination data. Calibration of thermal models would make it possible to predict cumulative-germination response under a wide number of potential field-temperature regimes without having to survey large numbers of alternative thermal treatments. The species in question, thickspike wheatgrass [*Elymus lanceolatus* (Scribn. and J.G. Smith) Gould], bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) Löve], Sandberg bluegrass (*Poa sandbergii* Vasey) and bottlebrush squirreltail [*Elymus elymoides* (Raf.) Swezey], were selected because they have been identified by the United States Department of the Interior, Bureau of Land Management as high-priority species for restoration of deteriorated rangelands in the Great Basin and Columbia Plateau.

Materials and Methods

Seeds for this experiment were purchased from Stevenson seed company (Ephraim, Ut.) which collected the seeds in 1991. Air-dry seeds were stored in cloth bags at room temperature during the course of the study.

Two experiments were conducted to evaluate variable-temperature effects on germination response. Experiment 1 was conducted between Oct. 1992 and Feb. 1993 to measure germination response under constant, alternating-constant and sine-wave temperature patterns. Experiment 2 was conducted between July 1993 and Nov. 1993 to measure germination response at constant temperature and under sine-wave temperature patterns of different amplitude.

Germination experiments were conducted inside 15 programmable environmental chambers (Hardegree and Burgess 1995). These chambers consisted of small refrigerators that were enhanced with incandescent and fluorescent lights, fans, and electrical resistance heaters. An electronic data acquisition/control system maintained temperature control to within ± 0.5°C. Chamber lights were programmed to have a 12 hour photoperiod. The temperature inside each box was monitored every 10 seconds for purposes of temperature control and an average temperature calculated and recorded for every 15 minute period.

In Experiment 1, separate environmental chambers were programmed to maintain constant temperatures in 5° increments between 5 and 35°C; alternating-constant night/day temperature regimes of 5/15, 10/20, 15/25, 20/30, and 25/35°C; and sine-wave patterns with an amplitude of 10°C and mean daily temperatures of 10, 15, 20, 25, and 30°C. In Experiment 2, environmental chambers were programmed to simulate constant temperatures in 5° increments between 5 and 35°C; and sine-wave patterns with a mean temperature of either 15, 20, or 25°C and temperature amplitudes of either 5, 10, 15, or 20°C. Each thermal regime was replicated 3 times in different germinators. As there were 17 separate thermal regimes in Experiment 1 and 19 in Experiment 2, all replicate treatments could not be evaluated simultaneously. Treatment order was randomized and treatments were evaluated in groups of 15 until all had been replicated 3 times.

Seeds were germinated on a cellulose dialysis membrane at the bottom of germination cups that were in contact with a water reservoir inside a clear-plastic snap-top vial (Hardegree and Emmerich 1992). Free water on top of the membrane was kept to a minimum by controlling the height of water in the reservoir and by daily suction when necessary.

One vial of each species was arranged randomly within each of 6 replicated blocks inside each germination chamber. Thirty seeds of each species (35 seeds for Sandberg bluegrass) were placed in each germination cup and dusted with Daconil fungicide (2,4,5,6-tetrachloro-1,3-benzenedicarbonitrile, wettable powder) at the beginning of a given experimental run. Additional fungicide was applied if the seeds developed fungal growth during the experiment. Germination vials were monitored daily for 21 days and seeds counted and removed when they exhibited radicle extension ≥ 2 mm.

Characterization of Subpopulation Germination Rates at Constant Temperature

The constant-temperature germination data were used to develop regression equations for estimating germination response under the alternating-constant and sine-wave temperature regimes. Cumulative-germination percentages were calculated for every combination of species and treatment for every day. The cumulative data were numerically transformed by dividing germination percentages by a scaling factor (Ellis et al. 1986). The scaling factor was equal to the maximum-mean-germination percentage achieved in the most favorable temperature treatment for that species. This transformation adjusted germination percentages for each species to a common scale with a maximum value of 100%. The scaling factors were 0.95 for thickspike wheatgrass, 0.91 for bluebunch wheatgrass, 0.82 for Sandberg bluegrass and 0.86 for bottlebrush squirreltail. Germination counts were pooled by species within each germinator box and the 3 within-box averages considered treatment replicates for model development and analysis.

For modeling purposes, the seed population was considered to be composed of subpopulations based on relative germination rate (Garcia-Huidobro et al. 1982a). Days required to achieve 5, 10, 15, 20, 25, 30, 35, 40, 45, 50, 55, 60, 65, 70, 75, 80, 85, 90 and 95% germination were calculated for each species and treatment by interpolating between points on the cumulative-germination curves (Covell et al. 1986). It was assumed that the seeds in a given population germinate in the same relative order, regardless of thermal environment (Garcia-Huidobro et al. 1982a). Inverse days required to achieve a given germination percentile, therefore, was considered to equal the per-day germination rate of the subpopulation represented by the percentile ranking (Garcia-Huidobro et al. 1982a).

Germination rates for each species and subpopulation were plotted as a function of temperature (Fig. 1). The relationship between germination rate and temperature appeared to be relatively linear for most species and subpopulations in the suboptimal temperature range of 5 to 20°C. The exception was for Sandberg bluegrass which exhibited nonlinearity in the slower germinating subpopulations above 15°C. Linear equations were calculated from the suboptimal temperature data relating germination rate (day^{-1}) to temperature for all species and subpopulations. Suboptimal linear regressions were extrapolated to the x-axis to obtain a value for the base temperature at which subpopulation germination rate was estimated to be zero (Arnold 1959).

Germination rate could not be calculated for subpopulations that exhibited zero germination during the 21-day test period. Lack of data for many subpopulations made it difficult to develop a uniform approach to characterizing supraoptimal temperature response. Supraoptimal temperature response, however, was clearly nonlinear (Fig. 1). Thermal response above 20°C (15°C for Sandberg bluegrass) was characterized by a series of linear equations used to interpolate between constant-temperature germination rates in 5°C increments.

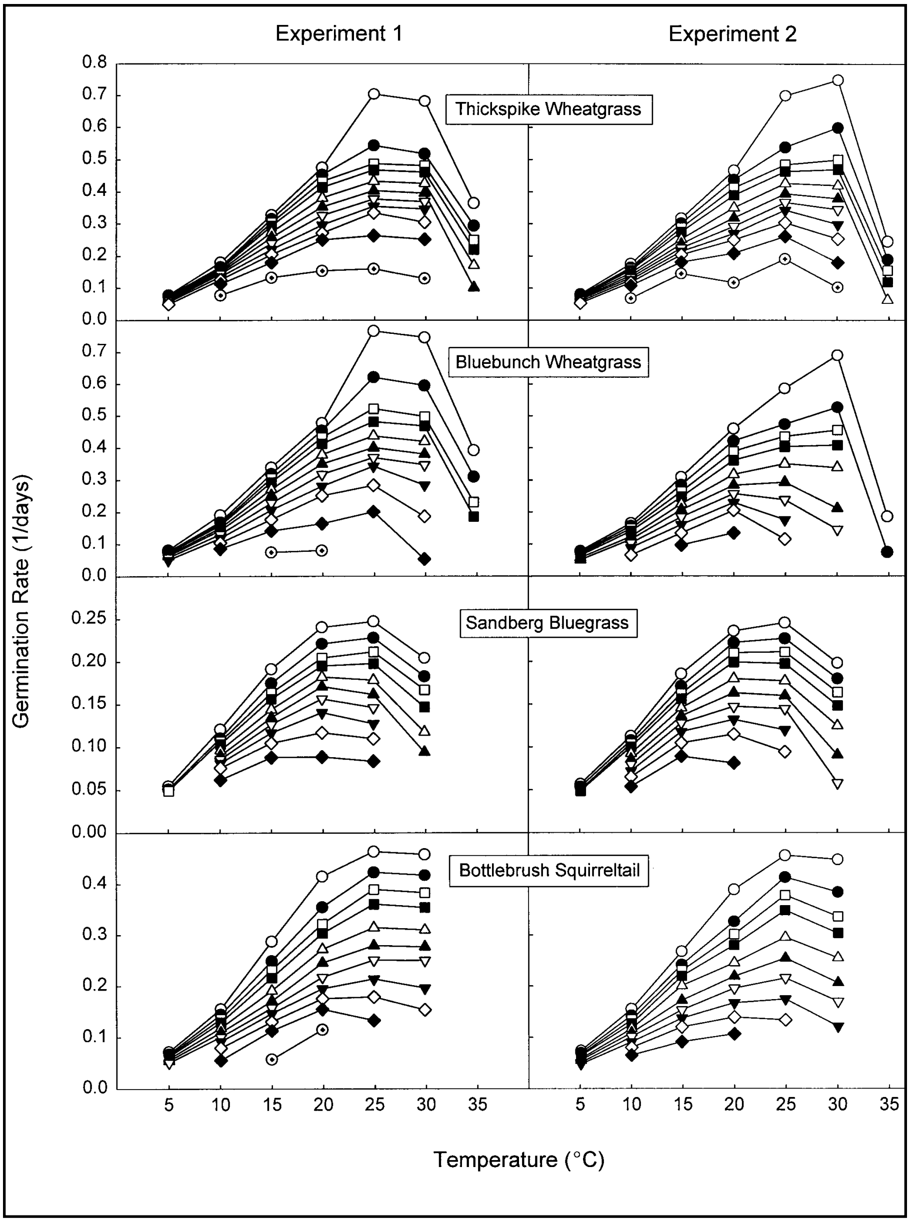

Fig. 1. Germination rate as a function of species, experiment, temperature and subpopulation for the constant-temperature treatments. For clarity only the 5 (○), 10 (●), 15 (□), 20 (■), 30 (△), 40 (▲), 50 (▽), 60 (▼), 70 (◊), 80 (♦) and 90% (⊕) subpopulations are represented.

Estimation of Variable-Temperature Response

A hypothetical example illustrates the procedure used to estimate cumulative-germination response in the variable-temperature treatment regimes. If subpopulation "a" requires 10 days to germinate at 10°C then its per-day germination rate will be 0.1 day^{-1} and it will progress 10% of the way toward germination for every day that it spends at 10°C. If the per-day germination rate at 10°C is 0.1 day^{-1} then the germination rate for a 15-minute period is equal to the per-day rate divided by 96 (the number of 15-minute intervals in a day). Subpopulation "a" would, therefore, progress 1.042% toward germination during a 15-minute interval at 10°C. If one assumes that the instantaneous germination rate of a given subpopulation is independent of thermal history, then progress toward germination can be predicted by the running sum of germination rate estimates for each 15-minute interval. Germination of the subpopulation should occur when the

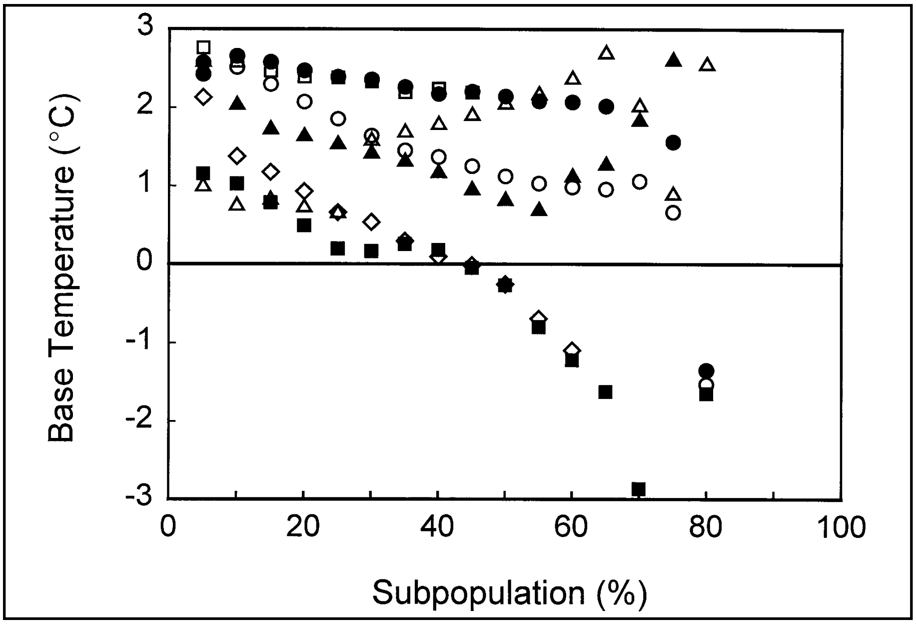

Fig. 2. Base temperature of thickspike wheatgrass [Expt. 1 (❍), Expt. 2 (●)], bluebunch wheatgrass [Expt. 1 (❐), Expt. 2 (■)], Sandberg bluegrass [Expt. 1 (∆), Expt. 2 (▲)] and bottlebrush squirreltail [Expt. 1 (◊), Expt. 2 (♦)] as a function of subpopulation. Base temperatures were estimated by extrapolation of suboptimal germination rates (Fig. 1) to the temperature at which germination rate was estimated to be zero.

running sum of these values reaches 1.

All environmental chambers were programmed to repeat the same temperature pattern every day. Average temperature over a given 21-day thermal treatment was calculated for each 15-minute interval of the diurnal temperature cycle. The germination rate for each 15-minute temperature interval was calculated for each species and subpopulation from the appropriate regression equations that were derived from the constant-temperature data. These 15-minute rate estimates were aggregated to produce a total daily (per-day, day^{-1}) germination rate for each combination of species, subpopulation, and variable-temperature thermal regime. The predicted time of germination (days) was determined to be the inverse of the aggregated per-day germination rate (Roundy and Biedenbender 1996). Some of the variable-temperature treatments overlapped temperature ranges for which constant-temperature germination was equal to zero. Germination times were not predicted for subpopulation-treatment combinations that were outside of the modeled-temperature range.

Results

Per-day germination rate across all subpopulations followed a general pattern. Germination rates were low at 5°C, increased with increasing temperature to a maximum in the 20–30°C range, and showed a relatively rapid decline at supraoptimal temperatures (Fig. 1). Peak germination rates tended to occur at relatively higher temperatures for the more rapidly germinating subpopulations. All subpopulations exhibited approximately linear, suboptimal temperature response over the temperature range of 5 to 20°C except for Sandberg bluegrass. Linear regression equations were derived for the data in this temperature range (5 to 15°C for Sandberg bluegrass) and base temperatures calculated by extrapolation to the temperature at which germination rate was estimated to be zero. Base temperature estimates tended to decrease with subpopulation but became highly variable for the most slowly germinating seeds (Fig. 2).

Suboptimal linearization of temperature response resulted in a general lack of model fit for the 5° constant-temperature treatments (Fig. 3). We believe that this lack of fit was caused by non-linearity of germination rate response at low temperature. The suboptimal-temperature models were recalculated using the same piece-wise linear interpolation procedure that was used for the supraoptimal temperature range. This approach greatly improved model fit for temperature regimes that included time spent in the 5 to 10°C

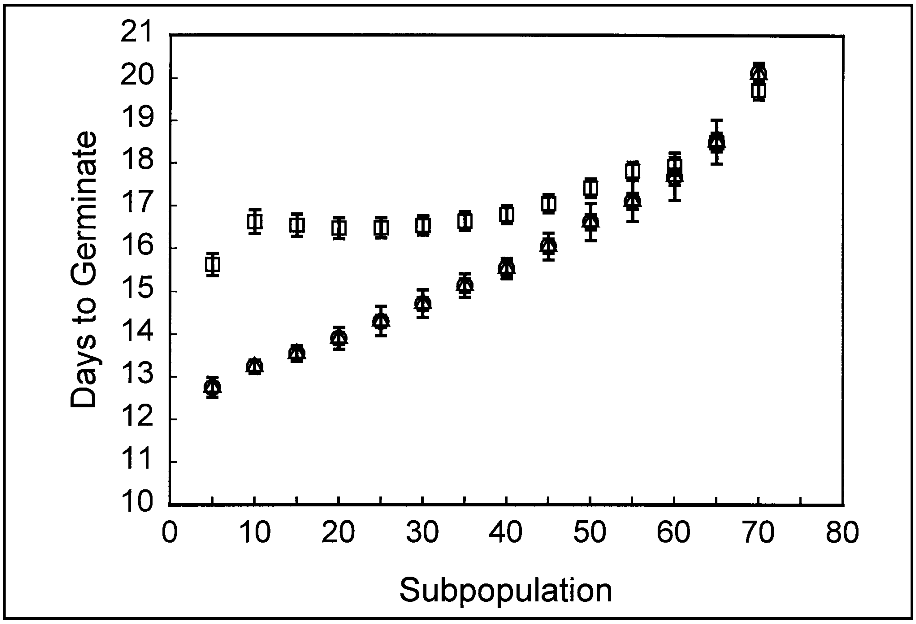

Fig. 3. Measured days to germinate (∆), predicted days to germinate in the constant –5 ˚C treatment for thickspike wheatgrass from the suboptimal-linear model (❐), and predicted days to germinate form the piecewise-linear model (❍). Error bars represent ±1 standard error.

Table 1. Mean residual (predicted - measured) values of germination time (days) for Experiment 1 as a function of species, temperature pattern and average temperature. Residual values were averaged separately for subpopulations ≤ 50% and subpopulations > 50%. Positive values indicate that measured germination was faster than predicted. Values in parentheses represent 1 standard error of the mean.

Species	Temp Pattern	Average Temperature (˚C) 10	15	20	25	30	10	15	20	25	30
		(5-50% Subpopulations) (days)					(50% + Subpopulations) (days)				
Thickspike	alt	–0.4(0.05)	0.1(0.02)	0.2(0.04)	0.1(0.04)	0.5(0.14)	0.5(0.20)	0.3(0.22)	0.3(0.10)	0.6(0.23)	–
	sin	–0.3(0.03)	-0.3(0.04)	0.1(0.03)	0.0(0.02)	0.3(0.10)	0.4(0.24)	-0.2(0.08)	0.5(0.17)	0.4(0.21)	–
Bluebunch	alt	–0.3(0.05)	0.1(0.06)	0.2(0.06)	0.1(0.01)	0.3(0.20)	0.8(0.22)	0.5(0.36)	0.0(0.09)	0.6(0.43)	–
	sin	–0.3(0.06)	–0.3(0.05)	0.0(0.03)	–0.1(0.02)	0.3(0.10)	0.4(0.16)	–0.4(0.05)	0.2(0.17)	–0.2(0.29)	–
Sandberg	alt	–0.1(0.05)	0.4(0.02)	0.4(0.08)	0.3(0.03)	–	–1.7(0.71)	1.5(0.46)	1.2(0.22)	–	–
	sin	0.1(0.09)	0.0(0.03)	0.4(0.04)	0.5(0.04)	–	0.9(0.19)	0.6(0.23)	1.5(0.28)	–	–
Squirreltail	alt	–0.1(0.06)	–0.4(0.04)	0.0(0.02)	0.0(0.02)	–	1.5(0.72)	0.6(0.53)	0.7(0.27)	0.1(0.03)	–
	sin	–0.2(0.04)	–0.1(0.01)	0.1(0.01)	0.1(0.03)	–	0.9(0.46)	–0.2(0.09)	0.2(0.08)	0.7(0.10)	–

range (Fig. 3). All further analyses were conducted on data residuals calculated from the piece-wise linear approach.

The residual values for predicted minus measured cumulative-germination response across all species, variable-temperature treatments and subpopulations are shown in Figure 4. The majority of predicted germination times corresponded to within a day of measured values. Model fit decreased in some of the slower-germinating subpopulations (Fig. 4, Tables 1, 2). Tables 1 and 2 present mean residual values for germination time (days) averaged across subpopulations in the 5–50% and >50% subpopulation ranges. Mean model fit for most species and treatments was less than 0.5 days for subpopulations in the 5–50% range but was as much as several days for some species and treatments in the later-germinating subpopulations. Figure 5 shows a graphical comparison of predicted and actual cumulative-germination response of some of the alternating-constant temperature treatments in Experiment 1.

Total germination percentage after 21 days as a function of temperature followed a similar pattern for all species and treatments (Fig. 6). A relatively high percentage of seeds germinated across the intermediate temperature range with reduced germination in the extreme high and low-temperature treatments. Some of the variable-temperature treatments of bluebunch wheatgrass and Sandberg bluegrass exhibited reduced germination for some of the higher average-temperature treatments (Fig. 6).

Discussion

Models for calculating thermal response of seed germination have been developed for many agricultural species but there has been little model validation under variable-temperature conditions (Garcia-Huidobro et al. 1982b). Thermal response models have been used to compare germination response of several rangeland species but not for the specific purpose of predicting the time course of cumulative germination under variable temperature regimes (Jordan and

Table 2. Mean residual (predicted - measured) values of germination time (days) for Experiment 2 as a function of species, average temperature and temperature amplitude. Residual values were averaged separately for subpopulations ≤ 50% and subpopulations > 50%. Positive values indicate that measured germination was faster than predicted. Values in parenthese represent 1 standard error of the mean. An asterick indicates a single subpopulation reporting.

Species	Avg. Temp. (˚C)	Temperature Amplitude (˚C) 5	10	15	20	5	10	15	20
		(5-50% Subpopulations) (days)				(50% + Subpopulations) (days)			
Thickspike	15	–0.2(0.02)	0.0(0.01)	0.0(0.01)	0.0(0.04)	0.0(0.07)	0.3(0.12)	–0.3(0.15)	–0.8(0.26)
	20	0.2(0.02)	0.1(0.02)	0.1(0.01)	0.2(0.03)	0.4(0.10)	0.1(0.04)	0.2(0.09)	1.5(0.76)
	25	0.1(0.01)	0.2(0.02)	0.0(0.07)	0.3(0.08)	0.1(0.26)	–0.5(0.78)	–	–
Bluebunch	15	–0.3(0.02)	–0.1(0.03)	0.0(0.01)	–0.1(0.06)	–0.5(0.29)	–2.0(0.97)	–0.4(0.08)	–0.1(0.07)
	20	–0.1(0.02)	0.0(0.02)	–0.5(0.09)	–0.7(0.18)	–0.7(0.29)	–0.5(0.28)	–1.5(*)	–2.5(*)
	25	0.3(0.08)	0.3(0.05)	–0.1(0.08)	0.2(0.12)	1.1(*)	0.2(*)	–	–
Sandberg	15	–0.1(0.03)	0.2(0.03)	–0.6(0.10)	–0.3(0.09)	–0.3(0.21)	0.7(0.16)	–3.1(0.92)	–1.8(0.39)
	20	0.3(0.05)	0.4(0.06)	–0.4(0.06)	–0.4(0.09)	1.0(0.20	1.2(0.35)	–	–
	25	0.5(0.08)	0.5(0.11)	–	–	–	–	–	–
Squirreltail	15	0.1(0.07)	–0.1(0.03)	–0.3(0.04)	–0.2(0.07)	0.0(0.26)	0.6(0.17)	–0.3(0.03)	–1.0(0.33)
	20	0.1(0.02)	0.2(0.03)	–0.2(0.05)	–0.1(0.05)	–0.3(0.29)	0.5(0.08)	–0.7(0.10)	–0.5(0.10)
	25	0.3(0.03)	0.2(0.04)	–	–	1.0(0.18)	0.8(0.17)	–	–

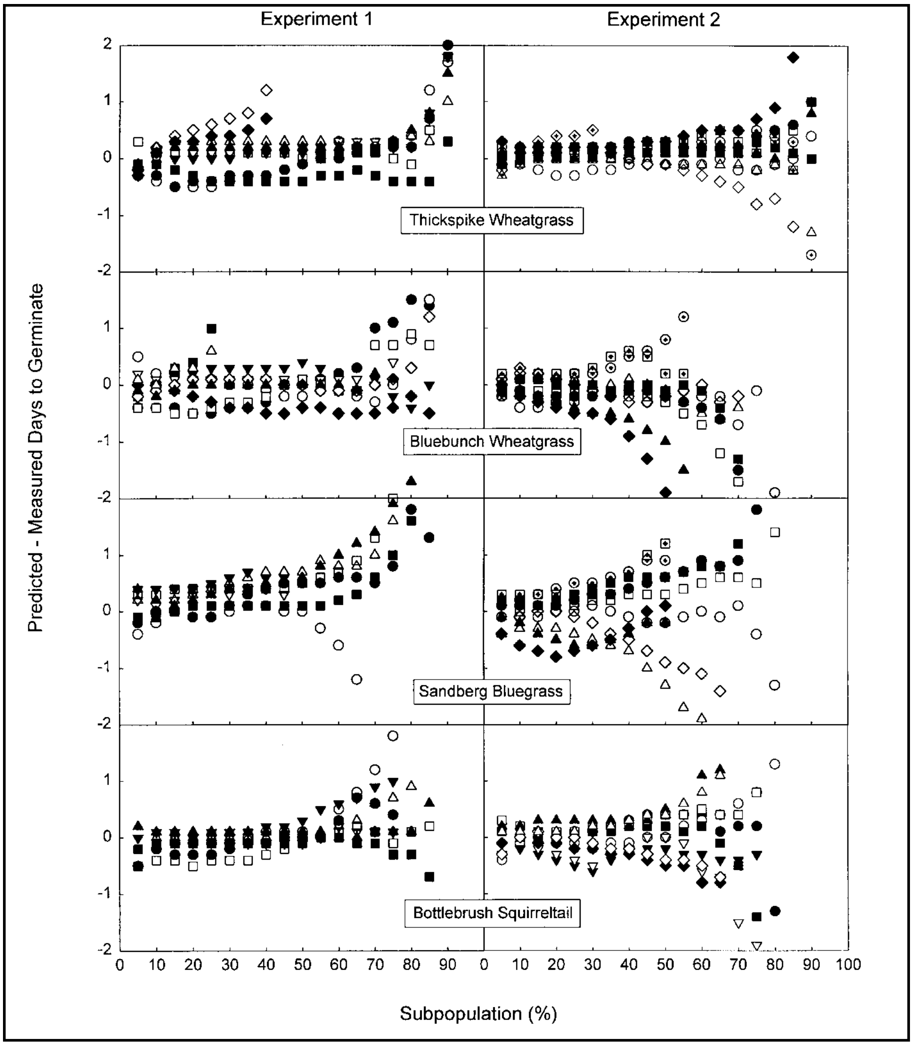

Fig. 4. Residual values of predicted minus measured days required to germinate as a function of subpopulation. Symbols for Experiment 1 represent alternating-temperature regimes with an average temperature of 10 (❍), 15(❒), 20 (△), 25 (▽), and 30˚C (◊); and sine-wave temperatures with an average temperature of 10(●), 15(■), 20 (▲), 25(▼) and 30˚ C (◆). Symbols for Experiment 2 represent sine-wave regimes with an average temperature of 15˚C and a temperature amplitude of 5 (❍), 10 (❒), 15 (△), 20 (◊); and an average temperature of 20˚C and a temperature amplitude of 5(●), 10 (■), 15 (▲) and 20 (♦) ˚C; and an average temperature of 25˚C and a temperature amplitude of 5 (⊕), 10 ( ), 15 ( ) and 20 ( ) ˚C.

Haferkamp 1989, Romo and Eddleman 1995, Roundy and Biedenbender 1996). Wester's (1991) survey of the range literature on seed germination documents a previous emphasis on the calculation of germination indices for treatment comparisons rather than predictive inference. Young and Evans (1982) summarized an extensive body of their previous work measuring germination response of range grass species to alternating-temperature regimes but their data emphasizes total germination percentage rather than germination rate. Thermal response models of the type described in the current study could be used to expand our level of inference to predict differences in cumulative germination under an unlimited number of potential field temperature scenarios (Garcia-Huidobro et al. 1982a).

The germination-rate response to temperature found in our study conforms to the general pattern found in previous experiments (Garcia-Huidobro 1982a, Covell et al. 1986, Benech Arnold et al. 1990). Subpopulation-germination rates tended to increase in a relatively linear fashion up to an optimal temperature, above which they declined rapidly (Fig. 1). Our data are also similar to those shown in previous studies in that optimal temperatures for maximum germination rate tended to decrease for later-germinating subpopulations (Covell et al. 1986, Garcia-Huidobro et al. 1982a).

Previous authors have accepted several assumptions about thermal-response data in order to simplify analysis and to facilitate comparisons among seedlots. Common assumptions include the following: subpopulations within a given seedlot share the same base temperature; germination rate response is linear over the suboptimal temperature range; germination rate response is linear over the supraoptimal temperature range; instantaneous germination rate is independent of temperature pattern; instantaneous germination rate is independent of thermal history; and subpopulations maintain their relative germination rate regardless of the thermal environment to which they are subjected (Garcia-Huidobro et al. 1982a, Covell et al. 1986, Benech Arnold et al. 1990, and Probert 1992).

We found significant differences in base temperature estimates as a function of subpopulation (Fig. 2). Previous studies have measured the same phenomenon (Garcia-Huidobro et al. 1982a) but most conclude that the assumption of a common base temperature is still useful (Covell et al. 1986, Carberry and Campbell 1989, Benech Arnold et al. 1990). A common base temperature makes it possible to develop a single equation for predicting the thermal-time requirements of all subpopulations in the suboptimal temperature range (Washitani 1985, Covell et al. 1986, Ellis et al. 1987, Benech Arnold et al. 1990). Equation coefficients can then be used as an objective tool for comparing seedlots (Covell et al. 1986, Ellis et al. 1986). If the base temperature assumption is false, however, thermal accumulation for a given temperature regime must be calculated separately for each subpopulation. Temperatures near the base temperature have a relatively large influence on germination times as the temperatures above the base are inversely

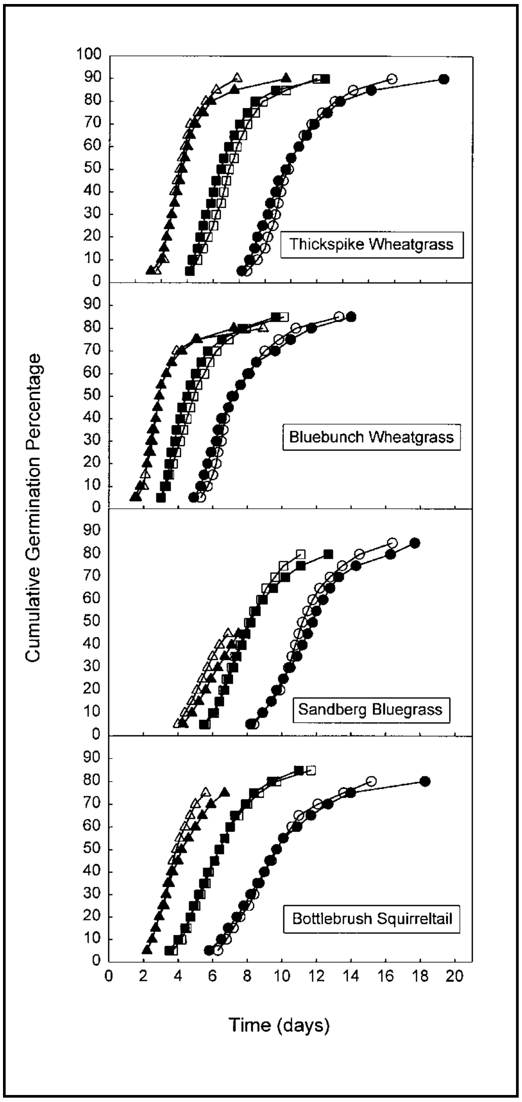

Fig. 5. Predicted (closed symbols) and measured (open symbols) cumulative-germination response under alternating-constant temperature regimes with an average temperature of 10˚C (circles), 15˚C (squares), and 20˚C (triangles) from Experiment 1.

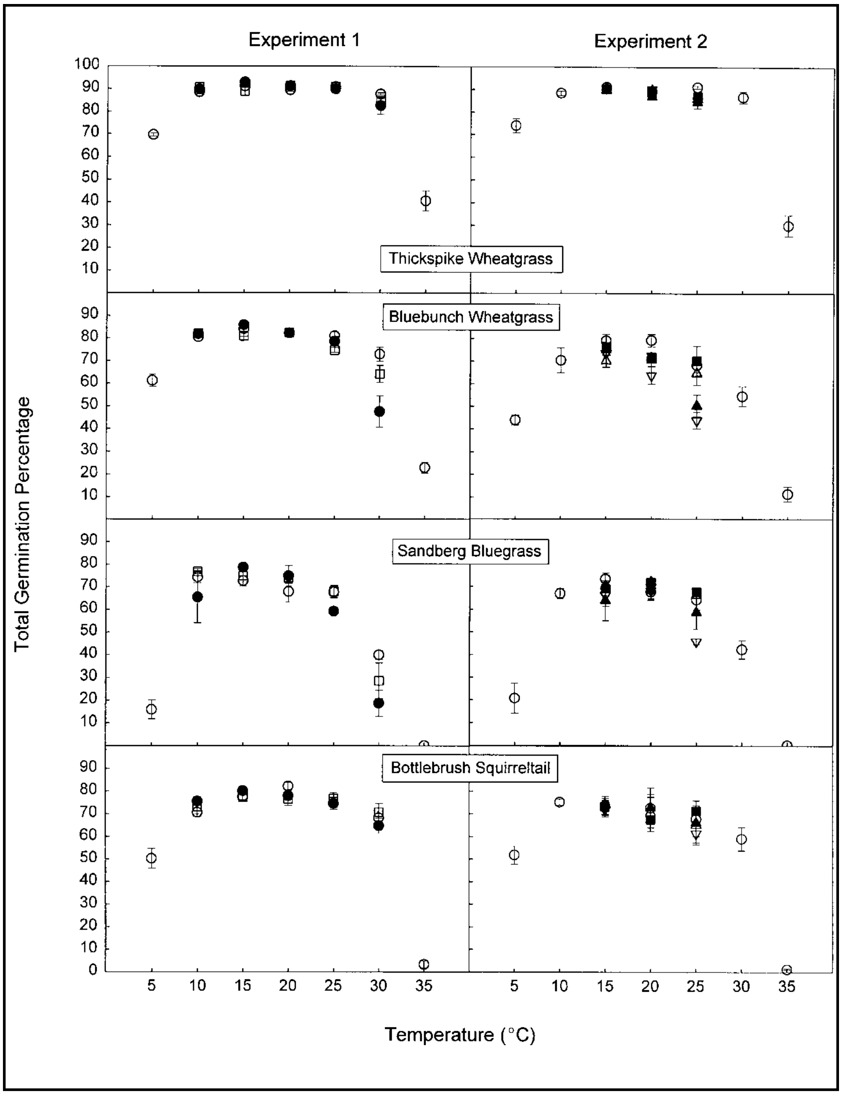

Fig. 6. Total germination percentage as a function of species, experiment, mean average temperature, and temperature pattern for Experiment 1 [constant temperature (❍), alternating temperature (●), sin-wave pattern (❐)], and Experiment 2 [constant temperature (❍), and sine-wave patterns with temperature amplitudes of 5˚ (■), 10˚ (∆), 15˚ (▲) and 20˚C (∇)]. Error bars represent ±1 standard error.

related to germination rate (Bierhuizen and Wagenvroot 1974). We chose not to accept the common-base-temperature assumption because model fit was more important than computational efficiency.

Many previous models assume linearity of germination rate at both sub- and supraoptimal temperatures. Acceptance of this assumption simplifies the experimental design for obtaining model data (Covell et al. 1986, Ellis et al. 1986, 1987). We did not have enough data points in the supraoptimal temperature range to test linear thermal-time models but found that a linear model for the suboptimal range tended to underestimate germination rate in some low-temperature treatments (Fig. 3). Similar results in previous studies have been attributed to errors in temperature control, and to the relative sensitivity of germination rate to temperatures near the base temperature (Covell et al. 1986, Carberry and Campbell 1989). We believe that our model-prediction errors were caused by nonlinearity in germination response at low temperature rather than random or systematic errors in the experimental design. These errors disappeared when we replaced the suboptimal linear equations over the 5–20°C range with separate equations for each 5° temperature increment (Fig. 3).

A common assumption of thermal-germination models is that the instantaneous germination rate is independent of temperature pattern (Garcia-Huidobro et al. 1982a, Probert 1992). This assumption has been shown to be invalid for species that remain dormant in a constant temperature environment (Thompson 1974, Thompson and Grime 1983, Murdoch et al. 1989). Models derived from constant-temperature data tend to underestimate variable-temperature germination response for these species (Garcia-Huidobro et al. 1982b, Benech Arnold et al. 1990). Our data do not show any stimulation of total germination percentage in alternating-constant and sine-wave temperature regimes (Fig. 6). The general conformity between predicted and measured germination times in our study also suggests that fluctuating temperatures did not increase germination rate except perhaps for some of the slowest subpopulations (Figs. 4, 5).

Another common assumption of germination-response models is that germination rate is independent of thermal history (Benech Arnold et al. 1990, Garcia-Huidobro et al. 1982a). This assumption is counter-intuitive and may only apply to the suboptimal temperature range. Germination shares a common temperature response with many other types of physiological processes. Suboptimal temperature response is generally attributed to the increased thermal activity of the molecules involved in metabolic reactions (Monteith 1977, Garcia-Huidobro et al. 1982a, 1982b, Probert 1992). Supraoptimal temperature response, however, is generally attributed to molecular dysfunction caused by membrane degradation, denaturation of enzymes and other, relatively irreversible, degenerative processes (Bewley and Black 1994). One would, therefore, not expect seeds to regain germinability after significant time spent at supraoptimal temperature (Garcia-Huidobro et al. 1982b, Ojeda and Trione 1990). This hypothesis is supported by our observation that ungerminated seeds in the low-temperature treatments would quickly germinate at the end of the experiment when germination vials were returned to room temperature. Ungerminated seeds in the high temperature treatments, however, did not germinate when temperatures were subsequently lowered. If the thermal-history assumption is false, one would expect total germination percentage to be lower than predicted for treatments that overlap both the suboptimal and supraoptimal temperature ranges. Our data show this phenomenon for bluebunch wheatgrass and Sandberg bluegrass for some of the higher-temperature treatments (Fig. 6). When this occurred, the effect was greater at alternating-constant temperatures than in sine-wave regimes that had equivalent mean daily temperature. This would be expected as the seeds in alternating-constant temperature regimes spend relatively more time at the maximum treatment temperature. The decline in germination rates at supraoptimal temperature was very rapid in our study and may not have been adequately characterized by a 5° temperature increment. Future studies using a smaller constant-temperature interval and inclusion of some treatments with a greater diurnal amplitude could be used to more rigorously test this assumption.

An additional assumption of thermal-response models is that the relative ranking of germination rate among subpopulations remains the same regardless of the thermal regime (Garcia-Huidobro et al. 1982a, Benech Arnold et al. 1990). There is no reason to expect that subpopulations adapted to germinate rapidly at low temperatures are the same subpopulations that are adapted to germinate rapidly at high temperatures. Violation of this assumption would also cause an underestimation of cumulative-germination rate in regimes that overlapped both high and low temperature ranges. This response was not apparent from our data but our experimental design did not allow for rigorous testing of the assumption.

Conclusions

Rangeland systems exhibit high spatial and temporal variability of seedbed microclimate (Pierson and Wight 1991). Field-planting trials integrate complex combinations of environmental variables, but statistical inference is limited by the unique set of conditions present during a given test (Hurlbert 1984). Laboratory experiments are easier to control and replicate but inferences are limited by the artificiality of the treatment environment. Previous studies have attempted to bridge the gap between the laboratory and field approaches by testing seeds under a large number of alternating-temperature scenarios (Young and Evans 1982). Our study showed that for the seedlots tested in this experiment, cumulative germination under a large number of variable-temperature regimes could be predicted from data generated by relatively few, constant-temperature experimental treatments. Future studies might, therefore, adopt a simplified experimental design for seedlots that do not have a dormancy response to fluctuating temperature regimes. Data from some previous constant-temperature experiments could perhaps be reevaluated and the data used to predict population-germination response to potential field-variable temperature regimes.

The variable-temperature treatments tested in this experiment differ from true field regimes in that diurnal temperature patterns were constant. Actual field regimes would vary in diurnal temperature range, temperature pattern, and longer-term trends in mean-daily temperature (Hardegree and Burgess 1995). Our experiment also ignored the effects of other abiotic and biotic seedbed variables (Hegarty 1973). Soil water availability is often the limiting factor for seedling establishment in the Intermountain West (Roundy and Call 1988). Hydrothermal modeling approaches have been developed for predicting the interactive effects of temperature and water stress on seed germination (Gummerson 1986, Bradford 1990) and these models have recently been applied to the prediction of dormancy release in the winter-annual weed *Bromus tectorum* L. (Christensen et al. 1996). Thermal and hydrothermal-response models, however, require additional validation under field-variable temperature and moisture conditions.

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Central Nevada riparian areas: Physical and chemical properties of meadow soils

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Abstract

Despite the importance of soil characteristics for classifying riparian ecosystem types and evaluating ecosystem or range condition, little information exists on western riparian area soils or the factors that influence them. We examined the effects of drainage basin geology and water table depth on soil morphology and soil physical and chemical properties of meadow sites in central Nevada. We described and analyzed the soils of meadows that occurred in 4 drainages with different geology and that exhibited high water tables (0 to –20 cm from the surface), intermediate water tables (–30 to –50 cm), and low water tables (–60 to –80 cm). Pedons of high water tables sites had thick O_e horizons, dark, fine-textured A horizons, no B horizons, and lower C horizons high in coarse fragments. In contrast, pedons of low water tables sites were characterized by deep, dark and organic-rich A horizons, cambic B horizons, and deep rooting profiles. High water tables sites had higher organic matter, total nitrogen, cation exchange capacity, and extractable potassium, but lower pH than low water table sites. Also, high water table sites had lower percentage sand, lower bulk densities, and higher soil moisture retention. The importance of organic matter was evidenced by strong positive product moment correlations for organic matter and total nitrogen, cation exchange capacity, and extractable potassium. Significant differences in pH, extractable potassium and extractable phosphorus existed among drainages that were explainable largely from the parent materials. Drainages with chert, quartzite, and limestone had higher silt and clay, neutral pH, and high levels of extractable phosphorus. Drainages formed in acidic volcanic tuffs, rhyolites and breccia were characterized by coarser textured soils and low pH and extractable phosphorus. In riparian areas, soil water table depth interacts with soil parent material to significantly affect soil morphology and soil physical and chemical properties. Because these factors vary over both large and small spatial scales, differences among sites must be carefully interpreted when classifying ecosystems or evaluating ecosystem condition.

Key Words: water tables, watershed geology, soil morphology, soil quality, ecosystem classification, ecosystem condition

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Resumen

A pesar de la importancia de las catacteríticas de los suelos para clasificar los tipos de ecosistemas ribereños y evaluar la condición de ecosistemas y pastizales existe poca información sobre los suelos del rea ribereña el oeste y los factores que los afectan. Examinamos el efecto de la geología del drenaje de la cuenca y la profundidad del manto freático en la morfología y propiedades fisico-químicas de los suelos de vega en la región central de Nevada. Describimos y analizamos los suelos de vega que ocurren en 4 dernajes con diferente geología y que tienen mantos freáticos alto (0 a –20 cm de la superficie), intermedio (–30 a –50 cm) y bajo (–60 a -80 cm). Los pedones de sitios con manto freático alto tuvieron horizontes O_c anchos, horizontes A obscuros y de textura fina, sin horizontes B y los horizontes C bajos con alto contenido de fragmentos gruesos. En contraste, los pedones de los sitios con manto freático bajo se caracterizaron por tener horizontes A profundos, obscuros y ricos en material orgánico, horizontes B cambicos y perfiles de enraizamiento profundos. Los sitios de manto freático alto tuvieron altos contenidos de materia orgánica, nitrógeno total, potasio extractable, alta capacidad de intercambio cationico y pH menor que los sitios con mantos freáticos bajos. Los sitio con manto freático también tuvieron un menor porcentaje de arena, menor densidad aparente y mayor retención de humedad del suelo. La importancia de la materia orgánica se evidenció or fuertes correlaciones positivas momento producto entre materia orgánicay nitrógeno total, capacidad de intercambio cationico y potasio extractable. Existieron diferencias significativa entre drenajes respecto a pH, potasio y fósforo extractables las cuales se explican en gran parte por el material parental. Drenajes con "Chert", cuarcita y piedra caliza tuvieron mas limo y arcilla, pH neutro y valores altos de fósforo extractable. Drenajes formados en tufas, riolitas y brechas volcánico ácidos se caracterizaron por suelos de textura gruesa, bajo pH y bajo contenido de fósforo extractable. En áreas ribereñas la profundidad del manto freático interactua con el material parental del suelo para afectar significativamente la morfología del suelo y sus propiedades físico- químicas. Debido a que estos factores varian en escales espaciales grandes y pequeñas, las diferencias entre sitos deben ser interpretadas cuidadosamente para clasificar los ecosistemas o evaluar la condición del ecosistema

Information on soil characteristics is essential for understanding riparian ecosystem patterns on the landscape and for assessing the effects of various land management activities on those ecosystems (Malanson 1993). Soil properties are commonly used to classify and delineate riparian ecosystem types (e.g., Hansen 1992, Weixelman et al. 1997). They are equally important for evaluating ecosystem or range condition (Wilson and Tupper 1982), although they are less frequently used for that purpose. Soil characteristics used to classify riparian ecosystems serve as indicators of the influence of regional factors such as climatic regime, geomorphic position, and hydrology on soil development, and for riparian ecosystems usually include soil type from pedon descriptions, depth to water table or saturation, and soil texture. In contrast, soil characteristics used to evaluate ecosystem condition serve as indicators of the combined influences of human-caused and natural disturbance on soil physical and chemical properties and biotic processes within ecosystem types (e.g., Breckenridge et al. 1995). Although soil characteristics for evaluating rangeland ecosystem conditions have not been standardized, measures of soil "quality" have been developed for agronomic situations that include measures of soil physical and chemical properties and biotic processes (Doran and Parkin 1994, 1996). When combined with the soil variables used to classify ecosystem types, these measures appear to be appropriate for detailed assessments of rangeland ecosystem condition (Harris et al. 1996).

Effectively using measures of soil characteristics to either classify riparian ecosystems or to assess ecosystem condition requires knowledge of the natural variability of the soils within these ecosystems. In riparian ecosystems, both drainage basin geology and depth to water table significantly influence soil characteristics. The geologic composition of watersheds influences physical soil characteristics such as coarse fragments and soil texture, and chemical characteristics such as pH and available phosphorus and potassium. Because of its effect on the depth to soil saturation and, thus, mineralization processes, water table depth influences soil properties such as organic matter, total nitrogen, cation exchange capacity, and pH (Mitsch and Gosselink 1993). In this study, we evaluated the degree of variability in central Nevada meadow ecosystem soils using several physical and chemical measures of soil "quality." The objectives were (1) to examine the relative influence of both watershed geology and water table on the physical and chemical soil properties of wet and mesic meadow ecosystems; and (2) to evaluate the implications of the results for classifying riparian ecosystems and for assessing ecosystem condition. This research was conducted as part of a USDA Forest Service ecosystem management project that is seeking to obtain a better understanding of the structure of central Nevada riparian ecosystems and to develop management guidelines for maintaining or restoring riparian ecosystem integrity (Chambers 1994).

Materials and Methods

Study Area

The study area is in the Toiyabe Mountain Range in central Nevada. Watershed elevations range from about 1,850 to 3,200 m. Precipitation ranges from 20 cm at the bases of the watersheds to 45 cm at the upper elevations with approximately 60% of the precipitation arriving as winter snow. Peak runoff is during snowmelt in early June, but convective summer storms also result in significant runoff and erosion. Valley floors are often characterized by salt desert vegetation, including shadscale (*Atriplex confertifolia* [Torr. & Frem.] Watts) and winterfat (*Ceratoides lanata* [Pursh.] J. Howell). At low to middle elevations, Wyoming big sagebrush (*Artemisia tridentata* spp. *wyomingensis* Beetle & A. Young) communities are interspersed with Utah juniper (*Juniperous osteosperma* [Torrey] Little) and single leaf pinyon (*Pinus monophylla* Torrey & Fremont) woodlands. At higher elevations, mountain big sagebrush (*Artemisia tridentata* spp. *vaseyana* Beetle) and limber pine (*Pinus flexilis* James) dominate. Riparian vegetation consists of stringers of quaking aspen (*Populus tremuloides* Michaux), narrow leaf cottonwood (*Populus angustifolia* James), river birch (*Betula occidentalis* Hook), willows (*Salix* spp.), and meadow communities. These ecosystems have been grazed by livestock since European settlers colonized the area.

The stream systems are typically located within confined valleys, exhibit high gradients, and are incised (USDA Forest Service 1996). Low flows in these stream systems range from about 0.0057 m^3 sec^{-1} to 0.0567 m^3 sec^{-1} (Hess and Bohman 1996). Meadow systems are associated with hillslope springs or seeps, or cross-valley alluvial fans or other nick points that block down-valley subsurface flows and result in locally higher water tables. Stream incision tends to be highest above the alluvial fans and meadow systems, but downcutting within the meadows can result in lowered water tables.

This study focuses on 4 drainages with varying geology—Kingston Canyon, Big Creek, Washington Creek, and San Juan Creek. The Toiyabe mountains are a typical north-south fault-blocked range with complex structural geology (Kleinhample and Ziony 1985). Bedrock geology of Kingston Canyon is dominated by Ordovician chert with minor greenstone, pillow lavas and shale with some areas influenced by deposition of Devonian-Silurian silty limestone. Bedrock geology of Big Creek is mostly Ordovician chert containing minor greenstone, pillow lavas and Ordovician-Cambrian phyllites and slate with laminated limestone. Washington Creek is dominated by Proterozoic quartzite with minor Ordovician shale and limestone, some locally metamorphosed to slate and marble. The San Juan watershed is dominated by a Tertiary rhyolitic to rhyo-dacitic welded ash flow tuff unit that is locally brecciated and somewhat argillized.

Field Methods

Within the 4 drainages, meadow sites were selected with perennially high water tables (0 to –20 cm from the surface), intermediate water tables (–30 to –50 cm), or low water tables (–60 to –80 cm). The study sites range from 2,180 to 2,330 m. Meadows with high water tables correspond to the Nebraska sedge ecosystem type and are dominated by Nebraska sedge (*Carex nebrascensis* Dewey), while those with low water tables are classified as the mesic graminiod ecosystem type and are dominated by Kentucky bluegrass (*Poa pratensis* L.) (USDA Forest Service 1996). Those with intermediate water tables are characterized by both Nebraska sedge and Kentucky bluegrass. In Kingston Canyon and Big Creek, only meadows with low and high water tables could be located for sampling, while in Washington Creek and San Juan Creek meadows with low, intermediate, and high water tables were located and sampled.

Soil pedons from each of the 10 meadow sites were described using standard methods (Soil Survey Staff 1984). Also, 4 replicate soil samples were collected from each of the meadow sites in August, 1994. Each sample was randomly located and consisted of a composite of 3 cores (10 cm diam.) taken 0.5 m apart. Samples were stratified by depth and were collected from the 0–5, 10–20, and 30–40 cm depths. In addition, 4 replicate bulk density measurements were made in the field on each meadow site using the rubber-balloon excavation method (Blake and Hartge 1986) and excavated holes of approximately 400 cm^2 surface-area and 15 cm depth. Depth to water table has been monitored from 3, 10 cm diam. wells (perforated PVC pipe) for each of the meadow sites in August of 1994, 1996, and 1997.

Laboratory Methods

Chemical and physical soil analyses of the < 2 mm fraction were conducted by the Soil, Plant, and Water Analysis Laboratory at Utah State University. All samples were analyzed for organic matter, total nitrogen, pH, extractable phosphorus, extractable potassium, and texture. In addition, samples from the Washington Creek meadows were analyzed for extractable cations, cation exchange capacity, and moisture retention. Total organic matter was determined by ashing (Storer 1984, Schulte 1988) and total nitrogen was evaluated with a modified micro-Kjeldahl digestion procedure (Bremner and Mulvaney 1982). A 1:1 ratio of soil:H_2O was used to determine pH (McLean 1982), and cation exchange capacity and extractable cations were evaluated using 1N NH_4OAc at pH 7 (Thomas 1982). Phosphorus was extracted using $NaHCO_3$ (Olsen and Sommers 1982). Percentage coarse fragments (> 2-mm) were determined by sieving. Particle-distribution of the < 2-mm fraction was determined by the hydrometer method (Gee and Bauder 1982). Soil water retention was determined using the pressure plate method at 0.03 MPa and 1.5 MPa (Klute 1982).

Statistical Analyses

Repeated-measures analyses of variance (ANOVA) were used to examine differences among drainages, soil water tables, and depths with depth as the repeated factor (Statistical Analysis System 1990). One analysis evaluated differences among all 4 drainages for the high and low soil water tables; a second examined differences among all 3 water tables for Washington and San Juan Creeks. For the soils data collected from the Washington Creek sites, the comparisons evaluated differences among water tables and depths. Mean comparisons were performed using Fisher's Protected LSDs (Steel and Torrie 1980). Product moment correlations were used to evaluate relationships among the different soil variables.

Results

Differences in soil profile characteristics among the 3 water table depth classes are summarized in Table 1. Pedons from meadows with high water tables are characterized by thick O_e horizons, dark, relatively fine-textured and organic-rich A horizons, and lower C horizons with higher coarse-fragment contents. Profile differentiation, as in the formation of B horizons is absent. Because of the high water table, gleyed soil matrix colors begin at 16 cm. In general, pedons with both

Table 1. Pedon descriptions representative of low (–60 to –80 cm), intermediate (–30 to –50 cm), and high (0 to –20 cm) water table depths.

Horizon	Depth	Munsell moist color	Texture	pH	Root abundance
Low water table - Aquic Cryoboroll					
	(cm)				
A	0–10	10YR 2/1	silt loam	6.6	many
Bw1	10–23	10YR 2/1	silt loam	6.6	common
Bw2	23–45	10YR 2/1	silt loam	6.6	common
Bw3	45–79	10YR 3/1	silt loam	6.6	common
Cg1	79–104	10YR 3/1	loam	6.8	few
Cg2	104–120	10YR 3/1	sandy clay loam	6.8	absent
Intermediate water table - Cumulic Cryaquoll					
A1	0–11	10YR 2/2	silt loam	6.8	many
A2	11–32	7.5YR 2.5/1	sandy loam	6.6	common
Ag	32–53	7.5YR 2.5/1	gravelly sandy loam	6.8	common
2C	53–115	10YR 3/1	v. gravelly sandy loam	7.0	few
	2 Cg	115–123 5GY 5/1	v. gravelly sandy loam	7.2	few
High water table - Typic Cryaquoll					
Oe	0–16	10YR 2/2	fibric	6.2	many
Ag	16–29	10YR 2/1	loam	6.2	many
A	29–54	10YR 2/1	gravelly sandy loam	6.4	common
2C	54–93	10YR 3/1	gravelly sandy loam	6.6	common
2Cg	93-	5GY 4/1	v. gravelly sandy loam	7.0	few

Table 2. August depth to water table for sites categorized as having low, intermediate, and high water tables in the study drainages. Values are mean ± S.E.; n = 3.

Water table category / Study drainage	Depth to water table 1994	1996	1997
	(cm)		
Low			
Kingston	67 ± 0*	88 ± 5	82 ±6
Big Creek	70 ± 0	77 ± 3	77 ± 3
Washington	50 ± 0	40 ± 7	56 ± 11
San Juan	63 ± 0	84 ± 8	83 ± 10
Intermediate			
Washington	30 ± 0	20 ± 2	29 ± 3
San Juan	54 ± 0	72 ± 12	70 ± 17
High			
Kingston	5 ± 0	18 ± 2	20 ± 0
Big Creek	0 ± 0	0 ± 0	2 ± 0
Washington	0 ± 0	0 ± 0	2 ± 0
San Juan	20 ± 0	--	--

*In 1994, n=1.

Table 3. Bulk densities (0-15 cm) for meadows with low, intermediate and high water tables in the four drainages. Upper case letters within rows indicate differences among soil water levels; lower case letters within columns indicate differences among drainages (Fisher's LSD, P ≤ 0.05).

Drainage	Bulk density: Low water table	Intermediate water table	High water table
	(Mg/m^3)		
Kingston	0.50 ± 0.40a A	—	0.26 ± 0.01a B
Big Creek	0.55 ± 0.06a A	—	0.11 ± 0.02b B
Washington	0.35 ± 0.03b A	0.43 ± 0.02a A	0.14 ± 0.02b B
San Juan	0.47 ± 0.05a A	0.40 ±0.07a A	0.16 ± 0.04b B

low and intermediate water tables lack O horizons. Pedons with intermediate water tables are characterized by thick dark organic-rich mineral A horizons that grade into C horizons with low organic-content and increasing coarse-fragment content. These pedons also show little evidence of profile differentiation. Pedons with low water tables are characterized by deep, dark and organic-rich profiles and the expression of cambic Bw horizons. All of the meadow types were characterized by abundant roots to depths of 50 cm or deeper.

Depths to the water table in August of 1994, 1996, and 1997 varied among sites, but most values are within the expected ranges based on initial surveys for the different soil water categories (Table 2). A potential outlier based on depth to water table is the Washington Creek site within the low soil water category.

Percentage coarse fragments in the soil are highly variable both among and within watersheds resulting in no statistical differences among water tables, sites, or depths (Fig. 1). Percentage sand is lower on the high water table sites than on the low or intermediate water table sites, and the highest percentages of silt and clay occurs on the low water table sites. The Kingston Canyon sites have significantly higher clay and silt and lower sand than the other sites for both the low and high water tables, potentially explaining some of the overall statistical differences in soil texture among water levels.

Bulk density of the 0-15 cm depth and soil moisture retention differ significantly among soil water tables. Bulk densities for high water table sites are consistently lower than for either low or intermediate water table sites, but there are no differences in bulk densities between low and intermediate water table sites (Table 3). Within water table categories, the Washington Creek site has lower bulk densities than the other low water table sites, while the Kingston Canyon site has higher bulk densities than the other high water table sites. For the Washington Creek meadows, soil moisture retention is higher on the high water table site than on the low or intermediate water table sites at both 0.03 MPa and 1.5 MPa (Table 4). Moisture retention tends to decrease with depth.

Both soil organic matter and total Kjeldahl nitrogen are highest on high water table sites and do not differ between low and intermediate water table sites (Fig. 2). Differences among sites exist and the San Juan site has lower organic matter and total nitrogen than the other low water table sites, while the Washington Creek site

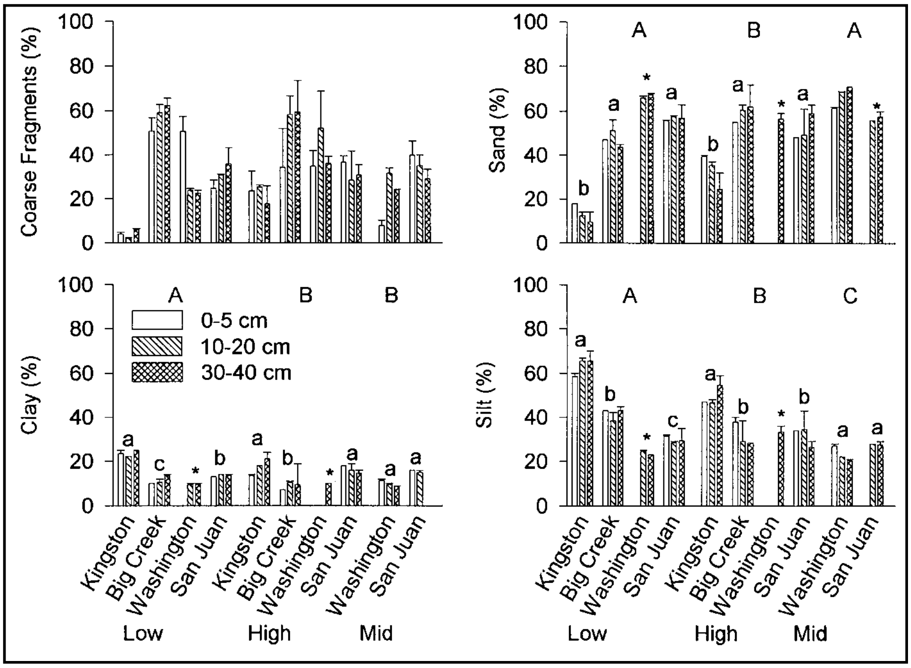

Fig. 1. Soil physical properties for low, high, and intermediate (mid) water tables for meadow sites within the 4 study drainages. Upper case letters indicate significant differences among water tables; lower case letters indicate differences among drainages within a soil water table category (Fisher's LSD, P< 0.05).

Table 4. Soil moisture retention for low, intermediate, and high water tables in Washington Creek. Upper case letters indicate differences among water tables; lower case letters indicate differences among depths within water tables (Fisher's LSD; P ≤ 0.05).

Water table and depth (cm)	Moisture retention 0.03MPa	Moisture retention 1.5MPa
	------------------ (% by weight) ------------------	
Low		
0 to –5	61.0 ± 7.9 a B	54.5 ± 11.1 a B
–10 to –20	20.8 ± 0.4 b	9.4 ± 0.2 b
–30 to –40	17.0 ± 0.1 b	6.4 ± 0.0 b
Intermediate		
0 to –5	37.6 ± 0.3 a B	27.9 ± 0.2 a B
–10 to –20	19.2 ± 0.8 a	8.2 ± 0.8 a
–30 to –40	16.1 ± 0.4 a	5.8 ± 0.4 a
High		
0 to –5	123.4 ± 16.9 a A	92.4 ± 20.4 a A
-10 to –20	60.4 ± 27.8 b	43.4 ± 23.9 b
–30 to –40	41.8 ± 5.0 b	22.2 ± 4.5 b

has higher organic matter and total nitrogen than the other high water table sites. Both organic matter and total nitrogen decrease significantly with depth (P < 0.001). The pH decreases with increasing water table level (Fig. 2). Significant differences exist among sites within water table levels with the San Juan sites having consistently lower pH values. Overall, pH decreases significantly with depth (P < .01). Extractable phosphorus levels are significantly higher on low water table sites than on either high or intermediate water table sites (Fig. 2). This is primarily because of the high levels of extractable phosphorus for the Kingston Canyon site within the low water table category. Within the high water table category, the Kingston Canyon site also exhibits higher levels of extractable phosphorus than the other sites. In contrast to extractable phosphorus, the high water table sites have higher levels of extractable potassium than the low water table sites. However, this again appears to be attributable to the high values for a single site—Washington Creek. Within water table categories, the San Juan sites have higher levels of extractable potassium than other sites for both the low and intermediate water tables. Levels of extractable potassium decline with depth across water table categories and sites (P < 0.001).

Cation exchange capacities measured for the Washington Creek meadow sites are higher on the high water table site than on the low or intermediate water table sites (Table 5). For all 3 water table categories, cation exchange capacity declined significantly with depth. Individual exchangeable cations did not differ among water table categories, but decreased with depth within water table categories.

Pearson product-moment correlations for the major soil properties are in Table 6. Negative correlations existed between pH, cation exchange capacity and potassium. However, pH was positively correlated with bulk density. As expected, levels of organic matter and total nitrogen were highly correlated among sites. Positive correlations existed for organic matter, total nitrogen, cation exchange capacity, potassium, and soil water retention. Organic matter, cation exchange capacity, and extractable potassium were negatively correlated with sand, but positively correlated with silt.

Discussion

In central Nevada meadow ecosystems, a high degree of natural variability in soil physical and chemical properties exists among sites characterized

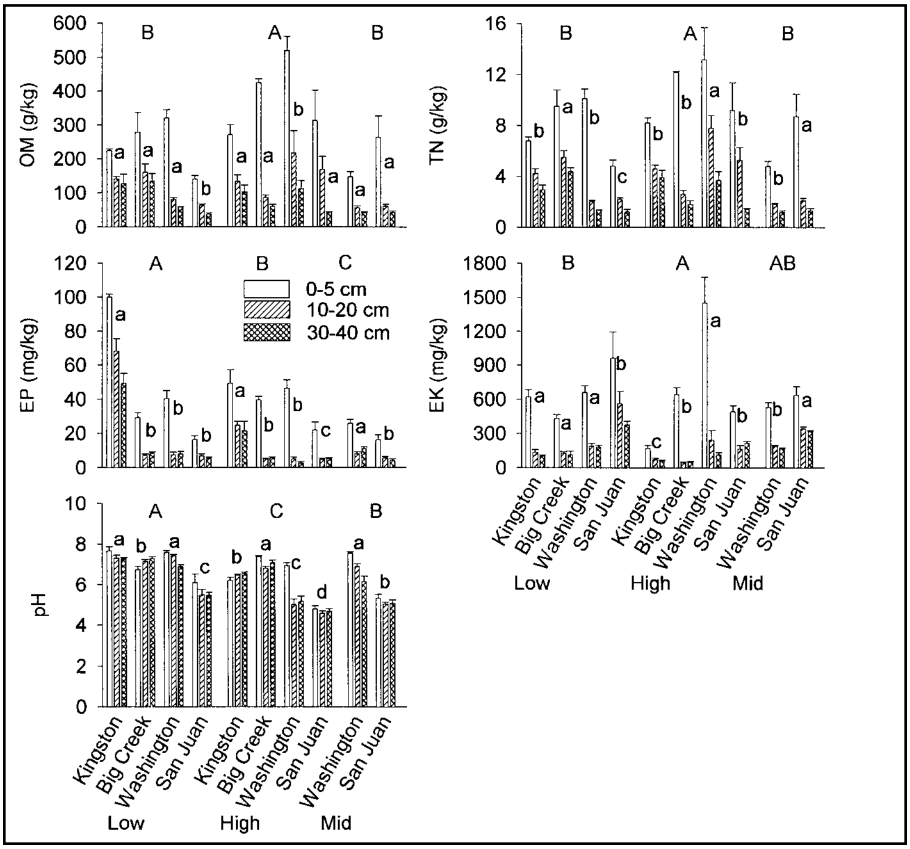

Fig. 2. Soil chemical properties for low, high, and intermediate (mid) water tables for meadow sites within the 4 study drainages. Upper case letters indicate significant differences among water tables; lower case letters indicate differences among drainages within a soil water table category (Fisher's LSD, P< 0.05).

Table 5. Cation exchange capacities and exchangeable cations for low, intermediate, and high water tables in Washington Creek. Upper case letters indicate differences among water table levels; lower case letters indicate differences among depths within water tables (Fisher's LSD; $P \leq 0.05$).

Water table and depth	Cation-exchange capacity	Exchangeable cations Ca	Mg	K	Na
(cm)	(cmol/kg)	(cmol/kg)			
Low					
0 to -5	49.9 ± 6.6a B	42.8 ± 1.7a	4.7 ± 0.3a	0.8 ± 0.1a	0.03 ± 0.08
-10 to -20	21.5 ± 0.7b	14.4 ± 0.4b	0.9 ± 0.1b	0.4 ± 0.1b	0.03 ± 0.00
-30 to -40	18.0 ± 1.0b	8.4 ± 0.1b	0.6 ± 0.1b	0.3 ± 0.1b	0.02 ± 0.01
Intermediate					
0 to -5	32.3 ± 1.4a B	31.2 ± 2.1a	2.9 ± 0.4a	0.8 ± 0.1a	0.01 ± 0.01
-10 to -20	19.8 ± 1.2b	10.4 ± 0.7b	0.8 ± 0.1b	0.3 ± 0.1b	0.02 ± 0.01
-30 to -40	16.3 ± 0.9b	7.1 ± 0.6b	0.6 ± 0.1b	0.2 ± 0.1b	0.02 ± 0.01
High					
0 to -5	78.5 ± 6.3a A	33.6 ± 8.8a	3.2 ± 0.7a	1.0 ± 0.1a	0.14 ± 0.09
-10 to -20	54.8 ± 19.0b	18.2 ± 0.5b	0.8 ± 0.4b	0.2 ± 0.1b	0.16 ± 0.13
-30 to -40	43.8 ± 7.8b	18.9 ± 4.0b	1.2 ± 0.4b	0.2 ± 0.1b	0.03 ± 0.00

by different water tables or located in different drainages. Soil development and morphological characteristics are strongly influenced by depth to water table. The thickness and organic matter content of surface horizons declines with decreases in average water table depth. This is not unexpected given that mineralization of organic matter decreases with increasing water content in these wet and mesic soils. Only the low water table (–60 to –80 cm), mesic graminiod sites has profile differentiation of a structural B horizon. Perpetually high water tables on the high water table sites (0 to –20 cm) limit the downward movement of colloids and solutes that would form B horizons (Duchaufour 1977). Moreover, continual saturation with water restricts soil shrink-swell which is important in the formation of structural B horizons.

Decreasing depth to soil water saturation results in higher organic matter, total nitrogen, cation exchange capacity and extractable potassium, but lower pH. Also, sites with lower depth to saturation have lower bulk densities and higher soil moisture retention. Levels of organic matter often increase with decreasing water table depth (e.g., Johnston et al. 1995) due to lower mineralization rates. Soil organic matter content influences many other variables (see Mitsch and Gosselink 1993) which is evident from the product moment correlations for the Washington Creek sites. Strong positive correlations exist for organic matter, total nitrogen, cation exchange capacity and extractable potassium, while a negative correlation exists between organic matter and pH. Higher levels of organic matter result in a greater number of cation exchange sites, and the tendency toward decreasing pH with higher levels of organic matter is common in meadow ecosystems (Naiman et al. 1994). The high correlation between extractable potassium and organic matter suggests that a large proportion of extractable potassium is associated with the soil organic fraction. This would be unusual because research has shown that the largest pool of extractable potassium is associated

Table 6. Product-moment correlation coefficients (and probability levels) comparing major soil properties for the central Nevada meadow sites.

	pH	OM	TN	CEC	EP	EK	Bulk density	Moisture retention	Sand	Silt
		(g/kg)	(g/kg)	(cmol/kg)	(mg/kg)	(mg/kg)	(Mg/m3)	(0.03MPa)	(%)	(%)
pH	–									
OM	-0.68 (0.13)	–								
TN	-0.68 (0.14)	(0.99) (0.001)	–							
CEC	-0.81 (0.05)	0.97 (0.002)	0.97 (0.001)	–						
EP	0.12 (0.82)	0.51 (0.30)	0.48 (0.34)	0.34 (0.51)	–					
EK	-0.81 (0.05)	0.97 (0.001)	0.94 (0.005)	0.99 (0.001)	0.35 (0.50)	–				
Bulk density	0.92 (0.009)	-0.46 (0.35)	-4.88 (0.33)	-0.64 (0.17)	0.41 (0.42)	-0.64 (0.17)	–			
Moisture retention	-0.84 (0.04)	0.96 (0.003)	0.97 (0.002)	0.99 (0.001)	0.23 (0.59)	0.97 (0.001)	-0.68 (0.133)			
Sand	0.74 (0.09)	-0.83 (0.04)	-0.75 (0.08)	-0.86 (0.03)	-0.39 (0.45)	-0.91 (0.01)	0.56 (0.25)	-0.8 (0.05)	–	
Silt	-0.72 (0.01)	0.83 (0.04)	0.75 (0.08)	0.86 (0.03)	0.37 (0.47	0.91 (0.01)	-0.55 (0.26)	0.80 0.05	-0.99 (0.001)	–
Clay	-0.54 (0.27)	-0.34 (0.51)	0.34 (0.50)	0.37 (0.47)	0.34 (0.51)	0.39 (0.44)	-0.41 (0.42)	0.39 0.44	-0.46 (0.36)	0.40 (0.44)

with 2:1 silicate clay minerals such as illite (Lindsay 1979). The high negative correlation between organic matter and soil bulk density is to be expected (Miller et al. 1965). The bulk density values obtained for the 0–15 cm depth here are similar to those for O horizons in other meadow soils (Johnston et al. 1995, Naiman et al. 1994) and for organic soils in general (i.e., 0.2 to 0.3 Mg/m^2) (Brady 1974).

The geological characteristics of the different drainage basins contributed significantly to the variability among sites, influencing soil texture and pH, extractable phosphorus, and extractable potassium. Kingston Canyon is characterized by high percentages of silt and clay, neutral pH, and high levels of extractable phosphorus. Big Creek also has high percentages of silt and neutral pH. These 2 drainages are in close proximity and consist primarily of erosion resistant chert and quartzite with a strong limestone component (Stewart and McKee 1977). While chert and quartzite are resistent to weathering, admixed limestone decomposes primarily to silts and clays resulting in nearly neutral soil pH values. Higher phosphate levels in Kingston Canyon can be attributed to a high content of Ca phosphate minerals in the parent materials. In Washington Creek soils are coarser-textured and tend towards lower pH and extractable phosphorus and extractable potassium levels. This is because quartzite (metamorphozed sandstone) with a minor limestone component is the principal catchment material (Stewart and McKee 1977). San Juan has fairly coarse-textured soils and the lowest soil pH and extractable phosphorus. Although the upper basins have parent material similar to that in Washington Creek, the lower areas above and surrounding the meadows are dominated by acidic volcanic tuffs, rhyolites, and breccias with lower base metal contents (Stewart and McKee 1977).

These results indicate that the physical and chemical soil characteristics of riparian areas exhibit high spatial variability and must be carefully interpreted when classifying ecosystems or evaluating ecosystem condition. The effects of differing soil water tables are often predictable for wetland soils (Mitsch and Gosselink 1993) and are fairly consistent among drainages in central Nevada. Soil water table depth significantly affects biotic processes in these ecosystems and, consequently, several soil properties, including bulk density, organic matter, total nitrogen, cation exchange capacity, and pH, are highly responsive to depth to saturation. In addition, drainage basin geology has large influences on soil texture, pH, extractable phosphorus and extractable potassium. This indicates that while depth to water table, soil descriptions, and soil properties such as organic matter and total nitrogen are reasonable characteristics for classifying meadow ecosystems, soil texture, pH, extractable phosphorus and extractable potassium are not. Also, effective use of the soil characteristics examined here for evaluating soil "quality" or riparian ecosystem condition will require classifying ecosystems within fairly narrow ranges according to soil water table. It will also require developing expected ranges for the various soil characteristics based on drainage basin geology as has been done for agronomic soils. These soil characteristics could be incorporated into sampling schemes for collecting the vegetation and soils data necessary for ecosystem classifications. Before we can accurately assess how these soils respond to human-caused and natural disturbance on a landscape basis, we need to increase our understanding of their natural variability.

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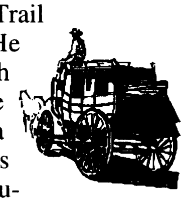
Book Reviews

The Merchant Prince of Dodge City—The Life and Times of Robert M. Wright. By C. Robert Haywood. University of Oklahoma Press, Norman, Oklahoma. 236 pages. US$27.95 hardbound. ISBN 0-8061-3073-3.

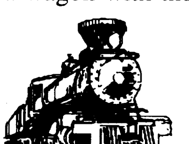
Growing up as the only daughter in my family during the early '50's, we viewed many TV westerns including *Bat Masterson* and *Gunsmoke.* When the book entitled, *The Merchant Prince of Dodge City—The Life and Times of Robert M. Wright,* arrived in the office of SRM, I was anxious to read it. I wanted to compare my memories of the hours I spent in front of our then new black-and-white TV with Haywood's thoughts in print. I was not disappointed. Mr. Haywood mesmerized me in the Preface, and I was ready to begin the adventure of Robert M. Wright.

In 1856 Robert left his home in the East to visit his aunt and uncle on a farm in St. Louis, Missouri. At the age of 19 he married Alice Armstrong, his 13-year-old cousin. Soon afterward Robert began his first overland trip which brought him to Pawnee Rock, the most famous landmark on the Santa Fe Trail. His mind had been saturated with stories that old freighters shared around the campfire of how the rock had become both a refuge from, and a source of, danger. It was at this turning point that he decided to spend the rest of his life in and around Kansas.



Robert made several trips on the Santa Fe Trail driving a team of oxen, in wagon trains. He went on to become a stage coach driver, which proved to be a milestone in his life, as he enjoyed having the power of control. Being a mule skinner, and making influential decisions on behalf of people, provided valuable opportunities to build character. Mr. Wright happened to be at the right place at the right time in Fort Dodge by being named post sutler or post trader, another rung in the ladder toward Wright's future business endeavors on Front Street in Dodge City.

It was said that Dodge City had its beginning in the back of a wagon with the sale of whiskey to the buffalo hunters. But the advent of the Topeka & Santa Fe railroad was the start of Dodge City's growth. Hunting buffalo to serve track layers brought people who were concerned with the waste of hides of animals that were shot and butchered. Some hides were sent east. They were determined to be of decent quality; more were ordered. This frontier town continued to grow quickly with a general merchandise store, a grocery, and merchant store, a dance hall, some primitive brothels and a blacksmith's shop. This growth caught Wright's attention. In 1872, he solicited friends to organize a town company to become involved on the *ground floor* of a booming town by purchasing land. Besides dealing in real estate, Wright became partners with Charles Rath and opened a two-story building on Front Street which was to become the heart of Dodge City. This store supplied every need that the buffalo hunters wanted to purchase, but eventually served as a bank as well. The Texas cattlemen spent their earnings there after they drove the cattle up from Texas. Years later Wright became sole owner of this store.



Haywood temporarily directs us from the town business of Robert Wright to the entrepreneur's political life. The year was 1874 and Kansas had experienced a terrible drought that began in the early 1870's and left western Kansas a barren brown. To make matters worse, the Rocky Mountain locusts arrived and finished off any edible' that remained. Robert Wright made his political debut as a state representative of the 130 District after the Governor of Kansas called for a special session to consider public aid for victims of these 2 disasters. Wright always had a soft spot for the Texas cattlemen and a lot of decisions that he made while in the legislature were made with the consideration of what was good for the Texas cattlemen who journeyed into Kansas. Later in Wright's life, he was elected mayor of Dodge City.

Haywood gives the reader a peek at some of the characters who lived in the early days of Dodge City. The brothels, dance halls, and 14 or more saloons helped give the town the title of *the Beautiful, Bibulous, Babylon of the Frontier.* Dora Hand, who was an actress and a dance hall girl was killed (quite by accident) sleeping in a borrowed bed; Ed Masterson, brother to Bat, was killed in the line of duty; Thomas O'Haran, also known as *Limping Tom* killed U.S. Marshall H.T. McCarty in the Long Branch saloon; and Wyatt Earp killed a cowboy named George Hoy.

Wright was always looking for, and doing, something new. He didn't spend much time at home as a husband and a father, but he was a good fiancial provider for his family. Tragedy hit the Wright household when their daughter Belle died. Married life became even more distant for Robert and his wife Alice. Belle was her mother's closest companion and her daughter's death was a terrible loss for her. After Alice passed away Robert married twice more.

The Merchant Prince of Dodge City contains many historical photographs spread throughout the book, which help one visualize the people and the town of Dodge City. Mr. Haywood wrote this account of Robert Wright in such a manner that I became personally acquainted with the Wright family. Robert Wright's life was colorful and his ventures cannot be put in a page of a book review. I recommend this book for all who are interested in the early years of our western heritage.—*Patty Rich*, SRM Headquarters Office, Denver, Colorado.

Monitoring Vertebrate Populations. By William L. Thompson, Gary C. White and Charles Gowan. 1998 Academic Press, San Diego, CA. 365 p. illus. US$64.95 hardcover. ISBN 0-12-688960-0.

State, federal, and private agencies have increasingly recognized that (1) management and use of our natural resources must be based on scientific data gathered via appropriate scientific methods and, (2) results must be statistically reliable and defendable if they are to withstand the rigors of increased public scrutiny and court battles. This recognition may have served in part, as the impetus for this book which was written as a general reference for wildlife biologists and resource managers who have the responsibility of monitoring vertebrate populations, yet may possess insufficient statistical training.

As the authors point out, the subject of this book is measuring changes in animal numbers and spatial distribution. However, successful detection of these changes in population parameters, i.e. in abundance, density, and distribution, is complex and influenced by the error and bias associated with various sampling designs and data collection procedures. They state *"...we have focused on both basic concepts and practical applications...we have attempted to combine classical finite population sampling designs with population enumeration procedures in a unified approach...we discuss approaches to minimize sampling error so that monitoring methods have a good chance of detecting trends in populations..."*

The book focuses on abundance estimation, seeking the inevitable trade-offs between minimum bias and maximum precision at a reasonable cost. Dealing more with survey design than experimental design, it focuses *"on methods for obtaining valid inferences from information on a portion of a population in order to detect a change in numbers over time, rather than on ways of manipulating a population to evaluate possible causes for a change in numbers over time."* They note that a good survey design cannot be implemented without proper knowledge of the species of interest. Surveys that are either poorly designed or poorly performed may mistakenly detect a population decline where none exists. They observe that poor surveys are probably no better than no survey at all; in fact no survey would be cheaper.

The first 6 chapters contain the fundamentals. Chapter 1 deals with basic statistical concepts and terminology associated with monitoring populations within a defined area over time (i.e. random and non-random sampling, variance, precision, and bias). The book discusses how plot size and shape affect both precision and the ability to detect a population trend (Chapter 2). It describes finite population sampling designs for moderate to abundant species—(simple random, stratified random, systematic random, Latin square +1, ranked set) as well as for rare or clustered populations. It also demonstrates which methods are best for decreasing variance. Chapter 3 presents enumeration methods—how to obtain either the actual abundance or an estimate of the abundance of animals on a sampling unit using complete counts (census) or incomplete counts (indices and adjusting for incomplete detectability). A community survey approach (Chapter 4) is compared to methods using single or multiple species approaches. Chapter 5 illustrates how to detect trends in population estimates through graphical, regression, randomization or nonparametric testing. The first half of the book concludes (Chapter 6) by using guidelines for planning surveys—determining the level of effort required to conduct a survey, plot design, sampling size, and power of the test to detect a trend.

Chapters 7 through 10 cover applications of concepts offered in the earlier chapters. They emphasize the importance of using pilot studies to assess cost and feasibility of proposed monitoring programs and present the more common survey methods for fish (7), amphibians and reptiles (8), birds (9), and mammals (10). Included for each vertebrate group are lists of scientific references and dichotomous keys for selecting among the methods for population enumeration. Finally, Appendices A through D contain a glossary of terms and notations, formulas for sampling estimators, and a list of both common and scientific names of vertebrates.

This test will enable the wildlife biologist/manager, natural resource administrator, or policy maker to better evaluate research concerning the status of wildlife populations. For the statistically impaired or statisiphobics among us, it offers hope and a lighted path toward meaningful data gathering and analysis. While it may not replace the mystery novel at your bedside table, it will no doubt earn a place among your most useful professional texts on your workshelf.—*Bruce B. Davitt*, Wildlife Habitat Lab, Dept. Natural Resource Sciences, Washington State University, Pullman, Washington.

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