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Diet selection of mountain lions in southeastern Arizona

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Abstract

Prey selection by mountain lions (Puma concolor) in the Aravaipa-Klondyke area in southeastern Arizona was studied from February 1991 to September 1993. Overall diet as determined from frequency of occurrence in 370 scats was 48% deer (Odocoileus virginianus cousi and O. hemionus combined), 34% cattle, 17% javelina (Tayassu tajacu), 6% rabbit (Sylvilagus spp. and Lepus californicus combined), 4% rodent, and 2% desert bighorn sheep (Ovis canadensis mexicanus). With respect to biomass consumed, cattle composed 44%, deer 40%, javelina 10.9%, rabbits 2.9%, and rodents 0.02%. Based on mean weights of prey consumed, the proportion of individuals killed and eaten changed to rabbits 52.7%, deer 16.3%, rodents 12%, javelina 10%, cattle 8%, and desert bighorn sheep 0.5%. Mountain lions selected deer less frequently than their availability would suggest, selected calves slightly more than their availability, and javelina as expected. We speculated that lions selected calves because they were more vulnerable to predation than deer.

Key Words: prey availability, cattle, diet selection, *Puma con*color, javelina, mule deer, white-tailed deer.

Livestock have been preyed upon by mountain lions since they were first introduced from Europe (Barnes 1960), and livestock loss remains a major rationale for controlling them. Arizona reportedly has some of the highest mountain lion kill rates on cattle in the United States (Christensen and Fischer 1976, Nowak 1976, Anderson 1983). Killing mountain lions that prey on livestock (i.e., depredation control) remains a legal, though controversial practice, and accounts for a substantial portion of the human-caused mortalities of Arizona mountain lions (Cunningham et al. 1995).

During 1987, the Aravaipa-Bonita Cattle Growers Association of southeast Arizona reported that mountain lions had killed more calves than historically. Consequently, they contracted with the Animal and Plant Health Inspection Service (APHIS), U.S. Department of Agriculture, to control

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Resumen

Presa seleccionada por el León de Montaña (Puma concolor) en el Sureste del Estado de Arizona en el area de Aravaipa Klondyke. El estudio fue conducido en el mes de Febrero del año 1991 a Septiembre de 1993. El alimento preferido fue determinado basado en la frecuencia que ocurrio en 370 ejemplos de escrementos y los resultados fueron los siguientes porcentajes: 48% Venado (Cola-Blanca y Venado Mula Odocoileus spp.), 34% Ganado Vacuno, 17% Cochi Javalin (Tayassu tajacu), 6% Conejo (Sylvilagus spp) y Liebre Lepus californicus), 4% Roedor y 2% Borrego del Decierto (Ovis canadensis mexicanus). Tambien fue estimado el porcentaje de biomasa y la proporción de especies casadas y consumidas por León de Montaña En cuanto al respecto de biomasa consumida, Ganado Vacuno fue 44%, Venado 40%, Cochi Javalin 10.9%, conejos 2.9%, y roedores 0.02%. De acuerdo con el promedio de peso de presa consumida por el León de Montaña la proporción de especies consumidas cambio a lo siguiente: 52.7% Conejo, 16.3% Venado, 12% Roedores, 10% Cochi Javalin, 8% Ganado Vacuno, 0.5% Borrego del Decierto. Tambien fue estimada la cantidad de diferente especies que pudieran existir en esta misma area usando un Helicoptero en 4 diferente vuelos, las siguientes especies fueron encontradas: (Venado, Ganado Vacuno, y Cochi Javalin). En los resultados observamos que el León de Montaña selecciono Venado con menos frequencia, comparado con la fiques sugerida, Ganado Vacuno (Crias) fue poco mas seleccionado de lo esperado, y Cochi Javalin como se esperaba. Especulamos que Leónes de Montaña seleccionarón Ganado Vacuno (Crias), porque fue mas vulnerable a la casa del León de Montaña que de lo que fue el Venado.

mountain lions. From 1987 through 1989, 57 mountain lions were killed within a 100,000 ha area. Ensuing public articles resulted in negative criticism of the control operation (B. Burkhart: Rancher, U.S. hunters kill wildlife without rein by State. Arizona Republic, June 15, 1989). We initiated an investigation of mountain lion-livestock interactions in the Aravaipa-Klondyke area of southeast Arizona. A main objective was to determine if mountain lions in the area selected livestock and other prey in proportion to availability.

This manuscript is dedicated to the memory of Dr. Carl R. Gustavson, an excellent biologist and better friend. This study was funded by the Federal Aid in Wildlife Restoration Act Project W-78-R. Constructive criticism on earlier drafts was provided by J. Truett, B. Wakeling, P. Beier, R. Schwiensburg, K. Logan, and J. deVos. We thank K. Sargent, J. Yarchin, and J. Simmons who were involved in data collection. We also thank the San Carlos Apache Nation for allowing us to conduct research on their land.

The Aravaipa-Klondyke study area (AKSA) consisted of 95,100 ha which included Aravaipa Canyon, portions of the Aravaipa Creek watershed, Galiuro Mountains, and the San Carlos Apache Indian Reservation (Fig. 1).

Elevations on the study area ranged from 750 to 2,300 m. Topography within all mountain ranges was steep and broken, with stone pinnacles, narrow and deep canyons, and rugged cliffs common at higher elevations. These formations merged downslope to comparatively level terraces near the bajadas of the Aravaipa Valley to the east, the Gila River Basin to the north, and the San Pedro River to the west.

The study area climate typified that of southeastern Arizona (Lowe 1964). Mean temperatures ranged from 8 to 26 C, and precipitation averaged 31.6 cm per year. Annual spring droughts were usually followed by late summer thunderstorms (monsoons) produced by moisture from the Gulf of Mexico. Winter rains were less episodic and more widespread, originating from Pacific fronts. Snowfall in the area was infrequent at higher elevations and rare in the lower valley areas.

The study area had a wide diversity of vegetation types. Seven of Brown and Lowe's (1974) biotic communities occurred in the study area; semidesert grassland (40% of area), Arizona upland Sonoran desert scrub (30%), interior chaparral (14%), Madrean evergreen woodland (13%), Great Basin conifer woodland (2%), petran montane conifer forest (<1%), and riparian strips along streams.

Livestock and Prey Occurrence

Both historic and current livestock operations on the study area could affect mountain lion diets. Beginning in the 1870s, >50,000 cattle (>125/km²) annually occupied the Aravaipa Valley. Cattle numbers were reduced after significant drought in the late 1890's, but were still grazed in larger numbers than today. By the 1920's, an additional 40,000 angora goats grazed the rougher parts of the Aravaipa watershed and 2,000 burros and 1,800 horses ran free (Hadley et al. 1991).

Grazing pressure declined during the 1930's. The value of mohair decreased,



Fig. 1. Boundaries of the Aravaipa-Klondyke study area where mountain lion diet selection was studied, 1991-1993.

leading to removal of most goats by 1940. The Federal government passed the Taylor Grazing Act in 1934, which called for removal of wild horses, fencing of public lands, and reductions (>50% in some areas) in the numbers of cattle grazed. During our study, there were 22 cattle grazing allotments on public lands (Commercial livestock area) with no restrictions on the San Carlos Indian Reservation (Fig. 1).

Wildlife has also varied in abundance on the study area during the past century. Hadley et al. (1991) reported that Apaches complained about the scarcity of game shortly after 1900. Large wild mammals remained scarce for another 2–3 decades, then began to increase. Based on interviews with local residents and natural resource managers, deer populations were larger during the period from the 1940s to the late 1960s than they were afterward.

Javelina populations have recently declined in the study area, but reasons for the decline were not well understood (Cunningham et al. 1995). Desert bighorn sheep were extirpated in the 1930's. In 1973, 22 bighorn sheep were reintroduced into the area and the population increased to >100 by 1985 (Cunningham et al. 1993).

Methods

Prey Availability

Densities of deer, calves and adult cattle, and javelina within the study area were estimated 4 times: October 1991, April and October 1992, and April 1993. We conducted aerial surveys for 4 days each estimate from a Bell Jet-Ranger helicopter along 52 10-km nonoverlapping transects following procedures of Anderson et. al. (1979) and Burnham et al. (1980). Transects were oriented at right angles to major drainages and were flown at an airspeed of 48 km/hr at 30 m altitude. Front and rear observers positioned on the right side of the helicopter made independent counts of prey species by group size up to 180 m from the helicopter. Cattle were divided into 2 groups based on size; calves (<180 kg) versus adults (>180 kg).

Based on line transect procedures, we had to assume equal visibility of the 3 key prey species (deer, javelina, and cattle). However our qualitative observations were that deer and javelina were not as visible as cattle in thicker vegetation at distances >100 m from the helicopter. This bias could result in lower deer and javelina density estimates and higher cattle density estimates than really existed.

Population density estimates were calculated using TRANSECT II software (Laake et al. 1979) as recommended by Burnham et al. (1980). Prey numbers among surveys and between the commercial livestock and San Carlos Indian Reservation portions of the study area were compared using MANOVA.

Prey Consumption and Selection

Two mountain lion scats were collected each month within 8 equal-sized subdivisions of the study area. We searched for scat by hiking or riding horseback along ridges and washes in each subdivision. We identified mountain lion scats by size and shape (Murie 1954); only scats >30 mm in diameter were collected which excluded most coyote (*Canis latrans*) and bobcat (*Felis rufus*) scats (Danner and Dodd 1982). Scats were judged to be <1 month old when dark and moist and were labeled as fresh; all others were labeled as old. While searching for scat, we also identified fresh (<1 month old) mountain lion kills by criteria described by Shaw (1989).

Prey items in scats were identified on basis of hair and skeletal remains. Scats were soaked in water and washed through 1- and 3-mm sieves. Skeletal material was compared with known reference materials. Hair was examined microscopically and compared with reference slides and photomicrographs from Moore et al. (1974). We did not differentiate between white-tailed and mule deer hair, or between cottontail and jackrabbit, or among rodent species.

We used frequency of occurrence data to estimate the relative number of each taxonomic group that were eaten using procedures described by Ackerman et al. (1984). Weights of white-tailed and mule deer were estimated from average live weights measured at deer hunt check stations near the study area (R. Olding, Ariz. Game and Fish Dept., unpubl. data). Weights of other species were from Burt and Grossenheider (1964).

Kill estimates were divided into 2 seasons; March–August (spring–summer) and September–February (fall–winter). We then analyzed diet versus availability when calf numbers were high and low. Scats considered fresh were pooled across years to increase sample size.

We compared estimates of abundance (i.e., availability) of deer, calves, and javelina with numbers estimated eaten by mountain lions (i.e.,use). We used Chi-square contingency tables to test for differences between prey use and availability by season and overall. If differences (P < 0.05) existed, Bonferroni confidence intervals were used to indicate in which instances use did not equal availability (Neu et al. 1974, Byers et al. 1984). For significant Bonferroni confidence intervals we used Jacobs' D selectivity index (Jacobs 1974) to indicate direction and magnitude of selection or avoidance of prey.

Results

Prey Availability

Overall, deer were the most abundant prey species surveyed in the study area (Table 1). Deer numbers were higher in fall (post-fawning) than spring. Calf numbers were higher in spring than fall as most calving occurred from December to February. Javelina numbers were relatively stable among the first 3 surveys, but were lower in April 1993. The number of javelina groups seen on the San Carlos Indian Reservation were too small to allow density estimation.

Prey densities (all species combined) were higher on the commercial livestock portion of the study area than on the Reservation (P = 0.043). However, there were no differences in relative proportions of prey species between the commercial and reservation areas and data sets were pooled.

Prey Selection

We found 41 mountain lion kills which included 16 white-tailed deer, 7 mule deer, 10 cattle, 4 javelina, and 4 desert bighorn sheep. Male:female ratio

Table 1. Large prey densities within the Aravaipa-Klondyke study area, Arizona, 1991–93, as determined by helicopter surveys.

Area	С	alves	Ad	ult cattle		Deer	Ja	velina	
Date	(<)	180 kg)	(>	180 kg)					
		95% CI		95% CI		95% CI		95% CI	
Commercial				(No./km ²)					
livestock portion	1								
Oct 1991	0.6	0.4 - 1.0	1.7	1.0 - 2.8	6.1	0.5 - 8.1	2.5	1.7 - 3.7	
Apr 1992	1.2	0.9 - 1.8	5.1	4.3 - 6.0	5.5	4.3 - 7.1	2.7	1.9 - 3.7	
Oct 1992	0.6	0.0 - 2.0	1.7	0.0 - 62.9	6.9	5.4 - 8.8	2.9	0.1 - 77.0	
Apr 1993	2.0	1.6 - 2.4	4.8	4.2 - 5.5	2.7	2.1 - 3.5	0.6	0.4 - 1.0	
x	1.1		3.3		5.3		2.2		
San Carlos India	n Reservation								
Oct 1991	0	0 - 0	0.4	0.2 - 0.9	3.6	2.6 - 4.9	0	0 - 0	
Apr 1992	2.3	0.0 - 56.5	1.8	1.2 - 2.8	2.5	1.5 - 4.1	27.5	0.3 - 2.7	
Oct 1992	0.03	0.0 - 0.3	0.1	0.0 - 0.4	2.5	1.6 - 3.8	0.6	0.3 - 1.0	
Apr 1993	0.05	0.0 - 0.9	1.8	1.0 - 3.3	6.3	4.3 - 9.4	0	0 - 0	
\overline{x}	0.6		1.0		3.7				

Table 2. Diet of mountain lions, based on the analysis of 370 scats, from the Aravaipa-Klondyke Study Area, Arizona, 1991-93. Percent biomass and relative number of individuals estimated consumed by mountain lions are calculated according to Ackerman et al. (1984).

Prev species	(A) Frequency of occurrence	(B) Estimated weights of individuals	(C) Correction factor	(D) Biomass	(E) Relative number of individuals consumed
riej species	occurrence	marridadio	140101	consumed	consumed
	(%)	(kg)	(kg/scat) ¹	(%)	$(\%)^3$
Deer	0.48	44	3.52	40.1	16.6
Calves	0.34	100	5.48	44.2	8.0
Javelina	0.17	20	2.68	10.9	10.0
Rabbit	0.06	1	2.02	2.9	52.8
Rodent	0.04	0.03	0.03	0.02	12.0
Desert bighorn	0.02	50	3.73	1.8	0.5

¹Estimated weight of prey consumed per collectible scat produced, when such prey is the only item in the scat (C = 1.98 ± 0.035 B).

 ${}^{3}E = (D \div B) / \sum (D \div B).$

was almost equal for white-tailed deer kills, but all mule deer kills were females. We found no deer fawn or juvenile javelina kills, but 3 of 4 bighorn sheep kills were lambs. Nine of 10 killed cattle were calves, and one was an adult cow; evidence indicated she was killed at the same time as her calf. Of the calves we found and 7 additional ones reported by ranchers, 8 were estimated <4 months of age, and 8 were estimated >4 months of age.

Deer remains were found in 48% of 370 scats and cattle remains occurred in 34% (Table 2). Javelina was the next most commonly-encountered food item (i.e., 17%), followed by rabbits, rodent, and desert bighorn sheep. Other prey such as birds, badger (*Taxidea taxus*), black bear (*Ursus americanus*), porcupine (*Erethizon dorsatum*), and skunk (*Mephitis* spp.) occurred in very few scats. Converted to biomass, diet of mountain lions was dominated by cattle (44%) and deer (40%). Javelina comprised 10.9% of the biomass, and rabbits, rodents, and bighorn sheep all comprised <3%.

Neither frequency of prey nor estimated biomass accurately reflected number of individual prey items eaten. Rabbits were the most frequently killed prey item, followed by deer, rodents, javelina, cattle, and desert bighorn.

During both seasons, rabbits were killed and eaten more than any other prey, but calves composed the majority of the biomass eaten (Table 3). During March-August (spring-summer), small prey (rabbits and rodents) were killed most frequently and were a greater proportion of the mountain lion diet than during September-February. The number of individual deer, calves, and javelina consumed in September-February (fallwinter) all increased more than 100% over spring-summer. Rabbits were still the most frequently killed prey in fallwinter, but the estimate of number of individuals consumed decreased 31.6%.

Over the entire study, mountain lions in the study area ate fewer deer than expected based on deer availability, slightly more calves than expected, and javelina in proportion to availability (Table 4). During the fall-winter season, mountain lions consumed fewer deer than expected, but consumed calves and javelina in proportion to availability. During the spring-summer season, all 3 species were consumed as expected based on availability.

Discussion

Prey Use

In our study, rabbits were the most numerous food item. Deer are the principal prey of mountain lions in many other areas based on frequency of occurrence in scats (Anderson 1983). Our data suggest that the importance of rabbits, rodents, or other small prey are masked by just using frequency of occurrence without a conversion factor. Studies where mountain lion kills are used for diet determination would also underrate small animals as most mountain lions would consume the whole animal. Also, Johnson and Aldred (1982) found that bobcats digested more bones and hair of smaller prey over larger prey. Mountain lions may digest almost all bones and hair of small species.

Based on the Ackerman et al. (1986) caloric needs model, and individual prey proportions eaten by mountain lions on the study area, we estimated the numbers of prey eaten each year. A resident female with 3 kittens would eat 35–40 deer, 17–19 calves, 21–24 javelina, 90–100 rabbits, 20–23 rodents, and 1–2 desert bighorn sheep. A resident female without kittens would eat 9–11 deer,

Table 3. Seasonal diet based on frequency of occurrence, percent biomass, and relative numbers of individuals consumed by mountain lions in the Aravaipa-Klondyke study area, Arizona, 1991–93.

	March–August (n = 82)			S	September–February (n = 54)				
	Frequency of occurrence	Biomass consumed	Number of individuals consumed	Frequency of occurrence	Biomass consumed	Number of individuals consumed			
				(%)					
Deer	36.6	33.2	8.6	44.4	37.9	21.0			
Calves	36.6	51.7	5.9	33.3	44.3	10.8			
Javelina	11.0	7.5	4.4	22.2	14.3	17.7			
Rabbit	12.2	6.5	73.3	3.7	1.7	41.7			
Rodent	4.9	0.02	7.5	1.9	0.01	8.0			
Bighorn	1.2	1.0	0.2	1.9	1.7	0.7			

 $^{^{2}}D = (A \times C)/\sum (A \times C).$

Table 4. Selection of 3 prey species by mountain lions based on frequency of occurrence in mountain lion scats and proportion available as determined from aerial surveys, Aravaipa-Klondyke Study Area, Arizona, 1991–93. (Rabbits, rodents, and desert bighorn sheep were not recorded during surveys).

Season Species	Frequency of occurrence	Relative number of individuals consumed	Proportion of prey species available	Bonferroni 95% CI	Jacobs' D ¹
Year-long diet					
Deer	48	47.3	58.0	0.41 - 0.54	-0.22
Calves	34	23.2	17.8	0.18 - 0.28	0.16
Javelina	17	29.5	24.1	0.24 - 0.35	
Fall diet					
Deer	47	42.6	63.1	0.27 - 0.59	-0.40
Calves	35	21.8	10.7	0.08 - 0.35	
Javelina	24	35.6	26.2	0.2 - 0.51	
Spring diet					
Deer	44	45.8	52.7	0.33 - 0.59	
Calves	44	31.2	25.8	0.19 - 0.43	
Javelina	13	22.9	21.5	0.12 - 0.34	

 1 A positive number means the item was selected for; a negative number means the item was selected against (Range = 1.0 to +1.0).

5–6 calves, 8–11 javelina, 7–9 rabbits, 5–7 rodents, and <1 desert bighorn sheep per year, while a resident male would eat 14–18 deer, 7–9 calves, 9–11 javelina, 36–46 rabbits, 8–11 rodents, and <1 bighorn sheep per year. Ackerman et al. (1986) estimated that young female or male transients would consume approximately 50% the prey of a resident female without kittens.

We estimated that mountain lions killed >600 deer and >225 calves each year on the study area (including both the commercial livestock and San Carlos Indian Reservation portions). If our deer kill estimates were accurate, we should have observed a reduction in deer numbers, but this did not occur. Conversations with ranchers suggested they believed livestock losses, though substantial, were not >225.

Several studies (see Ackerman et al. 1986 for review) have estimated that mountain lions kill a deer at 4 to 20 day intervals, depending on sex and age of prey. Although mountain lions have the ability to kill ungulate prey frequently, we suggest they may not do so if they opportunistically feed on smaller prey. However, this would be difficult to evaluate, and would require intense 24-hour tracking without affecting lion behavior.

Interaction with Cattle

Cattle, except for calves, are larger than most mountain lion prey. Prey selection is influenced by both prey availability and vulnerability (Sunquist and Sunquist 1989, Iriate et al. 1990). Only in Arizona have mountain lions been reported to prey heavily (>30% diet) on cattle (Tully 1991, Cunningham et al. 1995). Most reports come from mid-elevation chaparral and pine-oak woodlands in central Arizona; few cases have been documented in high-elevation or low desert areas (Shaw et al. 1988). In central Arizona, Shaw (1977) found cattle to comprise at least 37% of the mountain lion kills, and cattle remains occurred in 34% of the scats he analyzed; cattle kills peaked in spring.

Estimates of prey densities compared with mountain lion diet suggested that calves were selected by mountain lions in preference to deer. Deer densities in chaparral and forest vegetation types were probably higher than we estimated because of poor visibility during helicopter surveys. If correct, this bias would make mountain lion selection for calves over deer greater than our calculations suggested.

We speculate that calves were more vulnerable to mountain lion predation than deer. Hereford or crossbreed calves are more visible in thick or open terrain while deer are cryptically colored, quiet, and spend most of the day hiding. Deer are more alert and wary than calves. When we followed mountain lion travel routes we observed more calves than deer or javelina while prey surveys suggested deer and javelina densities were greater. Shaw (1981) suggested that increasing the deer:calf ratio may reduce cattle predation by mountain lions. However, we suggest that calf vulnerability was the major factor influencing kill rates, and increases in the deer prey base may not affect kill rates on calves. Also, changes in deer and javelina populations are highly influenced by climatic factors which are impossible for wildlife managers to control.

Shaw (1981) reported that the majority of calves killed were <4-months old and that calf predation was seasonal. We found mountain lions killed and ate calves of all ages year round. This also suggests that moderate increases in deer numbers (fall fawning period in our study) are unlikely to cause appreciable reduction in mountain lion predation on calves.

In our study area, many allottees have nowhere to graze cattle except in rugged terrain with relatively dense vegetation cover. Those with sufficient flat, open pasture hold their younger calves out of rugged areas as long as possible and generally experience fewer losses to mountain lions. Those without lower pastures experience greater losses of calves to mountain lions.

We believe that mature male mountain lions, rather than females and immatures, caused most of the livestock losses. During the study and statewide since 1990, females were killed in depredation control cases only during periods when small calves were abundant, and only 1 mountain lion <24 months of age was killed in connection with a depredation case (Cunningham et al. 1995). Although males are easier to catch than females (Anderson 1983), current strict controls on snaring and allowing dog hunting only in the vicinity of the kill increase the chance of killing the offending animal.

Anderson (1983) reported that male mountain lions weighed approximately 1.4 times more than females. Iriate et al. (1990) found that there was a positive correlation (r = 0.875) between mountain lion body size and prey size selected. Kruuk (1986) reported that felids are strictly carnivorous and select prey commensurate with their own body size. If mature males killed most of the livestock in this study, then our estimates of potential livestock losses to females with kittens were probably high. Also, additional bias may have occurred because we restricted scat collections to scats >30 mm in diameter; such scats may have been more representative of large lions. Regardless, our estimates indicate the potential for large economic losses from mountain lion predation.

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Is supplementation justified to compensate pastoral calves for milk restriction?

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Abstract

Competition for milk between calves and pastoral herders may reduce weaning weights, retard growth, and delay puberty in cattle. Calf supplementation could over-ride such effects and improve pastoral economies. To examine these issues in semiarid Ethiopia, 266 Boran calves (Bos indicus) were used in a 2 X 3 plus 1 factorial design contrasting graded levels of supplemental alfalfa hay (i.e., Medicago sativa L. with mean intakes of 0, 344, and 557 g head⁻¹ day⁻¹ on a DM basis) and supplemental water (i.e., with mean intakes of 0 and 3.8 liters head⁻¹ day⁻¹). The trial was repeated for animals born in 2 consecutive years. Treatments occurred over a background of simulated traditional management in which calves had limited access to grazing and water and were allowed to suckle about two-thirds of their dams' daily milk yield. Traditionally managed controls received no supplements while other (positive) controls received no supplements but had greater access to milk. After 10 months of treatment calves were weaned and monitored. Supplementation with the high level of hay plus water markedly enhanced (P<0.01) all productive features of calves at weaning compared to traditionally managed controls, and was an effective substitute for milk forgone in both years. Despite high variability in milk intake, access to supplements, and weaned body size as calves, all male cattle converged in liveweight and other productive features by 3.5 years of age, largely due to compensatory growth of traditionally managed controls. Heifers also converged in various attributes at maturity, but those which had received hay plus extra water as calves still conceived 2.6 to 4.3 months earlier (P<0.05) than traditionally managed controls. We concluded that supplementation with hay and water can indeed compensate a young calf for typical levels of milk restriction here. Carry-over effects, however, were insufficient to justify large investments in supplementation consid-

Resumen

La competencia por leche entre becerros y los pastores de sistemas pastoriles puede reducir los pesos al destete, retardar el crecimiento y retrasar la pubertad del ganado. La suplementación a los becerros puede anular o aminorar tales efectos y mejorar las economías pastoriles. Para examinar estos problemas en la Etiopía semiárida, se utilizaron 266 becerros Boran (Bos indicus) en un diseño factorial de 2 x 3 mas 1 para contrastar niveles graduales de suplementación de alfalfa (Medicago sativa L. con consumos medios de 0, 344, y 557 g cabeza⁻¹ dia⁻¹ en base a materia seca) y agua suplementaria (con consumos medios de 0 y 3.8 litros cabeza⁻¹ dia⁻¹). El ensayo se repitió para animales nacidos en 2 años consecutivos. Los tratamientos se diseñaron basado en antecedentes de un manejo tradicional simulado en el cual los becerros tenían acceso limitado a apacentar y al agua y se les permitió amamantar aproximadamente dos terceras partes de la producción diaria de leche de sus madres. Los controles fueron animales que recibieron el manejo tradicional sin recibir suplemento, mientras otros animales control (positivo) no recibieron suplemento pero tuvieron un mayor acceso a la leche. Después de 10 meses de tratamiento los becerros fueron destetados y monitoreados. La suplementación con un alto nivel de heno mas agua incremento marcadamente (P<0.01) todas las características productivas de los becerros al momento del destete en comparación con los becerros que recibieron el manejo tradicional (control) y esta suplementación fue un substituto efectivo de la leche de la que fueron privados los animales en ambos años. A pesar de la alta variabilidad en el consumo de leche, acceso a suplementos y tamaño corporal de los becerros destetados, a los 3.5 años, todos los machos fueron similares en peso vivo y otras características productivas. Esto debido principalmente al crecimiento compensatorio de los becerros que recibieron el manejo tradicional (control). Al llegar a la madurez, las vaquillas también fueron similares en varios atributos, pero aquellas que recibieron heno mas agua extra cuando eran becerras concibieron de 2.6 a 4.3 meses antes de las manejadas tradicionalmente. Concluimos que la suplementación con heno y agua puede compensar a los becerros jóvenes las restricciones típicas de leche a las que se someten. Sin embargo, los efectos totales fueron insuficientes para justificar las grandes inversiones en suplementación considerando los altos riesgos inherentes de la producción y tradiciones de mercadeo de animales maduros.

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ering the high inherent risks of production and traditions of marketing mature animals.

Key Words: Cattle nutrition, compensatory growth, puberty, seasonal environments, watering frequency, Borana pastoralists, Ethiopia.

Traditional African pastoralists rely on milk from livestock as their dietary mainstay. In cattle production systems pastoralists may take up to 65% of total milk yield, with the remainder left for calves (Dahl and Hjort 1976, Holden et al. 1991). It has been speculated that competition between calves and people for milk is a major contributor to lower weaning weights, stunting, and delays in time to puberty for cattle (Dahl and Hjort 1976, Waters-Bayer 1988, Preston 1989). Given that reliance on milk by pastoralists is unlikely to change, it has been hypothesized that a major production intervention would be to compensate calves for nutrients lost as a result of milk restriction. This strategy could have major implications for improving animal production if carry-over effects occurred as sustained improvements in mature weights and reductions in time to puberty for heifers (Cossins and Upton 1988). Improved nutritional management for calves could be implemented using cutand-carry feeding with improved forages and perhaps additional water in semiarid, pastoral production systems.

The core objectives of this work were to experimentally test hypotheses that supplementation of nursing calves with alfalfa hay (*Medicago sativa* L.) and/or water could: (1) compensate animals for moderate levels of milk restriction until weaning, and (2) elicit sustained and significant improvements in the subsequent performance of animals up to sexual maturity. A third objective was to use the experimental results to help answer the question of whether or not calf supplementation could be an economically viable means to improve the production system of Borana pastoralists in southern Ethiopia.

Materials and Methods

Study Area

Research was conducted on and near Demballa Wachu ranch, a government-

managed facility on the Borana Plateau 610 km south of Addis Ababa near the Kenya border. A semiarid climate supports perennial savanna vegetation. Annual rainfall averages 500 to 600 mm, with about 60% received during the long rains from April to May and 30% during the short rains from October to November. Rainy periods are separated by a cool dry season (June to September) and a warm dry season (December to March). The dominant ethnic group is the Boran, who are seminomadic and herd cattle. Forage resources are dynamic. Standing crops of herbaceous material can vary from 1.5 to 4.5 tonnes DM ha⁻¹ in dry and wet periods, respectively (Menwyelet 1990). Grazed portions of calf diets, on a DM basis, can have 17% CP and 73% in vitro digestibility in wet periods, and this can decline to <7% CP and 55% digestibility in dry seasons (Unpublished data, Coppock). Calving is highly seasonal, as 60% of births occur during the long rains. This birth peak is accompanied by a flush of milk production which subsequently declines in dry periods. Cattle drink from ponds in rainy periods. In dry periods cattle drink water lifted from deep wells using human labor. Watering frequency for adult cattle can vary from daily (rainy periods) to once every 4 days (at the end of dry periods). Limitations of water and forage, therefore, can constrain animal productivity. Water restriction is permitted by the relatively cool climate and is implemented to minimize labor (Nicholson 1987).

Animals, Diets, and Experimental Design

A growth trial was repeated for 2 groups of local Boran calves (*Bos indicus*) born in consecutive years. Alberro (1986) describes the dual-purpose Boran breed.

Early in 1986, 147 Boran cows in the third trimester of pregnancy were purchased from local pastoralists. Calves were born during March to May, 1986, stratified by sex and birthdate, and randomly allocated among 7 treatments (i.e., n = 21 for year 1). Cows were subsequently re-bred and produced 119 more calves during March to May, 1987. These calves were similarly assigned to the same 7 treatments (i.e., n = 17 for year 2). Local rainfall varied

from 477 mm in the first year (i.e., from April, 1986, through March, 1987) to 300 mm in the second year (i.e., from April, 1987, through March, 1988; Unpublished data, Coppock).

Six of the 7 treatments were incorporated into a factorial design involving supplementation with graded levels of water and alfalfa hay, offered to calves over a background of grazing and restricted access to milk and water. Treatments included 2 levels of supplemental water intake (i.e., ad-libitum and zero) and 3 levels of supplemental hay intake [i.e, ad-libitum (high), 60% of high (medium), and zero]. The high level of hay offered was set at 20% above the previous day's intake while the medium level offered was 60% of the high level. Alfalfa is not traditionally grown in these rangelands. It was selected because its feeding value is well-recognized and it offered the best possibility of eliciting improved cattle performance. Local legumes would have to substitute for alfalfa in new feeding systems for Boran calves (Coppock and Reed 1992). Alfalfa was harvested at 50% flowering, baled after sun drying, and chopped to 25-cm lengths before feeding. Chemical content (DM basis) was 21.2% CP, 65.6% IVDMD, and 42% NDF (Coppock and Reed 1992).

Supplements were offered nightly at 1800 hours in buckets to individual calves under confinement. The 6 factorial treatments were superimposed over a background that simulated traditional calf management from birth to weaning. As with other pastoralists, calf management by the Boran involves intensive hand-rearing, and, except for brief bouts of suckling, calves are kept from their dams to ensure sufficient milk for people. The background in our trial consisted of: (1) individually housing calves at night in small mud-and-thatch huts, (2) limiting daily milk intake for calves to around half of production by allowing calves to suckle 2 of 4 quarters from their dams for a few minutes in the morning and evening, (3) after 2 months of age, allowing calves to graze daily in a calf herd on Pennisetum mezianum Leeke range, and (4) altering watering frequency as water availability changed with season. Background watering frequency for all cows and calves in the trial varied from daily at the height of the rainy season to once every 3 to 4 days at the height of the dry season. A seventh treatment was not part of the factorial design and calves in this group did not receive supplements. The background for the seventh group only differed in that these calves received about 12 hours of continuous access to milk each night because they were corralled with their dams. The seventh treatment was intended to illustrate production potential in the absence of milk competition with people. It would also provide a comparative baseline to quantify whether supplementation could off-set effects of milk restriction.

Supplemental hay or water was first offered when calves began to graze, and supplementation continued until calves were weaned. The treatment period roughly occurred from July through March each year, ending at the onset of the long rains in April of 1987 and 1988. The treatment period thus covered an average of 9 months in 1986–7 (year 1) and 7 months in 1987-8 (year 2). Daily intake of supplements was expected to fluctuate according to seasonal resource dynamics and increase as calves grew. Range forage was senescent for about 5 to 7 months of the treatment periods in 1986–7 and 1987–8, respectively. Forage was green during and briefly after the short rains in October and November of both years.

Hay and water refusals were removed and measured each morning, and intake was estimated by difference. Milk intake was estimated bi-weekly for each calf using a weigh-suckle-weigh method (Coppock and Reed 1992). After suckling each cow was hand-milked and the residual yield was measured. This allowed estimation of total milk yields and percent of total yields received by calves. Background (i.e., non-supplemental) water intake was measured biweekly when all calves drank from known amounts in buckets. Daily water intake was calculated by dividing amounts consumed by watering frequency. Intake of the grazed diet was not measured because logistics in this remote area prohibited fecal collection for large numbers of nursing calves (Coppock and Reed 1992). We therefore focused on an empirical assessment of supplementation effects.

Prior to weaning liveweights and shoulder heights of each calf were measured bi-weekly. Shoulder height was measured from the base of the right front hoof to the top of the scapula.

Shoulder height was used to assess frame size and to derive a weight:height ratio as an index of body condition. After weaning, calves were no longer housed nightly in huts and managed by research staff, but were kept at nearby pastoral encampments. Research animals were maintained under traditional management until females reached puberty 3 to 4 years later. Pastoral management of immatures included corraling for about 12 hours each night and grazing by day in mixed savanna sites. Watering frequency again varied from daily (wet periods) to once every 3 to 4 days (dry periods). Travel to dry-season watering points required 20-km roundtrips from encampments.

At the encampments liveweights and shoulder heights of males were measured monthly. Females were similarly monitored until they were 24 months old, anticipated to be the earliest age at which they could become puberal. At 24 months females were run with breeding bulls at a ratio of 20:1. Every 10 days females were weighed and blood was collected from jugular veins for analysis of plasma progesterone. Blood was centrifuged on site and plasma was stored at -20° C for future analysis using the Enzyme-Linked Immuno Assay (ELISA) technique (Mukasa-Mugerwa et al. 1989) using Ovucheck test kits (Cambridge Veterinary Sciences, UK).

Onset of puberty was verified using 3 complementary methods: (1) animals were observed for successful mounts. recorded as to date and hour, (2) rectal palpations were conducted for pregnancy diagnosis (through detection of asymmetry of uterine horns and presence of enlarged embryonic vesicula) at 40 and 60 days post-mating, and (3) analysis of plasma progesterone was conducted for 4 samples collected within 10 days before and 30 days after an observed mount. Plasma progesterone levels over a threshold of 1.3 ng ml⁻¹ were considered indicative of a significant rise in hormone concentrations associated with estrous and an active corpus luteum. This conservative limit was specifically tailored for our sample population (Personal communication, Mukasa-Mugerwa). The value of 1.3 ng ml⁻¹ represented the upper limit of 2 standard deviations above the mean basal concentrations of plasma progesterone (Unpublished data, Sovani). If the pregnancy diagnosis and progesterone analyses were positive, the date of mating was considered to be the date of puberty. Routine rectal palpations were also conducted for all animals on a monthly basis to provide a backup in case matings were unobserved.

Statistics

Our experiment proceeded smoothly from April 1986, until June 1991. The first group of animals were successfully monitored as planned. The trial was scheduled to end by August 1991, after the second group of heifers would have all become puberal. Regional insecurity associated with an overthrow of the central government, however, required that work be abruptly terminated in mid-1991. This meant we had to use a piecemeal approach for data analysis given that the first group of animals had been fully evaluated and many in the second group had not. For example, because most heifers in the second group had not been observed to reach puberty, only reproductive data from the first group of heifers were analyzed. The main analyses included factorial ANOVA to assess: (1) effects of birth year, hay level, and water level on liveweight, shoulder height, and weight:height ratio for calves at weaning as well as average daily gain (ADG) and total gain from birth to weaning, (2) effects of birth year, hay level, and water level on liveweight, shoulder height, and weight:height ratio for the first group of heifers at puberty, as well as on ADG and total gain for these heifers from weaning to puberal age, and (3) effects of the same factors on the same response variables as just mentioned in (2), but using a terminal age of 3.5 years for the second group of heifers and both groups of males, with sexes analyzed separately. Other factorial ANOVA were used to assess patterns of hay, water, and milk intake of calves during treatment periods to confirm that the trial was adequately implemented and detect interactions among dietary components and year. Factorial ANOVA were also used to examine ancillary features of the trial such as total milk yield of cows, percent of total milk yield consumed by calves, background and total water intake, etc. Simple linear regression was used to calculate ADG per head and to correlate hay intake with total water intake for calves in each birth year. An ANOVA was used to contrast mean production responses of animals from each of the 6 factorial treatments with those from animals in positive control groups for both years. These analyses were conducted to evaluate responses from birth to weaning and weaning to a terminal age of 3.5 years. All ANOVA employed leastsquared means (SAS 1987) and milk intake (ml kg LW^{0.73}) was used as a covariate in ANOVA when positive controls were omitted. Variation among means was interpreted as significant when P<0.05. Dunnett's procedure (Day and Quinn 1989) was used to make 6 planned comparisons between the positive control group and each of the 6 factorial treatments in both years. Contrasts for linear trend were used to examine main effects of hay feeding level when higher-order interactions were absent (Winer et al. 1991).

Results

Trial Implementation

Intakes of supplements and milk by calves according to factorial treatment are illustrated in Table 1. There were some significant interactions involving year and intake of water, hay, and milk that merit brief review. It is useful to recall that year 1 had nearly 60% higher rainfall than year 2, and this had a marked influence on most aspects of the trial. Compared to year 1, the relative dryness of year 2 reduced the time that green forage was available for cows or calves and reduced availability of drinking water. Calves therefore tended to consume more supplements, and less milk, in year 2 than year 1.

Averaged across water levels and years, hay DM intake averaged 344 and 557 g head⁻¹ day⁻¹ for the medium and high levels offered, respectively (Table 1). Hay intake was affected by year and showed an interaction with supplemental water (both at P=0.0001). Averaged across the 2 levels of hay offered, calves ate 307 versus 595 g head⁻¹ day⁻¹ in year 1 and 2, respectively. Compared to year 1 and averaged across water levels, hay intake for animals on the medium level in year 2 increased by 103% from 227 to 462 g head⁻¹ day⁻¹ while hay intake for animals on the high level increased in year 2 by 87% from 387 to 727 g head⁻¹ day⁻¹. Calves in year 1 that received supplemental water ate 27% more hay than those which did not receive supplemental water (i.e., 271 versus 343 g head⁻¹ day⁻¹). In year 2 calves which received supplemental water ate 20% more hay than those which did not receive supplemental water (i.e., 541 versus 649 g head⁻¹ day⁻¹). Linear regression results for year 2 indicated that hay DM intake (y) in g head⁻¹ day⁻¹ was related to total water intake (x) in ml head⁻¹ day⁻¹ by the equation y = 0.036x + 322.8 (P = 0.0062; r² = 0.11; df = 66). No such relationship, however, was apparent for year 1 (P = 0.23).

Intake of supplemental water was 25% higher in year 2 compared to year 1 overall (Table 1). There was also a significant hay x water x year interaction (P < 0.001) indicating that calves on the high level of hay drank relatively more supplemental water than other groups, especially in year 2. In wetter year 1, targeted calves consumed an average of 3.2 liters head⁻¹ day⁻¹ of supplemental water. This increased intake of water 2.7-fold to 5.1 liters head⁻¹ day⁻¹ from a

background of 1.9 liters head⁻¹ day⁻¹ (not tabulated). In drier year 2, targeted calves consumed an average of 4.0 liters head⁻¹day⁻¹ of supplemental water. This increased intake of water 3.5-fold to 5.6 liters head⁻¹ day⁻¹ from a background of 1.6 liters head⁻¹ day⁻¹.

There were main effects of birth year on calf age at weaning, total milk yield of cows, and daily and total milk intake for calves (all at P < 0.01). Weaning age for the first and second groups of calves averaged 324 and 270 days, respectively. Daily milk intake by calves varied from an average of 1.12 to 1.05 liters head⁻¹ day⁻¹ in years 1 and 2, respectively. Daily milk intake exhibited a significant hay x water interaction (P = 0.002); milk intake was higher for traditionally managed controls over both years (Table 1). Total milk intake for calves varied from 363 to 283 liters head⁻¹. Total milk yield (i.e., intake plus offtake) averaged 1.79 to 1.67 liters cow⁻¹ day⁻¹ in years 1 and 2, respectively, or a total yield of 580 to 472 liters cow⁻¹ lactation⁻¹. Calf milk intake averaged 67% of total yield with no effect of year (P =0.77). For supplementation to compensate calves for milk restriction it would have to offset foregone milk volumes ranging from 189 to 217 liters head⁻¹ over the 2 years.

Treatment Responses: Birth to Weaning

The year x hay x water interaction (P = 0.0001) for weaning weight is shown in Figure 1; this primarily illustrates the effect of supplemental water in allowing animals to better utilize hay in both years. One source of the interaction of feeding treatment with year was annual

Table 1. Average daily intake ($\bar{x}\pm$ SE) of supplemental hay (g head⁻¹ day⁻¹ on a DM basis), supplemental water (liters head⁻¹ day⁻¹), and milk (liters Kg LW^{-0.73} day⁻¹) for calves in 6 factorial treatments over 2 years¹.

					Sup	plemental Hay	Level			
			Zero			Medium		High		
Year	Supplemental water?	Hay	Water	Milk	Hay	Water	Milk	Hay	Water	Milk
		(g head ⁻¹ day ⁻¹)	(liters head ⁻¹ day ⁻¹)	(liters kg LW ^{-0.73} day ⁻¹)	(g head ⁻¹ day ⁻¹)	liters head ⁻¹ day ⁻¹)	(liters head ⁻¹ LW ^{-0.73} day ⁻¹)	(g head ⁻¹ day ⁻¹)	(liters head ⁻¹ day ⁻¹)	(liters kg LW ^{-0.73} day ⁻¹)
1	No	0	0	1.3±0.07	207±3	0	1.0±0.07	333±5	0	1.1±0.07
	Yes	0	3.1±0.02	$0.9{\pm}0.08$	245±5	3.1±0.01	1.1 ± 0.08	441±4	3.5±0.01	1.2±0.09
2	No	0	0	1.3±0.07	460±4	0	1.0±0.09	621±5	0	0.9±0.09
	Yes	0	3.5±0.02	0.9±0.09	464±3	3.9±0.03	0.9±0.09	833±5	4.7±0.03	1.0±0.09

¹Based on n = 21 or 17 calves per treatment in years 1 and 2, respectively. Intake of supplements was measured daily while milk intake was measured bi-weekly. A seventh treatment of calves served as a "positive" control group. Calves in this treatment received greater access to milk but no supplemental hay or water. Milk intake was not measured for the seventh treatment because the calves had continuous access to their dam's milk overnight.



Fig. 1. Interaction of birth year, hay feeding level, and watering level on weaning weights of Boran calves (both sexes combined; P = 0.0001). The medium level of alfalfa hay intake (DM basis) averaged from 227 to 462 g head⁻¹ day⁻¹ in 1986–7 and 1987–8, respectively. The high level of alfalfa hay intake averaged from 387 to 727 g head⁻¹ day⁻¹ in 1986–7 and 1987–8, respectively. Intake of supplemental water averaged from 3.2 to 4.0 liters head⁻¹ day⁻¹ in 1986–7 and 1987–8, respectively.

variation in the relative impact of treatments compared to traditionally managed controls. For example, the water plus high hay treatment yielded weaning weights 31% higher than those of the controls in the first year (i.e., 108 versus 82 kg head⁻¹); in the second year this difference increased to 63% (i.e., 80 versus 49 kg head⁻¹). Other response variables exhibited qualitatively similar interactions and these data are reported in Table 2. Compared to the respective, traditionally managed controls in successive years, the water plus high hay treatment yielded ADGs from 38 to 138% higher, total gains from 41 to 108% higher, shoulder heights from 4 to 6% higher, and height:weight ratios 25 to 54% higher.

For animals born in year 1, the productive performance of positive controls (i.e., those which received over-night access to milk) exceeded that for all groups except those which had received the medium or high level of hay plus extra water (Table 3). For animals born in year 2, the performance of positive controls exceeded that for all groups except the one which received the high level of hay plus water. These results are interpreted to indicate that supplementation with hay and water indeed helped calves fully compensate for milk restriction. In the first year 116 kg of hay plus 924 liters of water helped offset 217 liters of milk foregone per calf. In the second year 175 kg of hay plus 987 liters of water helped offset 189 liters of milk foregone per calf.

Treatment Responses: Weaning to Maturity

Males

Overall, main effects of birth year had the most pervasive effects on growth features for males from weaning to 3.5 years of age (Table 4). Compared to males born in the second year, those born in the first year had growth rates that were 14% higher, with an advantage in total gain of 8%. At 3.5 years of age males born in the first year were 20% larger in weight and 9% taller at the shoulder compared to those born in the second year.

Main effects of hay or water supplementation were not significant for liveweights of males at 3.5 years of age (P>0.18). There was an interaction, however, of water x hay for liveweights of males at 3.5 years (P = 0.04). We interpreted this pattern to suggest that ani-

Table 2. Interaction of birth year with level of hay and water supplementation on calf growth features ($\overline{x\pm}SE$) from birth to weaning in 6 factorial treatments.

0 1	, a				0	1 17 .				
Supplemen	itation Group			Growth Feature						
		Average I	<u>Daily Gain</u>	Tota	l Gain	<u>Shoulde</u>	er Height	Weight:Sh	oulder Height	
Water level	Hay Level	1986–7	1987–8	1986–7	1987–8	1986–7	1987–8	1986–7	1987–8	
		(g head	$(g head^{-1} day^{-1})$ (kg head^{-1})		(c:	cm head ⁻¹) ¹ [(kg		:cm) head ⁻¹] ¹		
No	Zero	193±9.6	93±10.4	62±3.7	28±4.0	93±1.1	87±1.2	0.88±0.03	0.56±0.03	
No	Medium	199±10.5	140±13.8	64 ± 4.0	39±5.3	93±1.2	88±1.6	0.89 ± 0.03	0.68±0.04	
No	High	217±10.7	158 ± 13.8	70 ± 4.1	43±5.3	93±1.2	88±1.6	0.97 ± 0.03	0.71 ± 0.04	
Yes	Zero	209±11.5	140±12.9	66±4.4	38±4.9	92±1.3	89±1.5	0.93±0.04	0.67±0.04	
Yes	Medium	261±10.9	168±12.1	81±4.2	43±4.7	95±1.2	89±1.4	1.00 ± 0.03	0.72±0.04	
Yes	High	266±11.3	222±11.8	88±4.3	57±4.5	97±1.3	92±1.3	1.10±0.03	0.86±0.04	
F-test probability										
for 3-way in	nteraction ²		***	:	**		**		**	

,*Significant at the 0.01 and 0.0001 levels respectively.

¹Measurements taken at weaning.

²Where n = 38 calves per treatment over 2 years, with 224 error degrees of freedom in each ANOVA.

Table 3. Growth features (\bar{x} ±SE) from birth to weaning for cavles in "positive" control groups having overnight access to their dam's milk¹.

				Growth Feature			
Birth Year	n	Birth Weight	Weaning Weight	Average Daily Gain	Total Gain	Shoulder Height	Weight:Shoulder Height
1986–7	21	(kg head ⁻¹) 19±1.4	(kg head ⁻¹) 111±7.8	(g head ⁻¹ day ⁻¹) 253±20	(kg head ⁻¹) 97±7.9	(cm head ⁻¹) 99±2.4	[kg:cm)head ⁻¹] 1.10±0.06
Dunnett's test p positive control	robability of the versus:						
High hay plus	water	NS	NS	NS	NS	NS	NS
Medium hay p	lus water	NS	NS	NS	NS	NS	NS
All other facto	rial treatments	NS	**	**	**	**	**
1987–8	17	22±0.9	85±5.3	201±14	63±5.4	98±1.6	0.88 ± 0.04
Dunnett's test p positive control	robability of the versus:						
High hay plus	water	NS	NS	NS	NS	NS	NS
All other facto	rial treatments	NS	**	**	**	**	**

**Significant at the 0.01 level using the 2-tailed Dunnett's procedure.

¹To compare means with those of respective factorial treatments also see Table 1.

²Where Dunnet's procedure was used for pre-planned comparisons between the positive control and the response from 6 factorial treatments in each year. The high hay plus water group received 3.5 to 4.7 liters head⁻¹ day⁻¹ of supplemental water and 441 to 833 g head⁻¹ day⁻¹ of supplemental hay (DM basis) during years 1 and 2, respectively. The medium hay plus water group received 3.1 to 3.9 liters head⁻¹ day⁻¹ of supplemental water and 245 to 464 g head⁻¹ day⁻¹ of supplemental hay (DM basis) during years 1 and 2, respectively.

mals which had received supplemental hay and supplemental water as calves achieved higher liveweights at 3.5 years of age compared to those which had only received supplemental hay (Fig. 2). Another notable result was the trend for traditionally reared controls to have similar mean liveweights at 3.5 years of age compared to animals in the high hay plus water treatment; both of these groups had mean liveweights at 3.5 years of age

230

220

210

200

190

Liveweight (kg head⁻¹)

that tended to exceed those found for animals in the other 4 treatments.

Averaged over both birth years, the maximum range among treatments in terms of weaning weights for males was 28 kg head⁻¹ [i.e., 66 kg head⁻¹ (controls) versus 94 kg head⁻¹ (water plus the high level of hay), a relative increase of 42%]. By 3.5 years of age, however, males from the same 2 treatments, averaged over both years, exhibited no sig-

High



Females

The total number of heifers born in the first year was 67 across 7 treatments. Fifty four (81%) had become pregnant before the trial ended. Forty-two percent of heifers conceived at their first behavioral estrous. In 48% of the first behavioral estrouses, however, animals were physiologically non-puberal according to analysis of their plasma progesterone levels, which were <1.3 ng ml⁻¹. These animals tended to be younger and lighter in liveweight than those which exhibited sexual behavior that coincided with plasma progesterone concentrations >1.3 ng ml⁻¹ (Unpublished data, Sovani). Mating activity was a function of nutritional plane and was thus highly seasonal. Ninety-six percent of conceptions occurred during rainy or post-rainy periods. These were divided between the short and long rains in a bimodal pattern. Forty-two percent of all conceptions occurred during or just after the short rains in November and December, while 54% occurred during or just after the long rains in March through June.

Heifers first began to get pregnant during the short rains (October to November) of 1989, when some were



Medium

Hay Level Offered

 \rightarrow Supplemental watering

Traditional watering

Zero

Table 4. Main effects of birth year on growth features of male Boran cattle from weaning to 3.5 years of age as averaged across 6 factorial treatments

	Birt	h Year ¹	
Growth Feature	1986–7	1987–8	F-Test Probability
Average Daily Gain (g head ⁻¹ day ⁻¹)	151	132	**
Total Gain (kg head ⁻¹)	144	133	*
Weight at 3.5 years (kg head ⁻¹)	236	196	***
Shoulder Height at 3.5 years (cm head ⁻¹)	124	114	***
Weight:Shoulder Height [(kg:cm)head ⁻¹)	1.90	1.72	***

*,**,***Significant at the 0.05, 0.01, and 0.0001 levels respectively.

¹Where n = 63 males born in 1986–7 and n = 51 born in 1987–8, with 98 error degrees of freedom in the ANOVAs. The milk intake covariate was not significant for any case (P>0.10).

40 months old. Following a period of no sexual activity during the subsequent warm dry season, the next (and last) wave of pregnancies for the first group of heifers occurred during the long rains (April to May) of 1990, when the remaining animals averaged 48 months of age. The overall mean age (\pm SE) at conception was thus 43.4 \pm 1.5 months (or 3.6 years). The mean liveweight (\pm SE) at conception was 217 \pm 7.1 kg head⁻¹, roughly 96% of the mature weight for females (i.e., 225 kg head⁻¹; Alberro, 1986).

It was expected that heifers which had been born in the second year would begin to get pregnant starting during the short rains (October–November) of 1990. These rains, however, were sparse. Animals remained on a low plane of nutrition and few conceptions were recorded (Unpublished data, Sovani). The main wave of pregnancies for the second cohort was thus expected to occur in April to May of 1991, but this was when security collapsed and the trial had to be terminated.

Results from ANOVA which analyzed responses from weaning to puberty for females which had been born in the first year and conceived are shown in Table 6. These animals had exhibited the same interaction response to hay and water treatment in terms of weaning weight as previously reported; the group which received water plus the high level of hay exceeded the controls by 59% (i.e., 127 versus 80 kg head⁻¹). At puberty, however, these weight differences had largely disappeared. Groups also tended to be similar in terms of shoulder height and weight:height ratio at puberty.

That weight at puberty converged among treatments was not due to compensatory growth per se as observed for the males. In contrast to the males, which were analyzed at a common chronological age, time to puberty varied for females due to different factor levels and this complicated interpretation of results (Table 6). Heifers that had received extra water as calves became puberal 2.7 months earlier on average than those under traditional watering (i.e., 42.5 versus 45.2 months of age, respectively). Heifers which received the high level of hay became puberal 2.6 and 4.3 months earlier than those which received the medium and zero levels of hay, respectively (i.e., means of 41.6, 44.2, and 45.9 months).

Because of treatment variation in puberal age, groups differed in total gain from weaning to puberty, but did not differ in terms of ADG. Animals thus had to attain a similar target weight to become puberal, and this took different lengths of time depending on treatment. Total gain needed to achieve puberty after weaning varied in relation to

Table 5. Main effects of hay feeding level on growth of male Boran cattle from weaning to 3.5 years of age as averaged for animals across 6 factorial treatments born in 2 successive years.¹

	Hay Fee	eding Level ²		F-Tes	t Probability
Growth Feature	Zero	Medium	High	ANOVA	Linear Trend ³
Average Daily Gain (g head ⁻¹ day ⁻¹)	153	142	129	*	*
Total Gain (kg head ⁻¹)	151	139	127	*	*

*Significant at the 0.05 level.

¹Where each tabulated entry is the mean of n = 38 animals. Each ANOVA was based on 98 error degrees of freedom. The milk intake covariate was not significant for either case (P>0.10). ²Where the medium level consumed was 227 and 462 g head⁻¹ day⁻¹ and the high level was 387 and 727 g head⁻¹ day⁻¹,

"Where the medium level consumed was 227 and 462 g head" day" and the high level was 387 and 727 g head" day", in the first and second years, rspectively, on a DM basis. ³Linear contrast. whether animals received hay or water as calves (Table 6). Animals which did not receive extra water had to gain 128 kg head⁻¹, 16% more than those which had not received extra water (i.e., 110 kg head⁻¹). Puberty among animals which did not receive extra water was achieved over a period of time which was 6% longer than those which received extra water. Animals which did not receive hay had to gain 126 kg head⁻¹ after weaning to become puberal. This exceeded the gain needed by animals which received the high level of hay by 15% (i.e., 109 kg head⁻¹). Animals which did not receive hay, however, took 10% longer to achieve puberty.

Despite that an analysis of puberal features could not be conducted for females from the second cohort, data collected from weaning to termination of the trial allowed another factorial analysis of growth patterns from weaning to a common minimum age of 3.5 years for these animals (n = 8 to 9 per)treatment). Patterns again demonstrated convergence among treatments in liveweight, shoulder height, and weight:height ratios (all at P>0.05; not illustrated). This occurred even though hay and water treatments resulted in greater impacts on animals relative to respective controls in the second year compared to the first (Fig. 1).

Contrasts of Factorial Treatments with Positive Controls at Maturity

An ANOVA was conducted across all 7 treatments to analyze effects of birth year and treatment on total liveweight gain and ADG from birth to 3.5 years of age, and on liveweight, shoulder height, and weight:height ratio at 3.5 years of age. Birth year was significant (P<0.005) for all response variables. Considering the period from birth to 3.5 years of age, animals born in wetter year 1 had 25% higher mean (\pm SE) total liveweight gains (i.e., 204 ± 3.6 versus 163 ± 3.3 kg head⁻¹) and 26% higher mean ADG (i.e., 157 ± 3 versus 125 ± 3 g head⁻¹ day⁻¹). At 3.5 years of age animals born in wetter year 1 had a 21% higher mean liveweight (i.e., 223 ± 3.7 versus 185±3.4 kg head⁻¹), 10% greater mean shoulder height (i.e., 124 ± 1 versus 114 ± 1 cm head⁻¹), and a 12% greater weight: height ratio (i.e., $1.80 \pm$ 0.02 versus 1.62 ± 0.02 kg:cm head⁻¹). In contrast, however, there were no sig-

Table 6. Growth features from weaning to puberty, and time to puberty, for Boran heifers born in 1986 as influenced by supplementation in 6 factorial treatments.¹

						Feature			
Supplementatio	on Group								
Water Level	Hay Level	Weaning Weight	Puberal Weight	Total Gain	Average Daily Gain	Shoulder height ³	Weight:Height ³	Time:Weaning to Puberty	Age at Puberty
		(kg head-1)	(kg head ⁻¹)	(kg head ⁻¹) ²	$(g head^{-1} day^{-1})^2$	(cm head-1)	[kg:cm)head-1]	(days head-1)	(months head ⁻¹)
No	Zero	80±6.0	213±7.4	133±7.2	119±7.6	123±2.1	1.7±0.05	1,129±53.0	48.1±1.61
No	Medium	84±5.9	211±7.2	127±7.0	129±7.4	120 ± 2.0	1.7±0.05	1.009 ± 52.1	43.9±1.62
No	High	88±4.9	212±6.0	124±5.9	124±6.1	119±1.7	1.8 ± 0.04	993±43.3	43.7±1.31
Yes	Zero	91±6.3	210±7.7	119±7.5	125±7.9	122 ± 2.2	1.7±0.05	973±55.7	43.7±1.73
Yes	Medium	112 ± 5.6	230±6.9	118±6.7	121±7.0	124±1.9	1.8±0.05	974 ± 49.4	44.5±1.54
Yes	High	127±5.9	220±7.3	93±7.1	108 ± 7.5	128±2.1	1.7±0.05	872±52.4	39.5±1.62
F-test probabil	ity:								
Hay	•	**	NS	*	NS	NS	NS	NS	*
Water		***	NS	**	NS	*	NS	**	*
Hay x Water		*	NS	NS	NS	NS	NS	NS	NS
Linear Trend (I	Hay)	_		_	_	_	_	_	NS

*******Significant at the 0.05, 0.01, and 0.0001 levels respectively.

¹Where n = 8 to 9 animals per treatment. Entries are $\bar{x}\pm SE$. ANOVAs were based on 45 error degrees of freedom. See text for treatment details. The milk intake covariate was not significant in any case (P>0.13).

²From weaning to puberty.

³Measurements taken at puberty.

nificant effects of treatment on mean total liveweight gain (P = 0.48; range 174 ± 5.9 to 199 ± 10.7 kg head⁻¹), mean ADG (P = 0.35; range 134 ± 4 to $151 \pm$ 8 g head⁻¹ day⁻¹), or attributes at 3.5years including mean liveweight (P = 0.14; range 195 \pm 6.0 to 221 \pm 10.9 kg head-1) and mean weight:height ratio (P = 0.55; range: 1.65 ± 0.04 to 1.75 ± 0.07 kg:cm head-1). The only persistent effect of treatment was on shoulder height, which was significantly highest in the positive control group (P = 0.005). Averaged over both years, animals which received over-night access to milk as calves had a mean shoulder height of 126 ± 2.4 cm head⁻¹. This exceeded means for the 6 factorial treatments by an average of 7%. The range of mean shoulder heights for the factorial treatments was 116 ± 1.4 to 121 ± 1.2 cm head⁻¹. Overall, we interpret these results to indicate that effects of birth year on cattle growth were much more persistent compared to those from treatments. This illustrates the powerful role of environment on cattle productivity in this system.

Discussion

Cossins and Upton (1988) used analytical modeling to evaluate potential economic impacts of improved calf management in the Borana pastoral system. They estimated that if supplemental forage could fully compensate calves for milk taken by people, it could result in a 34% gross increase in the cash value of the lifetime output per cow. It was assumed that major impacts of supplementation would include a doubling of weaning weight from 47 to 94 kg head⁻¹ and a reduction in time to puberty for heifers from 4 to 3 years. This analysis supported the theory that lifetime performance of cattle in pastoral systems is significantly limited by competition between cattle and people for milk (Dahl and Hjort 1976, Pratt and Gwynne 1977, Wagenaar et al. 1986, Waters-Bayer 1988).

We interpret our results, however, to basically refute the proposition that enhancing calf growth via supplementation is an appropriate means to transform this particular pastoral economy. This perspective is based on a synthesis that includes empirical results from this trial, an improved understanding of pastoral production goals, and consideration of how risk and uncertainty affect production decisions. These are all considered further below.

Short-Term Effects: Birth to Weaning

Our trial results supported the hypothesis that supplementation could compensate calves in terms of weaning weight for a moderate loss of milk, but it is notable that extra water was required in addition to high-quality forage to achieve this effect. Traditional watering practices thus appear to limit dry matter intake for such calves, as noted in general for pastoral livestock in Africa by King (1983). Research intended to enhance livestock performance in Africa often has a sole focus on forage resources. Our findings indicate that benefits from improved forages would not be realized in a dry region such as this if watering constraints were ignored. Including water supplementation in our trial was therefore extremely useful.

Given our experimental results, an important question is whether calf supplementation should be promoted here or in similar systems in attempts to markedly improve weaning weights. This could be a valid point of intervention if higher weaning weights were an important production goal and offered an economic advantage to the producers. We have eventually learned, however, that neither of these conditions are generalizable to the Borana pastoral system. The critical point is that the traditional production rationale in the Borana system is not the same as that of a western cow-calf operator (Coppock 1994). In the Borana system overhead costs of production are relatively low, immature stock are commonly retained by producers to build-up herds, and mature cattle over 6 years years of age are the preferred animal for most households to sell. In contrast to selling mature stock, selling immatures is more common among poorer households who are forced to sell immatures because they have small and less-diverse inventories of animals and a chronic need to frequently buy cereal grains or other nonpastoral foods. Selling a mature male not only provides money for a household to buy various commodities, but also allows the seller to use the "change" to buy a couple replacement calves. The sale of a mature male thus simultaneously contributes to procurement of basic necessities as well as traditional values of herd building.

If we assumed higher weaning weights were an important production and marketing goal, could it be profitable to supplement calves? Assuming input costs of US \$0.15 per kg DM of legume hay and US \$0.03 per 10 liters of water based on labor profiles and other criteria (Mulugeta 1990), and considering calf performance in the high hay and water treatment over both years, 28 kg of extra weight was produced per calf as a result of 146 kg of hay (valued at US \$2.86) and 956 liters of water (valued at US \$21.90). The selling price for fattened calves is US \$1.00 per kg liveweight (Unpublished data, Coppock). A net return of US \$3.24 per calf does not appear very profitable, and importantly, the costs estimated by Mulugeta (1990) did not incorporate the substantial risks and problems of acquiring sufficient quantities of supplements. The true costs of supplementation were probably underestimated, further reducing profit.

We speculate that in contrast to improving weaning weights, supplementation to mitigate calf mortality under severe milk-restriction regimes is a more relevant production objective. This would be especially important to poorer households which have lower ratios of milking cows per person compared to middle-income or wealthier households. The poor tend to deprive their calves of milk to a critical extent in order to provide more milk for family members, especially children (Holden et al. 1991, Coppock 1994). Although we do not have empirical data on the amount of supplemental forage or water needed to mitigate calf mortality under extreme cases of milk deprivation, we expect that the benefit/cost ratio would be more favorable compared to using supplementation to stimulate gain. For example, if a female calf can make it to 2 years of age in the Borana system, the likelihood of subsequent survival, and hence benefit of a lifetime of productive output, dramatically increases (Coppock 1994).

Long-Term Effects

Growth Dynamics

Our results falsified the hypothesis that substantial increases in early growth rates and weaning weights would result in sustained increases in liveweight or frame features for these cattle. Regardless of what level of milk, hay, or water animals received as calves, and despite relative differences in weaning weights that exceeded 60% among treatments in some cases, the animals were remarkably similar by 3.5 years of age. Convergence was typically due to compensatory growth of traditionally managed animals. This is consistent with findings elsewhere which indicate that cattle can overcome early nutritional deprivation as calves (Laster et al. 1976, Richardson et al. 1978, Tawonezvi 1989). These authors found that differences in weaning weights of calves due to variable consumption of milk and/or solid foods only persisted from 1.5 to 11 months. This is not to say, however, that permanent stunting from a higher degree of milk restriction could not occur in some cases. Milk provides important bypass nutrients, and if these are severely restricted permanent stunting in cattle can result (Preston 1989).

Time to Puberty

The marked seasonality of conception observed in this study is common in pastoral Africa (de Leeuw and Wilson 1987). That Boran heifers conceived at 96% of mature weight is higher than figures reported elsewhere for Bos indicus (Macfarlane and Worrall 1970, Wilson 1987) or B. taurus (Dobson and Kamonpatana 1986). This suggests that Boran cows achieve physiological and physical maturity at roughly the same time (Fitzhugh 1976). The nonpuberal estruses and prepuberal rises in plasma progesterone levels observed here have been reported elsewhere (Nelsen et al. 1985, Rutter and Randel 1986), and justified use of several puberty detection methods. Bulls were also an important factor underlying seasonal patterns of conception. Bulls typically showed no sexual behavior until they had recovered body condition during wet seasons (Unpublished data, Sovani).

Our results are interpreted to suggest that early supplementation can result in a persistent reduction on time to puberty for heifers, despite convergence among treatments in liveweight and weight:height ratios. We speculate that supplementation resulted in subtle improvements in body condition, undetected by our monitoring system, that predisposed some animals to cycle one rainy season earlier during their puberal year (Mukasa-Mugerwa 1989). Reductions in time to puberty ranged from 2.6 to 4.3 months compared to traditionally managed animals, less than half of the advantage assumed in analyses by Cossins and Upton (1988).

While a reduction in time to puberty of 2 to 4 months would be very significant in western production systems where beef heifers become puberal at 12 to 15 months of age, it is important to once again view the benefits, costs, and risks of intervening in an African context where the typical heifer is sexually mature at 36 to 48 months of age and is reared in a much more challenging environment. One risk to a pastoral producer is the likelihood that hard-won gains in animal productivity due to supplementation investment could be lost in the future due to uncontrollable events. Such events include disease outbreaks, predation, and thievery; even our trial had to be terminated by 1991 because of insecurity. Even if these events could be mitigated, the problem of variable rainfall may be the most insidious. For example, 1 simple way to lose a hardwon, 2 to 4 month advantage in time to puberty is to merely have the first rainy season fail in a heifer's puberal year. As observed in our trial, failure of one rainy season could adversely affect nutrition of heifers and bulls and delay conception until the next favorable rainy period 6 months (or more) later. Another aspect is the often calamitous impact of drought. Herd dynamics in southern Ethiopia indicate that up to 50% of the cows may die every 5 to 8 years, largely due to interactions among stocking rate, rainfall fluctuation, and bottlenecks in regional marketing systems (Coppock 1994). Such a situation clearly mitigates against substantive investments to improve animal productivity over the long term. Such risk perspectives were not incorporated into the deterministic analyses of Cossins and Upton (1988).

Conclusions

Our empirical results indicated that nutritional supplementation could help Boran cattle compensate for moderate levels of milk restriction experienced as calves. Supplemental water was required in addition to legume hay, however, and underscores the crucial role of watering constraints in this and similar systems. The compensatory effect of supplementation was most apparent at weaning, and there was also a slight carry-over effect in terms of a 2 to 4 month reduction in time to puberty for heifers. Most other production features, however, had completely converged by the time animals reached maturity. This was largely due to compensatory growth of control animals. Despite some of these results, further consideration of the rationale and realworld risks of pastoral production has led us to conclude that supplementation to enhance anything but animal survivorship is a highly risky, and a likely wasteful, use of scarce resources. Lowinput management is therefore justified when production risks are high. All things considered, our work also undermines the notion that moderate levels of milk consumption by pastoralists constitutes a significant loss for the animal production system; in our case this was on the order of 189 to 217 liters of milk per calf. Finally, the future risks of losing benefits of past investments in animal production must be considered and incorporated into stochastic economic analyses of production interventions. Such risks are particularly important in traditional pastoral production systems.

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Stream channel and vegetation responses to late spring cattle grazing

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Abstract

A 10-year riparian grazing study was conducted on a cold, mountain meadow riparian system in central Idaho in response to cattle grazing-salmonid fisheries conflicts. Six pastures were established along Stanley Creek to study the effects on riparian habitat of no grazing, light grazing (20-25% utilization), and medium grazing (35-50%) during late June. Stream channels narrowed, stream width-depth ratios were reduced, and channel bottom embeddedness decreased under all 3 grazing treatments as the area responded to changes from heavier historic grazing use. Streambank stability increased and streamside willow communities (Salix spp. L.) increased in both height and cover under all 3 treatments. Plant species richness increased on both streamside and dry meadow areas during the years of grazing and moderate drought. The numbers of species receded to near original levels in the ungrazed and light grazed pastures in 1996, a wet post-grazing year, primarily due to a decrease in forb species. Streamside graminoid height growth was similar among treatments after 1 year of rest. Most measurements of streamside variables moved closer to those beneficial for salmonid fisheries when pastures were grazed to 10 cm of graminoid stubble height; virtually all measurements improved when pastures were grazed to 14 cm stubble height, or when pastures were not grazed. Many improvements were similar under all 3 treatments indicating these riparian habitats are compatible with light to medium late spring use by cattle.

Key Words: riparian, mountain meadow, streambank stability, width/depth ratio, willow, species richness, salmonid, fisheries, livestock management

Riparian areas are among the most important features of natural landscapes. Their biotic productivity and diversity stand out within the surrounding mosaic of terrestrial habitats (Kondolf et al. 1996). They typically function to moderate flood intensity, store water, and maintain water quality by acting as nutrient and sediment sinks (Hawkins 1994). These ecological attributes make riparian areas and the included

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Resumen

Se condujo un estudio de apacentamiento de áreas ribereñas con una duración de 10 años. El estudio se llevó a cabo en la región central de Idaho en un sistema ribereño frío de pradera de montaña y fue motivado por los conflictos surgidos entre el apacentamiento de ganado y las pesqueras de salmones. Se establecieron 6 potreros a lo largo del arroyo Stanley para estudiar los efectos que el no apacentamiento, apacentamiento ligero (20-25% de utilización) y apacentamiento moderado (35-50%) a fines de junio tienen sobre el hábitat ribereño. Los canales del arroyo se estrecharon, las relaciones ancho-profundidad de los arroyos se redujeron y los depósitos en el fondo del canal decrecieron, esto ocurrió bajo los 3 tratamientos de apacentamiento conforme el área cambio de un uso histórico de pastoreo fuerte. La estabilidad del banco del arroyo se incrementó y las comunidades de "willow" (Salix spp. L.) presentes a los lados del arroyo se incrementaron tanto en altura como cobertura, esta respuesta se obtuvo en los 3 tratamientos de apacentamiento. Durante los años de apacentamiento y seguía moderada, la riqueza de especies vegetales se incrementó tanto a lado del arroyo como en las áreas de pradera seca. En 1996, un año húmedo después de la estación de apacentamiento, el número de especies vegetales de los potreros que recibieron apacentamiento ligero o no apacentamiento regresó a niveles cercanos a los originales, esta respuesta se debió principalmente a una disminución de las especies de hierbas. Después de un año de descanso, el crecimiento en altura de las gramíneas de los lados del arrovo fue similar entre tratamientos. Cuando los potreros se apacentaron a 10 cm de altura del rastrojo remanente, la mayoría de las mediciones de las variables tomadas a los lados del arrovo se movieron a niveles cercanos de los que son benéficos para las pesqueras de salmones. Cuando los potreros se apacentaron a 14 cm de altura del rastrojo remanente o no se apacentaron, virtualmente todas las mediciones mejoraron. Muchas de las mejorías fueron similares bajo todos los tratamientos, indicando que estos hábitats son compatibles con el uso ligero o moderado por el ganado durante la primavera.

streams highly valued for many human uses. One of these uses is livestock grazing. Major concerns about the impacts of grazing on riparian areas have been raised in the last 2 decades (Swanson 1988, US GAO 1988, Armour et al. 1994).

In earlier years, livestock grazing practices rarely addressed

Support by personnel of the Sawtooth National Recreation Area and the Sawtooth National Forest made this study possible. Appreciation is expressed to John W. Kinney and various field crew members assisting in field data collection, and to Rodger L. Nelson for instruction and assistance in stream channel measurements. Livestock were provided by the Stanley Basin Grazing Association.

the needs of riparian areas (Winward 1994). Conflicting reports over the effects of livestock grazing on riparian areas have pointed to a critical need to examine grazing practices that can potentially permit livestock production while simultaneously preserving the riparian characteristics needed for wildlife habitat, native fisheries, and water quality (Waters 1995). Despite the need for objective management strategies, most current recommendations for improvement of riparian grazing are based on collective experiences and case studies. Experimental examination of specific management hypotheses has occurred at only a limited number of sites, including locations in Colorado (Schulz and Leininger 1990), Montana (Marlow and Pogacnik 1986), Oregon (Bryant 1985, Green and Kauffman 1995), and Wyoming (Siekert et al. 1985).

The need for more grazing management information has been apparent in the Pacific Northwest as concern for the dwindling numbers of anadromous salmonids heightened riparian habitat issues. A review of the Sawtooth National Recreation Area by the Chief of the Forest Service and representatives of The Wildlife Society, American Fisheries Society, and other concerned parties defined several courses of action to improve fish reproduction and migration, including development of improved riparian grazing systems (Peek and Gebhardt 1980). The present study was initiated in response to the identified concerns about grazing-fisheries conflicts in the Sawtooth National Recreation Area. This study spanned a 10-year period and examined the response of a cold mountain meadow riparian system to 3 intensities of controlled late June cattle grazing.

Study Area

The grazing study was initiated on Stanley Creek, Sawtooth National Recreation Area, Sawtooth National Forest, central Idaho in 1987. The study area is about 6 km northwest of Stanley, Ida., in portions of sections 19, 29, and 30 T11N, R13E (Lat 44°15'46"N, Long 114°59'02''W) where Stanley Creek flows through a broad, flat valley with a westerly aspect at an elevation of 1,950

m. Stanley Creek is a 3rd order, C4 stream (Rosgen 1994). Soils are Typic Cryaquepts formed in alluvium and lacustrine sediments derived from granite. They have moderately slow to moderate permeability. The upper 23 cm is typically a silty clay loam overlying a sandy to coarse sandy clay loam. Below 76 cm the profile contains 60% pebbles, cobbles, and stones (Personal communication, D.R. Gilman). National Weather Service records are incomplete, but annual precipitation during the treatment years (1987–1995) appeared to have been approximately 20-25% below the 389 mm average. This below average precipitation period is referred to as a drought in the current study. The post-grazing year (1996), when final measurements were taken, precipitation was 570 mm or approximately 46% above average. Average temperature during the June grazing period is 11°C; average annual temperature is 2°C (Personal communication, Idaho Climate Services).

The area is representative of the mountain meadows ecosystem in the forest zone of the mountain West containing wet to intermittently wet sites (Garrison et al. 1977). Typical streamside plant species included: Kentucky bluegrass (Poa pratensis L.), tufted hairgrass (Deschampsia cespitosa [L.] Beauv.), water sedge (Carex aquatilis Wahl.), beaked sedge (C. rostrata Stokes), Baltic rush (Juncus balticus Willd.), foxtail (Alopecurus spp. L.), timber danthonia (Danthonia intermedia Vasey), thick-stemmed aster (Aster integrifolius Nutt.), cinquefoil (Potentilla spp. L.), gentian (Gentiana spp. L.), Lemmon's willow (Salix lemmonii Bebb), and Drummond willow (S. drummondiana Barratt). The streamside area, 7% of the pastures (Clary and Booth 1993), was incised an average of 0.38 m below the surrounding drier meadow and averaged 16 m in width.

Idaho fescue (*Festuca idahoensis* Elmer), western needlegrass (*Stipa occidentalis* Thurb.), and mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle) were common in the portion of the area away from the stream. These areas, referred to as the "dry meadow," were typically dry from about mid July into fall, but bog-like areas and other areas of excess moisture were present in all years.

Stanley Creek and the surrounding meadows have had a long history of use

and disturbance by European man. Placer gold was discovered in Stanley Basin in 1863 (Van Noy et al. 1986). Mining in the upper portion of Stanley Creek began in the early 1870's by ground sluicing. Dredge mining was conducted from 1900 to 1914. Various forms of placer mining occurred from 1933 to 1938 (Choate 1962). Obvious signs of mining activity are still present immediately upstream from the study pastures. Other indications are also present that suggest heavy use by early settlers. Water diversion ditches and trail roads are apparent in a number of locations. A log-supported stream crossing is still present within the boundaries of 1 study pasture.

Sheep grazing began by 1879 and up to 200,000 sheep grazed during summers in the Sawtooth Valley, although there is no current sheep use of the study area. Cattle grazing in Stanley Basin apparently started in 1899, but records of grazing use are not available earlier than 1939 and little attention was given to grazing management until the 1970s (Sawtooth mountain area study: history. 1965. Copy on file Sawtooth National Recreation Area, Ketchum, Ida.) (Environmental analysis report: Stanley Basin revegetation and rehabilitation project. 1974. Copy on file Sawtooth National Recreation Area, Stanley, Ida.). Until fenced at the beginning of this study, the study area was grazed as part of the Stanley Basin cattle allotment. Limited utilization records suggested a 60-65% utilization rate of the dry meadow, tufted hairgrass sites, but no information was available on utilization rates for streamside locations (Personal communication, L. Burton). Streamside utilization rates were assumed to have been high because some cattle usually had access to Stanley Creek throughout the summer (Personal communication, B. Webster). No significant utilization by wild herbivores was apparent during the study.

Methods

Field Procedure

Six experimental pastures, 3.7 to 9.0 ha, were established along Stanley Creek in fall 1986 (Fig. 1). Grazing was conducted annually with cow-calf pairs in the last half of June from 1987 to 1995; except for 1993 when concerns



Fig. 1. Layout of experimental pastures on Stanley Creek in central Idaho. Treatments are medium (M), light (L), and no grazing (N). Black area represents the slightly incised stream and streamside area.

about federal listing of chinook salmon as a threatened species precluded grazing. The last half of June corresponded in nearly all years to the period when the dry meadow vegetation had made substantial growth, and yet had sufficient soil moisture remaining to maintain forage succulence. Since the dry meadow pre-study utilization rates of 60-65% exceeded the recommended 55% maximum to maintain healthy tufted hairgrass communities (Reid and Pickford 1946) and the grazing appeared to have negatively impacted the riparian habitats, the target utilization rates on the dry meadow portions of the pastures were 50, 25, and 0% for the medium, light, and no grazing grazing treatments. Two pastures were assigned to each of 3 treatments: medium grazing (average of 2.20 animal unit months [AUM] ha⁻¹), light grazing (average of 1.27 AUM ha-¹), and no grazing. Stocking was adjusted so all pastures were grazed for a similiar period (usually 14 days).

A 4-ha, 100-point sampling grid was established within 5 pastures with interpoint distances of 20 m; the 6th pasture had interpoint distances of 17 m. At each point a 0.25-m² plot was sampled for various vegetation and soil attributes. Distribution of the 100-plot grid between streamside and dry meadow locations varied among pastures because of the variable size and location of the streamside areas. A second set of forty 0.25-m² plots was concentrated near the stream to provide a more detailed sample of the streamside area in each pasture. Analyses were based on 140 plots per pasture (100-plot grid plus 40 additional plots) with 45 to 59 of the plots per pasture sampling the streamside area and 81 to 95 sampling the dry meadow area.

Plant canopy cover, by graminoids, forbs, and shrubs, and litter were visually estimated (Daubenmire 1959); herbaceous plant height was measured in centimeters, and number of species was recorded by plant life form. Plant attributes were determined in each 0.25-m² plot in 1987, 1990, 1994, and 1996. Height of the willow closest to each plot was measured in centimeters at the beginning and at the end of the study (1987 and 1996). Plant community-type classifications were made within a radius of 3 m from each 0.25-m² plot in 1988 and 1996 following the general approach of Tuhy and Jensen (1982). Plant and soil moisture contents and their relationship to grazing distribution on the study area were reported in Clary and Booth (1993).

Percentage utilization to the nearest 5% was determined by visual estimation (Pechanec and Pickford 1937) by graminoid, forb, and shrub categories based on comparison with 6 reference cages per pasture. The cages were relocated at the start of the grazing period each year. Beginning in 1988, mean residual stubble heights were measured to the nearest centimeter immediately after each grazing period. Autumn remeasurements were initiated in 1989 to determine season-end heights.

Thirty-one channel cross-sections were systematically located along the stream within the boundaries of the plot grid in each pasture and measured mid summer in 1986, 1990, 1994, and 1996. Variables measured included wetted width, average wetted depth, bank stability (based on estimated protection from erosion provided by vegetation or by boulders and rubble), bank alteration (based on linear proportion of active banks estimated to be slumped, broken, or eroding), channel bottom embeddedness (rated as the proportion of the average perimeter of individual gravel, rubble, and boulder particles covered by fine (<4.7 mm diameter) sediment), and channel bottom textural composition (Platts et. al 1987, Zweygardt and Buckhouse 1996).

Analyses

Although the pastures appeared to have similar characteristics when fenced; it became apparent that each one was somewhat unique. Therefore, to partially compensate for these initial differences, analyses were based on comparisons between the initial reading for a variable (1986 or 1987) and later readings (1990, 1994, or 1996). Stream profile variables were analyzed as proportional changes because stream channel width and width/depth ratio were physically limited in their potential response. Other variables were analyzed based on numeric differences between initial and later readings.

Variables were transformed as necessary to normalize data distributions. Transformations used were logarithm, square root, and arc sine for continuous variables, counts, and percentages and angles. Average values presented in tables were transformed back into the original data form. Analyses of treatment effects were conducted by Analysis of Variance (ANOVA) using a General Linear Model. Repeated measures analysis was used when data included more than 1 response year. Plant community-type frequency of occurrence was examined by Chi-square analysis. Significant differences among means in the ANOVA tests were identified using a protected Fisher's Least Significance Difference (LSD). Additional T-tests were conducted to determine if responses within individual treatments differed from the initial readings in 1986 or 1987. This was used as an aid in interpretations of treatment trends, even when no significant differences were defined among treatments. Probabilities of 0.05 or less were considered significant in all analyses. The analysis of changes for most data are presented in 2 periods: 1990 and 1994 during the grazed drought years compared with initial year (1986 or 1987); and 1996 the post-grazing, high precipitation year compared with the initial year.

R

Graminoid utilization averaged 35.2% at streamside and 51.8% in the dry meadow for the medium grazing treatment; 21.6% at streamside and 25.0% in the dry meadow for the light grazing treatment. The residual stubble heights for graminoids immediately following grazing were 10.5 cm (4.1 in) at streamside and 7.1 cm (2.8 in) on dry meadow for medium grazing and 14.1 cm (5.6 in) at streamside and 13.4 cm (5.3 in) on dry meadow for light grazing. Seasonend streamside stubble heights were 12.9 cm (5.1 in) for medium, 16.4 cm (6.5 in) for light grazing, and 26.2 cm (10.3 in) for no grazing. These utilization levels were less severe and the season of grazing more restricted than had been the situation on the study site for most of this century.

Stream Channel

Stream Channel Profile and Streambank Ratings

A decrease in stream width occurred under all treatment regimes from 1986 to 1996 (Table 1). The average amount of narrowing was inversely associated with grazing intensity. The change in depth was more erratic among years than the change in width. Depths decreased during the drouthy grazing years, but had increased in the wet posttreatment year. The ungrazed pastures, which displayed the greatest narrowing, showed the greatest increase in depth

compared to 1986. The width/depth ratio decreased under all treatments as compared to pre-study conditions at study end; the ungrazed treatment produced greater decreases than did either grazed treatment (Table 1).

Ratings of streambank stability improved at a similar rate for the 3 grazing treatments (Table 2). Ratings of streambank alteration decreased under all treatments by the end of the study; the ungrazed treatment showed the most reduction (Table 2).

Channel Bottom

Embeddedness changed differently among treatments. Embeddedness had decreased in all treatments at study end; the least change occurred under medium grazing (Table 3). The surface area composed of fine textured sediments increased or showed no change with medium grazing. Both the light and ungrazed pastures showed little reduction in surface fines during the grazed years, although the lightly grazed pasture illustrated a significant reduction from initial conditions by the end of the study (Table 3).

Riparian Vegetation

Streamside Willows

Willows in the streamside area were scattered along most the length of Stanley Creek included within the study area. Willow heights increased during

Table 1. Proportional changes in channel profile characteristics, Stanley Creek pastures.¹

esults	5
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	Stream profile characteristics									
	Width	1 <u> </u>	Depth	L <u> </u>	Width/depth ratio					
Grazing treatment	1990&1994	1996	1990&1994	1996	1990&1994	1996				
		(Prop	ortion of initial	measurement	2)					
Medium grazing	0.821 Cb ³	0.856 Bb	0.812Ab	1.598 Ab	1.011 Ba	0.536 Bb				
Light grazing	0.665 Bb	0.824 Bb	0.730 Ab	1.585 Ab	0.912 Ba	0.520 Bb				
No grazing	0.591 Ab	0.687 Ab	0.861 Ab	2.336 Bb	0.686 Ab	0.294 Ab				

¹1990 and 1994 measurements were taken during grazed, droughty years; 1996 measurements were taken in ungrazed, wet conditions 1 year following cessation of treatments.

Data presented are the proportional changes from initial measurements, therefore, the units are dimensionless

³Treatment means sharing an upper case letter within a characteristic and year are not different

at P≤0.05. Lower case letters indicate: a=not different from initial reading, or b=significantly different from initial reading.

Table 2. Changes in streambank ratings, Stanley Creek pastures.¹

		Streambank characteristics								
	Streamban	<u>k stability</u>	Streamban	alteration						
Grazing treatment	1990&1994	1996	1990&1994	1996						
		(Change from initial rating ²)								
Medium grazing	12.4 Ab^3	12.0 Ab	3.3 Bb	-17.4 Bb						
Light grazing	11.2 Ab	11.8 Ab	-1.3 Ba	-22.6 Bb						
No grazing	16.7 Ab	19.5 Ab	-11.0 Ab	-35.2 Ab						

¹1990 and 1994 measurements occurred during grazed, droughty years; 1996 measurements occurred in ungrazed, wet conditions 1 year following cessation of treatments.

²Characteristics were rated on a scale of 0-100. Table values indicate direction and magnitude of rating change.

³Treatment means sharing an upper case letter within a characteristic and year are not different

at P<0.05. Lower case letters indicate: a=not different from initial reading, or b=significantly different from initial reading.

Table 3. Changes in channel bottom characteristics, Stanley Creek pastures.¹

		Channel bottom characteristics						
	Embe	ddedness	Fine s	ediments				
Grazing treatment	1990&1994	1996	1990&1994	1996				
	(Coverage of	(Coverage of large particles)		hannel bottom)				
Medium grazing	6.7 Bb ²	-16.5 Cb	15.0 Bb	6.9 Ba				
Light grazing No grazing	-2.6 Ab -8.6 Ab	-33.3 Ab -20.0 Bb	–1.0 Aa –2.8 Aa	-14.0 Ab -4.0 Ba				

¹1990 and 1994 measurements occurred during grazed, droughty years; 1996 measurements occurred in ungrazed, wet conditions 1 year following cessation of treatments.

²Treatment means sharing an upper case letter within a characteristic and year are not different at P≤0.05. Lower case letters indicate: a=not different from initial reading, or b=significantly different from initial reading.

Table 4. Streamside willow responses to grazing management from beginning to end of study, Stanley Creek pastures.

Willow characteristics								
Grazing treatment	Change in height	Change in cover ¹						
Medium grazing Light grazing No grazing	(m) 0.35 Ab ² 0.28 Ab 0.40 Ab	(%) 28.89 Ab 37.13 Ab 56.39 Bb						

¹Based only on plots containing willows throughout the study. ²Treatment means sharing an upper case letter within a

Treatment means sharing an upper case letter within a characteristic are not different at $P \le 0.05$. Lower case letters indicate: a=not different from initial reading, or b=significantly different from initial reading.

the study period, but the changes did not differ among treatments (Table 4). Willow cover increased with all treatments; the greatest increase occurred in the absence of grazing.

Plant Species Richness

The grazed pastures increased in graminoid species in all years compared to the initial reading (Table 5). The grazed pastures also showed an increase in forb species during the grazed years. The year after grazing ceased and precipitation was high all pastures lost forb species richness. The average number of shrub species per plot increased slightly from the initial readings; the response was similar among treatments. Overall, the grazed treatments experienced a greater increase in total plant species during the period of grazing than did the ungrazed treatment. In the year following the end of grazing when a general reduction of forb species occurred, only the medium grazed treatment maintained a significant increase in total species richness compared to initial readings (Table 5).

Plant Community-Types

No significant changes occurred in frequencies of individual plant community-



Fig. 2. Proportional change in several streamside plant community-type group frequencies during 1988 to 1996. The shift in community-types typified by strongly rooted, late seral graminoids compared to all other herbaceous plant community-types was significant at P=0.01.

types in the streamside locations. A significant change did occur in the frequency of the entire group of strongly-rooted, late seral species (beaked sedge, water sedge, bluejoint reedgrass [*Calamagrostis canadensis* (Michx.) Beauv.], and Baltic rush) (USDA-FS 1992)(P=0.01). An increase in this group occurred in the ungrazed and lightly grazed pastures (Fig. 2). This increase was nearly matched by a non-significant downward trend in the Kentucky bluegrass community-type (P=0.07).

Plant Cover and Litter

Little change in graminoid canopy cover occurred. No treatment differed significantly from the initial measurements at the end of the study (Table 6). The forb cover tended to increase variably in the grazed treatments and to decrease significantly in the ungrazed treatment. Changes in total herbaceous plant cover did not differ among treatments in the grazed years. The no grazed treatment ended in 1996 with a lower total plant cover than the initial reading. Litter tended to decrease in the moderately grazed pastures, gain in the no grazing treatment, and change minimally in the light grazing treatment (Table 6).

Plant Height

Graminoid heights were similar among treatments after the cessation of grazing for 1 year (P=0.56). Average streamside graminoid heights were 28.2, 28.1, and 29.4 cm for medium, light, and no grazing treatments, respectively. These results suggest that similar growth rates of herbaceous plants were attained among treatments within 1 year after grazing stopped.

Table 5. Changes in numbers of streamside plant species, Stanley Creek.¹

		Plant growth form										
Grazing	Gram	inoid	F	Forb		Shrub		Plant				
treatment	1990&1994	1996	1990&1994	1996	1990&1994	1996	1990&1994	1996				
		Change in no. 0.25-m ⁻²										
Medium grazing	0.73 Bb ²	0.64 Bb	0.59 Bb	-0.01 Aa	0.08 Ab	0.09 Ab	1.40 Bb	0.72 Bb				
Light grazing	0.65 Bb	0.35 ABb	0.47 Bb	-0.45 Ab	0.13 Ab	0.20 Ab	1.25 Bb	0.10 ABa				
No grazing	0.14 Aa	0.06 Aa	0.04 Aa	-0.45 Ab	0.12 Ab	0.18 Ab	0.30 Ab	-0.21 Aa				

¹1990 and 1994 measurements were taken during grazed, droughty years; 1996 measurements were taken in ungrazed, wet conditions 1 year following cessation of treatments. ²Treatment means sharing an upper case letter within a characteristic and year are not different at P≤0.05. Lower case letters indicate: a=not different from initial reading, or b=significantly different from initial reading. Table 6. Changes in streamside litter and herbaceous plant cover, Stanley Creek pastures.¹

	Plant growth form									
Grazing	Ι	Litter	Gran	Graminoid		Forb		Total herbaceous plant		
treatment	1990&1994	1996	1990&1994	1996	1990&1994	1996	1990&1994	1996		
(Change in % cover) —										
Medium grazing	–1.19 Aa ²	-3.39 Ab	-3.20 Aa	–2.91 Aa	0.82 Ba	4.28 Bb	-2.38 Aa	1.37 Ba		
Light grazing	1.50 Bb	–0.66 Ba	–1.95 Aa	-4.89 Aa	3.62 Bb	0.02 Ba	1.67 Aa	–4.87 ABa		
No grazing	2.82 Cb	2.77 Cb	8.44 Ab	1.93 Aa	-6.36 Ab	-7.83 Ab	2.08 Ab	-5.90 Ab		

¹1990 and 1994 measurements were taken during grazed, droughty years; 1996 measurements were taken in ungrazed, wet conditions 1 year following cessation of treatments. ²Treatment means sharing an upper case letter within a characteristic and year are not different at P≤0.05. Lower case letters indicate: a=not different from initial reading, or b=significantly different from initial reading.

Dry Meadow Vegetation

Species Richness

The graminoids were greater in both the grazed period and in the post-grazing year in comparison to initial values (Table 7). The forb species richness exhibited a general increase across treatments during the grazed years, but declined in the ungrazed treatment in 1996, a wet year. This indicates that both drought and grazing stresses provided the opportunity for an increase in forb species. A slight increase in number of different shrubby species occurred from initial readings in the light and ungrazed treatments, although no differences among treatments were detected. During the grazed period, the average number of total species recorded increased for all treatments. In the year after grazing ceased, only the medium grazed treatment showed an increase in number of total plant species compared to the initial reading (Table 7).

Plant Community-Types

There was greater evidence of a change in the frequencies of community-types in the dry meadow portion of the pastures than in the streamside areas. The frequency of the tufted hairgrass type (P<0.01) and the Kentucky bluegrass type (P<0.01) increased inversely to grazing pressure at the expense of the thick-stemmed aster type (P<0.01), the primary forb type on the study area. The greatest change occurred in the ungrazed pastures. A group of late seral graminoid community-types (beaked sedge, water sedge, bluejoint reed grass, and Baltic rush), that inhabited the more moist locations in the dry meadow area, decreased in all treatments (P<0.01).

Plant Cover and Litter

On the dry meadows graminoid cover decreased during the period of study with no difference among treatments (Table 8). Forb cover increased in all treatments during the grazed years, but 1 year after grazing stopped the medium grazing treatment was the only treatment different than the initial measurement. There were no changes in shrub cover. Total plant cover decreased on the dry meadows during the grazed years, but in 1996 only the no grazed treatment had less total cover than initial readings (Table 8). Generally, less litter was recorded during the study than in the initial readings, although little difference occurred among treatments.

Discussion

Streamside

Grazing along streambanks probably does as much or more damage to stream-riparian habitats through bank alteration as through changes in vegetation biomass (Winward 1986). Overuse by cattle can easily destabilize and break down streambanks as vegetation is weakened and the physical forces of hoof impacts shear off bank segments (Marlow and Pogacnik 1985, Trimble and Mendel 1995). As grazing and trampling damage are reduced, the residual vegetation aids in trapping of sediments that serve as base material to rebuild streambanks (Clary et al. 1996). The channel narrowing and the reduced width/depth ratio of all 3 treatments in this study suggest the grazing stress applied during treatment was within the sites' capabilities for annual recovery and that the original degree of degradation did not preclude an improving trend under these conditions. Because the degree of change in these variables was associated with grazing intensity, this study illustrates that streambank and aquatic habitat impacts can be controlled through grazing management. When streambanks rebuild and channels narrow, the decreased width/depth ratio improves the stream's hydraulic and sediment transport efficiency (Morisawa 1968, Olson-Rutz and Marlow 1992, Leopold 1994) and provides potential increases in fish hiding cover (Meehan et al. 1977, Kozel et al. 1989, Bjornn and Reiser 1991, Overton et al. 1995).

All treatments decreased in substrate

Table 7. Changes in numbers of dry meadow plant species, Stanley Creek.¹

Plant growth form									
Grazing	Graminoid Forb				Shi	rub	Total	plant	
treatment	1990&1994	1996	1990&1994	1996	1990&1994	1996	1990&1994	1996	
					no. 0.25-m ⁻² —				
Medium grazing	0.98 Bb^2	0.91 Bb	0.84 Ab	0.44 Bb	0.01 Aa	0.02 Aa	1.83 Bb	1.37 Bb	
Light grazing	0.58 Ab	0.34 Ab	0.54 Ab	-0.16 Aa	0.03 Ab	0.04 Ab	1.15 Ab	0.22 Aa	
No grazing	0.46 Ab	0.37 Ab	0.52 Ab	-0.23 Ab	0.03 Ab	0.05 Ab	1.01 Ab	0.19 Aa	

¹1990 and 1994 measurements were taken during grazed, droughty years; 1996 measurements were taken in ungrazed, wet conditions 1 year following cessation of treatments. ²Treatment means sharing an upper case letter within a characteristic and year are not different at P≤0.05. Lower case letters indicate: a=not different from initial reading, or b=significantly different from initial reading.

Table 8. Changes in dry meadow ground cover, Stanley Creek.¹

					Ground cover c	haracteristics	5			
Grazing	L	itter	Grau	ninoid	For	rb	Sh	rub	Tota	l plant
treatment	1990&1994	1996	1990&1994	1996	1990&1994	1996	1990&1994	1996	1990&1994	1996
					Change in %	6 cover				
Medium grazing	-3.15 Ab ²	-3.60 Ab	-14.38 Ab	-11.43 Ab	5.00 Ab	11.09 Cb	0.01 Aa	0.01 Aa	–9.37 Ab	–0.33 Aa
Light grazing	1.63 Bb	-1.22 Ab	-11.71 Ab	-5.27 Ab	3.04 Ab	1.83 Ba	0.02 Aa	0.03 Aa	-8.65 Ab	–3.41 Aa
No grazing	0.80 Aa	-1.62 Ab	-16.00 Ab	-8.67 Ab	3.75 Ab	-2.04 Aa	0.02 Aa	0.04 Aa	-12.23 Ab	–10.67 Ab

¹1990 and 1994 measurements were taken during grazed, droughty years; 1996 measurements were taken in ungrazed, wet conditions 1 year following cessation of treatments. ²Treatment means sharing an upper case letter within a characteristic and year are not different at P \leq 0.05. Lower case letters indicate: a=not different from initial reading, or b=significantly different from initial reading.

embeddedness by the end of the study, but the decrease in proportion of the surface composed of fine sediments was variable. This response may have been affected by downstream movement of old dredge mining sediments. Channel bottom conditions are greatly affected by sediments contributed by upstream sources and may not respond rapidly to on-site management (Rinne 1988). The channel substrate status is important to spawning and incubation of stream fishes, production of aquatic invertebrates for salmonid food, and cover for young fish (Bjornn and Reiser 1991).

Willow height and cover increased in all treatments of this study. The maintenance of an adequate herbaceous forage supply (Winward 1994, Pelster 1998) and control of season of grazing undoubtedly reduced impacts on the willow community as compared to historic grazing procedures (Kovalchik and Elmore 1992, Winward 1994). Some impact on willows is typical even under managed grazing (Myers and Swanson 1995), thus the positive growth response of willows in this study exceeded expectations. The benefits of streamside vegetation canopies, particularly of various species of willow are: provision of hiding cover, modulation of stream temperatures, and contribution of leaf detritus and terrestrial insects that expand food sources for fish (Meehan et al. 1977, Murphy and Meehan 1991, Kovalchik and Elmore 1992, Li et al. 1994).

Plant species richness in the grazed pastures increased in all categories during the treatment years. The continued grazing stress in the grazed pastures, together with the below normal precipitation that was present for the bulk of the study, apparently opened the stand and allowed new plant establishment. Changes in species richness in the ungrazed treatment were noticeably less, as was expected (Hayes 1978, Green

and Kauffman 1995). In 1996, one year after cessation of grazing and a year of above average precipitation, forb species numbers dropped to less than initial counts for the lightly grazed and no grazed treatments as grazing and moisture stresses were reduced. The increase in frequencies of strongly-rooted, late seral graminoid communitytypes in streamside locations under light or no grazing was expected (Green and Kauffman 1995). The extent and strength of the roots and rhizomes of these plants provide essential stability to the banks (Kleinfelder et al. 1992, Dunaway et al. 1994), thus allowing undercuts to form as habitat segments for salmonids (Platts 1991). The lack of differences among treatments in height of graminoids, after 1 year of rest from grazing, suggests that any loss of vigor from the current grazing treatments was largely recovered after 1 year. A similar response was suggested from studies of simulated grazing (Clary 1995).

Although substantial changes occurred in a number of characteristics that benefit the stream environment and aquatic habitat, changes of herbaceous plant characteristics along the stream edge at Stanley Creek were limited. Overall, stream channel characteristics of the Stanley Creek riparian area seemed to respond more rapidly than the vegetation characteristics—a sequence differing from studies in some other locations (Kondolf 1993, Knapp and Matthews 1996).

Dry Meadow

During this study we were applying differential grazing treatments and the regional climate was applying drought stress for most of the years of grazing. These combined stresses opened the stands sufficiently to provide an opportunity for additional species to thrive. Stress conditions on dry meadows, particularly grazing stress, typically provide disturbance conditions favorable for increases in species richness and diversity (Dobson 1973, Hayes 1978, Green and Kauffman 1995). After protection from grazing, dry meadows characteristically experience a reduction in the forb component while retaining the exotic Kentucky bluegrass component (Kauffman et al. 1983, Green and Kauffman 1995). Reduction in graminoid cover during the study was probably a result of drought because the ungrazed treatment decreased as well. There were mixed directions of successional changes. The increase in tufted hairgrass and a decrease in forb dominance under reduced grazing pressure suggest improved meadow conditions. A decrease in wet-site rhizomatous graminoids during drought suggests a depletion of meadow conditions (Reid and Pickford 1946, Hansen et al. 1995).

Management Implications

No single management approach is best for all situations, nor perhaps is even required for a given situation (Clary and Webster 1989, Ehrhart and Hansen 1997). There are, however, management approaches that work well in many circumstances. For instance, several authors have emphasized the potential benefits of late summer grazing (Kauffman et al. 1983, Marlow and Pogacnik 1985). Alternatively, spring grazing has shown promise in many areas of the western United States (Hayes 1978, Platts and Nelson 1985, Siekert et al. 1985, Goodman et al. 1989, Kovalchik and Elmore 1992, Pelster 1998). The combination of succulent upland forage, cool temperatures, and wet soils near water sources acts to encourage a more dispersed spring grazing pattern (Krueger 1983, Marlow and Pogacnik 1986, Kovalchik 1987, Myers 1989, Clary and Booth 1993).

Grazing strategies employed in this study were designed to stay within the annual tolerance of the site for plant or streambank/channel impacts each year. Even though many riparian forage plants have season-long access to adequate soil moisture, their ability to withstand grazing has limits (Allen and Marlow 1994, Lamman 1994, Clary 1995, Hall and Bryant 1995, Dovel 1996). Willows are notably vulnerable to cattle use in late summer (Kovalchik and Elmore 1992, Lamman 1994, Winward 1994, Myers and Swanson 1995), particularly as the forage supply is reduced (Pelster 1998). Heavy trampling on streambanks is typically very damaging (Trimble and Mendel 1995), especially when the banks are moist (Marlow and Pogacnik 1985). The strategy in the Stanley Creek study was to limit grazing to the early season when less grazing use occurred near the water's edge. The Stanley Creek streambank substrate composition was amenable to this grazing approach; its relatively permeable streamside soils were not likely as susceptible to spring trampling damage as other more fine textured soils (Chaney et al. 1993) (Personal communication, D. Dallas and C. Marlow). Cattle congregated on the dry meadows during those weeks the forage there was still green and succulent, rather than concentrating on the wetter streamside areas (Clary and Booth 1993). Grazing was terminated each year before herbaceous vegetation on the dry meadows had matured.

Riparian grazing recommendations for the recovery of depleted meadow riparian systems, presented after initiation of this study, suggested that 10-15 cm of forage stubble height should remain on streamside areas at the end of the growing season, or at the end of the grazing season after fall frost, to limit potential impacts to the herbaceous plant community, the woody plant community, and streambank stability. Spring or early summer grazing was recommended where feasible (Clary and Webster 1989, 1990). The grazing strategy on the Stanley pastures closely paralleled these recommendations even though the grazing rates were originally based on use of the dry meadow sites. Compared to historic management patterns, the total forage utilization in this study was less, and

mid to late season grazing was eliminated. This approach appears to have been successful. Most riparian area changes in grazed pastures were in a similar direction, but in different magnitudes, to those in the ungrazed treatment here and in other ungrazed mountain meadows (Knapp and Matthews 1996). At the end of the study the conditions on Stanley Creek were continuing to improve, but it was not known how much additional change could have been expected under either carefully grazed or ungrazed conditions. Stanley Creek appeared to be approaching relatively stable conditions when compared to undisturbed meadow systems (Overton et al. 1995), .

Although changes were slow in this cold mountain valley, these early season grazing regimes allowed improvements in stream channel conditions and streamside vegetation characteristics. Most measurements improved to some degree under all 3 treatments; this suggests that early season grazing practices that leave 10 to 14 cm of residual forage stubble height provide an avenue for riparian habitat improvement while maintaining substantial livestock use of the meadow area. Potential changes in other riparian meadow situations will vary depending on past grazing management, streambank substrates, weather, and other factors.

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Late-summer forage on prairie sandreed dominated rangeland after spring defoliation

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Abstract

The potential of using spring defoliation to improve latesummer nutritive value of prairie sandreed [Calamovilfa longifolia (Hook.) Scribn.] on rangeland was studied with a factorial array of replicated 1-year treatments that included clipping plots at ground level or at a 5 or 10 cm height on 1 April, 26 April, 20 May, or 14 June. Vegetative tillers accounted for 83% of prairie sandreed herbage on unclipped control plots. After spring treatments, late-summer crude protein content (CP) in vegetative tillers of prairie sandreed ranged from 5.0 to 7.9% and in vitro dry matter digestibility (IVDMD) ranged from 45 to 52% compared to 5.0% CP and 45% IVDMD for unclipped plots. Reductions in mean weight of prairie sandreed vegetative tillers after April and May treatments were offset by 20 to 30% increases in tiller density. Treatments that increased tiller density had little or no effect on forage nutritive value when applied more than 90 days before herbage was sampled. Nutritive value of prairie sandreed and total yield from all species in mid-September were unchanged after April treatments. After sandreed tillers began to emerge in early May, late-summer nutritive value improved as clipping was delayed and degree of defoliation increased during May and June, however, yield was inversely related to nutritive value. While mid-September nutritive value of prairie sandreed was comparable to mid-summer values after June treatments, clipping reduced projected, late-summer stocking rates by 58 to 100% compared to control. It may be possible to improve mid-September forage nutritive value with moderate stocking rates in June with less reduction of total late-summer herbage because of selective herbivory. Measurable increases in prairie sandreed yield after complete defoliation of associated species in late April indicated prairie sandreed populations might be increased by concentrating cattle in selected pastures during late April.

Key Words: *Calamovilfa longifolia*, clipping date, cutting height, yield, crude protein, in vitro dry matter digestibility, tiller demographics

Resumen

Se estudio el potencial de utilizar la defoliación en primavera para mejorar el valor nutritivo a fines de verano del zacate "prairie sandreed" [Calamovilfa longifolia (Hook.) Scribn]. El estudio se condujo en un pastizal bajo un arreglo factorial de tratamientos repetidos 1-año que incluyeron parcelas defoliadas a nivel del suelo, o a 5 y 10 cm de altura. La defoliación se realizo el 1 de abril, 26 de abril, 20 de mayo o 14 de junio. En las parcelas sin defoliar (control), los hijuelos vegetativos aportaron el 83% del forraje producido por el "prairie sandreed". Después de los tratamientos de primavera, el contenido de proteína cruda (PC) de los hijuelos vegetativos a fines del verano fluctúo de 5.0 a 7.9% y la digestibilidad in vitro de la materia seca (DIVMS) estuvo en un rango de 45 a 52% comparado con 5.0% de PC y 45 % DIVMS de las parcelas sin defoliar (control). Las reducciones del peso promedio de los hijuelos vegetativos del "prairie sandreed" ocurrida después de aplicar los tratamientos de abril y mayo fueron compensados por un incremento del 20 al 30% de la densidad de hijuelos. Cuando los tratamientos que incrementaron la densidad de hijuelos vegetativos fueron aplicados 90 o más días antes del muestreo de forraje estos tuvieron poco o ningún efecto en el valor nutritivo del forraje. El valor nutritivo del "prairie sandreed" y el rendimiento total, a mediados de septiembre, de todas las especies no cambio después de los tratamientos de abril. Después de que los hijuelos de "prairie sandreed" comenzaron a emerger a inicios de mayo, el valor nutritivo a fines del verano mejoro conforme la defoliación se retrasó y el grado de defoliación incrementó durante mayo y junio, sin embargo, el rendimiento fue inversamente relacionado al valor nutritivo. Mientras el valor nutritivo del "prairie sandreed" a mediados de septiembre fue comparable al de mediados del verano después de los tratamientos de junio, la defoliación redujo la carga animal proyectada para fines del verano, la reducción fue del orden de 58 a 100% en comparación con el control. Puede ser posible mejorar el valor nutritivo del forraje de mediados de septiembre utilizando cargas animales moderadas en junio teniendo menos reducción de forraje total de fines de verano debido a la herbívora selectiva. Incrementos medibles en el rendimento de "prairie sandreed" después de completar la defoliación de las especies asociadas a fines de abril indica que las poblaciones de "prairie sandreed' podrían ser incrementadas por la concentración de ganado en potreros seleccionadas durante fines de abril.

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The feasibility of using spring grazing to reduce seasonal declines in forage nutritive value associated with plant maturity has not been reported for semiarid rangeland. Some studies have examined the effects of defoliation on nutritive value in a following season, but initial dates of defoliation have been confounded with additional clipping dates between first cutting and final harvest (George and Obermann 1989, Willms 1991, Willms and Beauchemin 1991, Belsky and Fedders 1994, 1995). In early spring, seasonally low forage allowances of green herbage for livestock can cause severe defoliation of initial plant growth. Given the potential for a wide range in degree of spring defoliation, improvement in late-summer nutritive value could be caused by reduced stem development (Perry and Baltensperger 1979), reduced average age of tiller populations (George and Obermann 1989, Culvenor 1993, Bullock et al. 1994), and/or reduced composition of reproductive tillers (Cook and Stoddart 1953, Murray 1984, Ganskopp et al. 1992, Brummer 1994). In the semi-arid region of western Nebraska and adjoining states, the duration of temperature and soil moisture conditions required for rapid plant growth is relatively short. Studies of interactions between date and degree of spring defoliation are needed to understand the mechanisms by which end-ofseason forage quality might be improved. Extensive rhizomes and deep roots enhance prairie sandreed's [*Calamovilfa longifolia* (Hook.) Scribn.] ability to tolerate drought and produce large quantities of herbage compared to associated plant species on sandy soils throughout the northern Great Plains (Lodge 1963, Welch 1968, White 1977). Our objective was to quantify the effects of spring defoliation on late-summer nutritive value of prairie sandreed and yield of all species on rangeland dominated by prairie sandreed.

Material and Methods

A 3 x 4 factorial array of 1-year spring clipping treatments was replicated on sandy range sites dominated by prairie sandreed at 2 locations in 1993 and 1994 (Table 1). Eight sites were selected at each location in March 1993 and

 Table 1. Average species composition based upon herbage biomass in control plots clipped in September, 1994.

Species ¹	Buffalo Creek	Wildcat Hills
		-(%)
Calamovilfa longifolia (Hook.) Scribn.	54	52
Stipa comata Trin. and Rupr.	29	4
Poa pratensis L.	0	22
<i>Carex</i> spp. ²	3	11
Bouteloua gracilis (H.B.K.) Lag. ex Griffiths	4	9
Agropyron smithii Rydb.	2	1
Forbs	8	1

¹Nomenclature follows The Great Plains Flora Association (1986).

²Carex species were predominantly C. filifolia Nutt. and C. heliophila Mack.

ranked by relative abundance of prairie sandreed. Within comparable levels of abundance, sites were randomly assigned to years to include similar variation in species composition each year. All vegetation in 1.0 m² plots was clipped at ground level or at a 5 or 10 cm height on 1 April, 26 April, 20 May, or 14 June. This provided deferment periods of about 165, 140, 115 and 90 days between spring defoliation and late-summer harvest in mid-September. Current-year prairie sandreed tillers were counted and clipped from the interior 0.5 m² of plots when spring defoliation treatments were applied. All other herbage clipped in the spring was discarded. Prairie sandreed tillers harvested from plots clipped at ground level were cut into segments of 0-5, 5-10, and above 10 cm to estimate degree of spring defoliation at the 5 and 10 cm heights. In addition, each site included 3 control plots. Mean response of control plots for each site was used for analysis of variance. Late-summer, current-year herbage was harvested at ground level from the interior 0.5 m² of plots in mid-September, separated into prairie sandreed vegetative and reproductive tillers and other species, and oven dried at 60°C to a constant weight. Tillers with exposed seed heads were classified as reproductive. Plant composition at each location was estimated in late summer by clipping and weighing species individually from 12 control plots at each location on 1994 study sites.

Locations were the Buffalo Creek Wildlife Management Unit, 9 km southwest of Melbeta, Nebr. and the Wildcat Hills State Park, 11 km south of Gering, Nebr. Livestock had been excluded from both locations for 10 years or more. Soils at Buffalo Creek are mixed, mesic Entic Haplustolls. Soils at the Wildcat Hills location are a mosaic of mixed, mesic Typic Haplustolls and mixed, calcareous, mesic, shallow Typic Ustorthents. Precipitation during April to September 1993 was about 193 mm at both locations and 239 mm at Buffalo Creek and 282 mm at Wildcat Hills in 1994 compared to the long-term average of 293 mm for this 6-month period (NOAA 1994). Long-term average annual precipitation is 410 mm and the average frost-free period is 136 days.

Forage samples were analyzed to determine concentrations of crude protein (CP) and in vitro dry matter digestibility (IVDMD) by near infrared reflectance spectroscopy (NIRS) using the protocol described by Windham et al. (1989). Reflectance measurements $(\log 1/R)$ were collected for all samples from 1,100 to 2,500 nm and recorded in 4-nm intervals using a Pacific Scientific 6250 (NIRS Systems, Silver Spring, Md) scanning monochromator. Based upon spectral characteristics, a subset of 60 samples representing the entire range of H values (Mahalanobis distance) was selected for NIRS calibration (Shenk and Westerhaus 1991a). Estimates of CP and IVDMD were determined for calibration samples using the micro-Kjeldahl and rumen fermentation (Marten and Barnes 1980) procedures, respectively. All analyses were done in duplicate and averages of duplicate samples were used as analytical values. Calibrations were developed using modified partial least squares regression (Shenk and Westerhaus 1991b). Coefficients of determination and standard errors for calibration and cross validation were, respectively, 0.93, 1.47 and 1.86 for IVDMD and 0.99, 0.09 and 0.16 for CP. Calibration statistics were within acceptable limits for all variables (Windham et al. 1989).

Experimental units were 0.5 m^2 quadrats centrally placed in 1.0 x 1.0 m

treated areas. Data were analyzed as a randomized complete block using the General Linear Models Procedure (SAS 1986). Level of probability selected for significance was $P \le 0.05$. Single degree of freedom orthogonal contrasts were used to select variables for equations to describe significant main effects and interactions. Equations for main effects were fit to treatment means from both study years, and equations for spring clipping date by cutting height interactions were fit to factorial means averaged over years using the Regression Procedure (SAS 1986). Dunnett's test was used to compare control with each clipped treatment (Dunnett 1955). The Least-Squares Means Procedure within SAS was used for mean separation among defoliation treatments (Searle et al. 1980).

Results

Composition of prairie sandreed on control plots in mid-September ranged from 24 to 93% among study sites. While the mean composition of prairie sandreed was comparable between locations, differences in the composition of cool-season species occurred between locations. Needleandthread (Stipa comata Trin. and Rupr.) was the primary cool-season species at Buffalo Creek (Table 1). In contrast, the primary coolseason species at Wildcat Hills were kentucky bluegrass (Poa pratensis L.) and sedges (Carex spp.).

Prairie Sandreed Tiller Responses

All prairie sandreed tillers emerged after 26 April and growing points in reproductive tillers were elevated less than 5 cm above the soil surface on 14 June at both locations in both years. When growing-season precipitation was 34% below the long-term average in 1993, complete defoliation at Buffalo Creek increased the density of reproductive tillers by 82% after 1 April treatments and 29% after clipping on 26 April compared to control (28 m⁻²). However, percent of late-summer herbage composed of reproductive tillers was unchanged after April treatments because of concurrent increases in vegetative tiller density. After prairie sandreed tillers emerged, complete defoliation in May or June at Buffalo Creek



Fig. 1. Effects of spring clipping date (D = days after 31 Mar) on late-summer density of prairie sandreed vegetative tillers.

generally eliminated reproductive tillers which comprised about 25% of prairie sandreed herbage on control plots in mid-September. In the following year when growing-season precipitation was near average, spring defoliation had no effect on reproductive tillers regardless of cutting height.

Clipping in April or May increased late-summer density of vegetative tillers by 20 to 30% (Fig. 1) compared to 300 m⁻² for control. Changes in vegetative tiller density diminished as the amount of herbage removed from prairie sandreed increased from May to June (Fig. 1, Table 2). Mean weight of vegetative tillers in mid-September was reduced by about 15%, compared to control, when plots were clipped in April (Fig. 2a). After prairie sandreed tillers emerged in May, reductions in tiller weight increased as the degree of spring defoliation increased and clipping date was delayed (Fig. 2a, Table 2). Removing 53 to 100% of the herbage from prairie sandreed in mid-June reduced late-summer mean tiller weight by 32 to 55%, compared to control.

Levels of CP content in vegetative tillers within comparable weights were higher under drought conditions in 1993 than in 1994 when near average precipitation occurred (Fig. 3a, Table 3). Crude protein declined rapidly as tiller weight increased with about 75% of the change occurring between the low and midrange tiller weights. Average IVDMD of prairie sandreed vegetative tillers was not different between years, but the rate at which IVDMD declined with increasing tiller weight was about 2 times greater when precipitation was near

Table 2. Percent defoliation of prairie sandreed in the spring, crude protein (CP) content and digestibility (IVDMD) of vegetative tillers of prairie sandreed in mid-September, and projected late-summer stocking rate after clipping at 0, 5, or 10 cm on 20 May or 14 June.

	Spring Cutting Height ¹						
Spring Clipping Date	0 cm	5 cm	10 cm				
20 May							
Spring Defoliation (%)	100	61	29				
Late-summer ²							
CP (%)	6.0	(5.4)	(5.1)				
IVDMD (%)	46.7	(45.4)	(45.0)				
Projected Stocking Rate (AUD ha ⁻¹)	15	23	31				
<u>14 June</u>							
Spring Defoliation (%)	100	78	53				
Late-summer ²							
CP (%)	7.9	6.1	5.6				
IVDMD (%)	52.2	48.9	47.2				
Projected Stocking Rate (AUD ha ⁻¹)	0	5	17				

¹Values in parentheses are not significantly different from control based on Dunnett's test, P>0.05. ²Late-summer values for control were 5% CP, 45% IVDMD, and 40 AUD ha⁻¹. Projected stocking rate was calculated by dividing herbage available for livestock consumption by 11.8 kg to estimate potential animal unit days (AUD).



Fig. 2. Spring cutting height by clipping date interaction effects on (a) mean tiller weight and (b) yield of prairie sandreed vegetative tillers in mid-September. Columns with dots (●) are different from control, P<0.05.

average in 1994 compared to drought conditions in 1993, e.g. 5.5 compared to 2.8 percentage points decline in IVDMD per 100 mg increase in mean tiller weight (Fig. 3b, Table 3). While CP content was generally higher in vegetative than in reproductive tillers, the range in treatment means for IVDMD of each tiller type was comparable in both years. Mean weight, CP content and IVDMD of reproductive tillers ranged from 465 to 1,970 mg tiller⁻¹, 3.2 to 4.6%, and 45 to 51%, respectively.

Herbage Responses

Vegetative tillers accounted for 77 to 98% of prairie sandreed herbage after spring clipping compared to 83% for control. Yield of herbage from vegetative tillers in mid-September ranged from 520 to 1,330 kg ha⁻¹ (Fig. 2b) compared to 1,080 kg ha⁻¹ for control. Latesummer yield from vegetative tillers was unchanged by clipping at any cutting height in April or May except for complete defoliation in late April (Fig. 2b). Complete defoliation of plots on 26 April, before prairie sandreed tillers emerged, increased prairie sandreed yield by 23% compared to control. Removing 53 to 100% of the currentyear herbage from prairie sandreed in mid-June (Table 2) reduced mid-September yield of prairie sandreed herbage from vegetative tillers by 35 to 52% (Fig. 2b).

About 75% of herbage from other species was produced by cool-season grasses or sedges (Table 1). Mean yield of herbage from other species on control plots was 610 kg ha⁻¹. When averaged over spring clipping dates, little change occurred in late-summer yield of herbage from other species after clipping at 5 compared to 10 cm (Fig. 4a). However, predicted late-summer yield declined rapidly as cutting height decreased from 5 to 0 cm. Late-summer herbage from species other than prairie sandreed also declined about 26 kg ha⁻¹ for each week that spring clipping was delayed after 1 April (Fig. 4b).

Average, current-year herbage from all species that occurred on control plots in mid-September was about 1,900 kg ha⁻¹. Projected, late-summer stocking rates were based on leaving 950 kg ha⁻¹ (half of control herbage) for ecosystem functions and utilizing 50% of the remaining herbage (Table 2). The balance, 50% of herbage beyond the target level of 950 kg ha⁻¹ in remaining herbage, was an estimate of losses by factors other than cattle. Herbage available for livestock forage was divided by 11.8 kg to calculate projected animal unit days (AUD). The average projected stocking rate in mid-September for control was about 40 AUD ha⁻¹. Removing an average of 29 and 61% (10 and 5 cm height) of current-year herbage from prairie sandreed in mid-May reduced projected, late-summer stocking rates by 22 and 43%, respectively, but did not improve nutritive value of prairie sandreed (Table 2). Clipping prairie sandreed in mid-June at 10 or 5 cm heights increased mean defoliation to 53 and 78% causing measurable increases in late-summer nutritive value of prairie sandreed, but reduced projected stocking rates by 58 and 88%, respectively.

Discussion

While crude protein content was lower in reproductive compared to vegetative tillers of prairie sandreed, the occurrence of reproductive tillers had little effect on average IVDMD of late-summer herbage. Density of reproductive tillers was also affected by spring clipping at only one location in a single year. Consequently, the risks of reduced livestock performance in May or June, damage to associated plant species, and reduced infiltration and site stability caused by the severe defoliation needed to reduce density of reproductive tillers can not be justified. Additionally, carbohydrates from the relatively large photosynthetically active surface areas of

Table 3. Polynomial equations for spring cutting height (H) by clipping date (D = days after 31 Mar) interaction effects on late-summer vegetative tiller weight and yield of prairie sandreed from vegetative tillers and regression equations for the effects of late-spring cutting height and late-summer tiller weight (W) on crude protein (CP) content and digestibility (IVDMD) of late-summer herbage from vegetative tillers of prairie sandreed in mid-September.

Late-summer Dependent Variable	Equation ¹	R ²	
	Spring Cutting Height by Date (Figure 1)		
Tiller Weight	$Y = 315 + 0.55 \text{ D} - 0.032 \text{ D}^2 - 1.018 \text{ H} + 0.12 \text{ DH}$.94	
Yield	$Y = 1090 + 8.54 \text{ D} - 0.203 \text{ D}^2 + 0.27 \text{ DH}$.91	
	Spring Cutting Height (Table 2)		
СР	$Y_{May} = 6.04 - 0.18 H + 0.0082 H^2$.45	
	$Y_{Jun}^{May} = 7.90 - 0.49 H + 0.0262 H^2$.75	
IVDMD	$Y_{Mav} = 46.7 - 0.34 H + 0.017 H^2$.63	
	$Y_{Jun} = 52.2 - 0.82 H + 0.032 H^2$.99	
	Late-summer Tiller Weight (Figure 2)		
СР	$Y_{93} = 15.3 - 0.055 \text{ W} + 7.6 \text{ x } 10^{-5} \text{ W}^2$.93	
	$Y_{94} = 16.3 - 0.077 \text{ W} + 12.7 \text{ x} 10^{-5} \text{ W}^2$.89	
IVDMD	$Y_{93} = 55.6 - 0.028 \text{ W}$.81	
	$Y_{94} = 59.9 - 0.055 W$.84	

¹Cutting height by clipping date treatment means (n=12) were used to compute equations for Figures 1 and 2. Year by cutting height treatment means within clipping dates (n=6) were used to compute equations for May and June.



Fig. 3. Relationship between mean weight of prairie sandreed vegetative tillers and (a) crude protein (CP) and (b) digestibility (IVDMD) in mid-September.

reproductive tillers not grazed in late summer may be a significant source of energy for root, rhizome, and/or bud development (Brejda et al. 1989, Nixon 1993, Reece et al. 1996).

Degree of defoliation of associated species increased and opportunity for cool-season species to recover before rapid growth of prairie sandreed declined as clipping date was delayed from 1 April to 20 May. However, increases in density of prairie sandreed vegetative tillers after clipping in April or May appeared to be caused primarily by micro-environmental changes (Briske and Richards 1995), rather than release from competition, because yield of prairie sandreed increased only after complete defoliation in late April.

The inverse relationship of nutritive value to mean weight of vegetative tillers and measurable declines in mid-September mean tiller weight when clipping treatments improved nutritive value indicated that the average age or maturity of tiller populations was reduced (Hendrickson et al. 1997, Northup and Nichols 1998). In our study, CP content and IVDMD of tiller populations with improved nutritive value in midSeptember were comparable to levels reported for prairie sandreed tillers harvested from ungrazed pastures in mid-June to mid-July (Northup 1993, Hendrickson et al. 1997). Rapid decline in nutritive value during early development of new cohorts of prairie sandreed tillers reported by Hendrickson et al. (1997) would explain the declining differences in nutritive value between progressively earlier spring clipping treatments and control when measurable increases in tiller recruitment occurred.

The sum of late-summer herbage from prairie sandreed plus herbage from other species was not affected by defoliation in April at any cutting height. In contrast, total yield of herbage in mid-September declined after clipping in mid-May because of 30 and 20%

yield reductions in other species after complete defoliation and clipping at 5 cm, respectively. Increases in prairie sandreed tiller density compensated for up to 15% reductions in mean weight of vegetative tillers. After clipping in mid-June, total late-summer yield was about 30 to 70% below control because of reductions in herbage from prairie sandreed and other species. All reductions in the yield of prairie sandreed corresponded to 20% or more reductions in mean weight of vegetative tillers.

While the largest increases in nutritive value of prairie sandreed occurred after complete defoliation, projected stocking rates for mid-September after clipping at ground level in May were 30% below control and complete defoliation in June precluded projected grazing until the following growing season because of inadequate herbage (Table 2). Clearly, defoliation at ground level in mid-May or mid-June was not a sustainable practice when repeated in consecutive years (Reece et al. 1996). However, this level of defoliation documents the physiological upper limits in mean CP and IVDMD levels in prairie sandreed in late summer after spring defoliation.

Additionally, complete defoliation in mid-May is unnecessary because deferring until mid-June and removing only 50% of current-year herbage from prairie sandreed would provide similar nutritive value and mass of forage in mid-September with reduced risks (Fig. 2b, Table 2).

Differences in yield and quality responses to spring defoliation may occur between clipping and grazing because of selective herbivory. Seasonal changes in preferred plant species, which correspond to plant maturity (Northup 1993), and selection for current-year versus carry-over herbage may reduce the magnitude of changes to micro-environment and plant competition caused by clipping. Defoliation of current-year herbage by livestock should be similar to clipping in April because cool-season species are in vegetative stages and highly palatable while prairie sandreed tiller emergence would be limited. Selection for cool or warm-season species may also be similar in mid-May because most cool-season species are in vegetative or boot stages and warm-season grass tillers are in early vegetative stages. In contrast, most cool-season species will initiate inflorescences in mid-June and cattle will selectively graze prairie sandreed and other warmseason grasses thus removing less herbage from cool-season species than removed by clipping (Streeter et al. 1968, Northup 1993). Consequently, competition from cool-season species may reduce growth of prairie sandreed and reduce the relative value of improved late-summer forage quality in prairie sandreed after grazing in June.

Conclusion

Precipitation, which occurs primarily during the summer for much of the rangeland dominated by prairie sandreed, will have a measurable effect on how vegetation responds to spring defoliation. Soil moisture deficits will reduce or stop plant growth after spring grazing (Dahl 1963, Ganskopp 1998). Drought is a common and unpredictable component of semi-arid ecosystems. Regional drought has occurred in about 20% of the years since 1940 in the northern Great Plains (Holechek et al. 1989). Shortages in the quantity of herbage are



Fig. 4. Effects of (a) spring cutting height and (b) clipping date on yield of current-year herbage from species other than prairie sandreed in mid-September.

generally of greater economic importance than nutritive value under drought conditions. Additionally, CP content was higher when drought occurred in our study than when near average precipitation occurred.

A limited opportunity may exist in June for some improvement in late-summer nutritive value of prairie sandreed with minimal risk to livestock performance and rangeland resources. Small but measurable increases in CP content and IVDMD after 50% defoliation of prairie sandreed in mid-June would not fully meet nutritional requirements of growing and/or lactating cattle (NRC 1984) and less than half of the potential number of animal unit days (AUD) of grazing would be available in late summer compared to ungrazed control. However, the sum of AUDs or gain in livestock weight from mid-June and mid-September grazing periods may equal or exceed the total from a single mid-September grazing period. Conversely, if late-summer forage quality is the primary concern, it may be possible for cattle to select a diet of equal quality for an equal number of AUD's in pastures that are deferred until late summer with no risk to rangeland resources.

Prairie sandreed is commonly more abundant on spring-grazed compared to summer-grazed pastures on sandy range sites throughout the northern Great Plains. Heavily grazing pastures in late April before prairie sandreed tillers emerge may be an effective method of maintaining or increasing prairie sandreed populations. Cattle will selectively graze cool-season species in the spring (Streeter et al. 1968). Feeding relatively large numbers of cattle on selected pastures during late April should provide adequate nutrition for livestock and allow cattle to defoliate cool-season species to the physical limit of their foraging ability. Excluding livestock from these pastures from the time of tiller emergence to the end of the growing

season should allow prairie sandreed to fully benefit from late-April grazing when average or above average precipitation occurs. Herbage in these pastures could then be used for dormant-season grazing, or left for watershed or wildlife habitat management objectives.

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Season-long grazing of seeded cool-season pastures in the Northern Great Plains

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Abstract

In the semi-arid Northern Great Plains, seeded cool-season grasses are primarily recommended for spring and fall grazing because their nutritive quality is perceived as too low to support acceptable animal weight gains during mid-summer. This perception is caused in part by traditional use of high spring stocking rates, which leave little forage remaining for mid-summer use. A study was conducted near Mandan, N.D. to determine the effect of moderate (1.6 AUM ha⁻¹) and heavy (2.4 AUM ha⁻¹) stocking rates on weight gains of yearling Hereford steers grazing crested wheatgrass (Agropyron desertorum [Fisch. Ex Link] Schult.), western wheatgrass (Pascopyrum smithii [Rydb.] Löve), smooth bromegrass (Bromus inermis Leyss.) and flat (class II and III) and rolling (class IV and VI) native rangelands. Studies were conducted over a 140-day grazing season during 3 summers from 1992-1994. Grazing was initiated in mid-May and terminated the last week of September or the first week of October each year. At the end of each grazing season forage samples were clipped inside and outside of cages randomly located in each pasture to estimate end of season standing crop and forage utilization. Animal activity data were collected for 9 days during August and September 1994. Steer weight gains were not different among crested wheatgrass, western wheatgrass, smooth bromegrass and flat native pastures, but weight gains of steers grazing rolling native pastures were lower (P<0.05) than gains on other pastures. Weight gains per steer were 8% higher (P<0.05) on moderately grazed pastures, but weight gains per hectare were 39% higher on heavy grazed pastures. Steers spent more (P<0.05) time grazing on smooth bromegrass than western wheatgrass, crested wheatgrass, or flat native pastures and they also spent more (P<0.05) time grazing on heavy than moderately grazed pastures. Seeded cool-season grasses produced season-long yearling steer weight gains comparable to flat native, and superior to rolling native pastures, even when grazed at a stocking rate that was 80% heavier than the rate recommended for native rangeland by the USDA-SCS (1984). These results suggest that seeded cool-season grasses can be successfully grazed season-long in the Northern Great Plains where environmental conditions and precipitation patterns are comparable to central North Dakota.

Resumen

En la región semiárida de las Grandes Planicies del Noreste, los zacates de crecimiento invernal son recomendados principalmente para el apacentamiento de primavera y otoño porque se percibe que su calidad nutritiva es muy baja para producir ganancias de peso animal aceptables a mediados del verano. Esta percepción es causada, en parte, por el uso tradicional de altas cargas animal en primavera, lo cual deja poco forraje remanente para utilizar a mediados del verano. Se condujo un estudio cerca de Mandan, N.D. para determinar el efecto de la carga animal moderada (1.6 UAM ha⁻¹) y alta (2.4 UAM ha⁻¹) en las ganancias de peso de novillos de año raza herford apacentando "crested wheatgrass" (Agropyron desertorum [Fish. Ex Link] Schult), "western wheatgrass" (Pascopyrum smithii [Rybd]Löve), "smooth bromegrass" (Bromus inermis Leyss.) en pastizales nativos planos (clase II y III) y ondulados (clase IV y VI). Los estudios se realizaron durante 3 veranos, de 1992 a 1994, y la estación de apacentamiento fue de 140 días. El apacentamiento fue iniciado a mediados de mayo y terminado la última semana de septiembre o la primera de octubre. Al final de la estación de apacentamiento se cortaron muestras de forraje fuera y dentro de jaulas localizadas aleatoriamente en cada potrero, esto con el fin de determinar la biomasa en pie al final de la estación de crecimiento y la utilización del forraje. Durante 9 días, entre agosto y septiembre de 1994, se tomaron datos de actividad animal. Las ganancias de peso de los novillos no difirieron "crested wheatgrass", "western wheatgrass", "smooth bromegrass" y pastizales planos. Sin embargo, las ganancias de peso de los novillos apacentando pastizales ondulados fueron menores (P<0.05) que las ganancias obtenidas en otros potreros. Las ganancias por novillo fueron 8% mayores (P<0.05) en los potreros con carga animal moderada, pero las ganancias por hectárea fueron 39% mayores en los potreros con carga alta. Los novillos pasaron mas tiempo (P<0.05) apacentando "smooth bromegrass" que "western wheatgrass", "crested wheatgrass o pastizales planos. Los novillos de la carga alta pasaron mas tiempo apacentando que los de la carga moderada. Los zacates de crecimiento invernal produjeron ganancias de peso comparables a las obtenidas en pastizales planos y superiores a la de los ondulados, aun cuando fueron apacentados con una carga animal 80% mayor a la recomendada por el USDA-SCS (1984) para pastizales nativos. Estos resultados sugieren que en las Grandes Planicies de Noreste, donde las condiciones ambientales y patrones de precipitación son comparables a los de la región central de North Dakota, los zacates invernales pueden ser exitosamente pastoreados a lo largo de la estación.

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Key Words: native rangelands, seasonality, crested wheatgrass, smooth bromegrass, western wheatgrass

Seeded cool-season grasses are usually recommended for spring or fall grazing in the Northern Great Plains because it is widely believed that their nutritive quality in mid-summer is too low to support adequate livestock weight gains. This pattern of use was first suggested by Sarvis (1941) and Williams and Post (1945), when they suggested that crested wheatgrass and smooth bromegrass were best used in the spring when they provided nutritious forage for grazing 2–3 weeks earlier than native grasses. They also indicated these grasses should be completely utilized by about 1 July. Rogler et al. (1962) reported that "most cool-season grasses lose quality rapidly heading in late after June". Nevertheless, both Sarvis (1941) and Williams and Post (1945) demonstrated that crested wheatgrass and smooth bromegrass could be grazed season-long and produce animal weight gains comparable to native range. Heavy stocking rates and early starting dates were used by Williams and Post (1945), thus grazing periods ranged from 79 to 180 days for crested wheatgrass and 69-160 days for smooth bromegrass depending on yearly precipitation patterns. Because producers needed a dependable summerlong forage supply, the practice of fully utilizing cool-season grasses in spring, followed by grazing native rangeland in summer was adopted. Later Frischknecht et al. (1953) suggested that crested wheatgrass could also be used for fall grazing, if regrowth was adequate. In the 1970's extensive coal mining in the Northern Great Plains (Ries et al. 1977) brought the related need to stabilize reclaimed land with perennial grasses. Before mining, about 51% of this land was in native rangelands and used for grazing. Reseeding mined land to native grass mixtures was expensive, slow, and difficult, while introduced cool-season grasses could be more readily established at lower cost and grazed more quickly after seeding. Hofmann and Ries (1989) using moderate stocking rates based on recommendations resulting from lessons learned in the 1930's drought (Dyksterhuis 1949), found that cool-season grasses could be grazed season-long (126 days) on reclaimed mined

et al. (1993) also demonstrated that cool-season grasses seeded on nonmined land and grazed at the same season-long (133 days) stocking rate as native range produced comparable yearling steer weight gains. In that study both cool-season and native pastures were stocked at 1.5 AUM ha⁻¹, which was 15% greater than the USDA-SCS (1984) recommended stocking rate for native range in this area. However, forage utilization rates were only 30-40%, indicating that a higher stocking rate might be warranted. The objective of the study reported here was to determine the effect of moderate (1.6) and heavy (2.4)AUM ha⁻¹) season-long (140 days) stocking rates on forage utilization and the performance of yearling steers grazing crested wheatgrass, western wheatgrass, smooth bromegrass, and flat and rolling native range.

Materials and Methods

land in central North Dakota. Hofmann

Grazing studies were conducted near Mandan, North Dakota for 140 days each summer from 1992-1994. Grazing periods were from 14 May to 30 September 1992; 20 May to 6 October 1993; and 19 May to 5 October 1994. Seeded species were 'Nordan' crested wheatgrass (Agropyron desertorum [Fisch. Ex Link] Schult.), 'Rodan' western wheatgrass (Pascopyrum smithii [Rydb.] Löve), and 'Lincoln' smooth bromegrass (Bromus inermis Leyss.). Native pastures were located on adjacent class II and III, 2-6% slope (flat native) and class IV and VI, 9-25% slope (rolling native) land. Seeded and native pastures included 2 replications at both moderate and heavy stocking rates. Seeded pastures were established on fine-silty, mixed Pachic Haploborolls

and fine-silty mixed Typic Haploborolls soils. Flat native pastures were located on soils comparable to the seeded pastures, but rolling pastures were located on loam, silt loam, and silty clay Entic and Typic Haploborolls soils.

The 73 ha of land to be seeded was divided into 6.1 ha plots and randomly seeded to 1 of the 3 cool-season grasses by no-till seeding into spring wheat stubble (Triticum aestivum L.) in the fall of 1985 (Hofmann et al. 1993). Four, 6.1 ha plots were fenced on both flat and rolling native rangelands (Hofmann et al. 1993). In the current study there were 5 pasture treatments, 2 stocking rates and 2 replications of each pasture treatment by stocking rate combination for a total of twenty pastures. Stocking rates were established by adjusting pasture size to 5.7 and 3.8 ha for moderate and heavy stocking rates, respectively.

Pastures were stocked with 3 Hereford steers (*Bos taurus*) weighing approximately 294 kg at the beginning of each grazing season. Due to limited forage utilization (30-42%) in the previous study (Hofmann et al. 1993) stocking rates of 1.6 (moderate), and 2.4 AUM ha⁻¹ (heavy) were established. None of the pastures were fertilized for at least 10 years before the current study was initiated in 1992, and pastures received no fertilizer during this study.

Rolling and flat native pastures differed in species composition as well as topography. Flat native pastures contained blue grama (*Bouteloua gracilis* [H.B.K.] Griffiths), green needlegrass (*S. viridula* Trin.), needleandthread (*Stipa comata* Trin. and Rupr.), western wheatgrass, sedges (Carex spp.), threeawn (*Aristida* spp.) and Kentucky bluegrass (*Poa pratensis* L.). Rolling native pastures contained the same species as flat native pastures plus little bluestem (*Schizachyrium scoparium* [Michaux]

Table 1. Precipitation (mm) and mean monthly ambient air temperatures (C) between April and October for 1992–1994 and the 80-year average.

1992		1	1993		1994)-yr avg	
Month	Precip.	Temp.	Precip.	Temp.	Precip.	Temp.	Precip.	Temp.
April	8	6	36	6	31	6	38	6
May	38	15	69	13	18	16	58	12
June	117	17	114	16	71	19	89	18
July	69	17	343	18	48	19	56	21
August	41	17	48	19	5	19	51	21
Sept	23	13	5	12	69	16	41	14
Oct	5	7	0	6	147	9	20	8
Total	301		615		389		353	
Table 2. Pasture means averaged over stocking rate and years for end of season standing crop (standing crop), forage utilization, and yearling steer weight gains for 140-day grazing seasons in 1992–1994)¹.

	Standi	Standing Crop		St	eer perforn	nance
Pasture	Ungrazed	Grazed		Gain steer-1	ADG	Gain ha ⁻¹
	(kg ł	1a ⁻¹)	(%)		(kg)	
Smooth bromegrass	2,898 ^d	1,946 ^b	31 ^a	143 ^a	1.02 ^a	93 ^a
Western wheatgrass	5,018 ^a	3,476 ^a	$28^{\rm a}$	141 ^a	1.01 ^a	91 ^a
Crested wheatgrass	4,367 ^b	3,164 ^a	27 ^a	136 ^a	0.97^{a}	89 ^a
Flat native	3,885 ^{bc}	3,134 ^a	19 ^a	131 ^a	0.94^{a}	86^{a}
Rolling native	3,371 ^{cd}	2,470 ^b	25 ^a	115 ^b	0.82^{b}	75 ^b
SE	202	175	3	4.5	0.03	3.2

¹Means within a column with different letters differ (P<0.05).

Nash) and patches of western snowberry (*Symphoricarpos occidentalis* Hook), and buffaloberry (*Shepherdia argentea* [Pursh] Nutt.).

End of the grazing season standing crop was estimated by hand clipping forage at a 5 mm stubble height from 36 by 36-cm plots, randomly located inside 0.9 by 4.3-m cages used to prevent grazing. Similar procedures were used to collect forage samples at random locations outside of each cage to estimate the amount of residual forage where grazing occurred. Samples were clipped far enough from cages to eliminate any animal-cage effects. One sample was clipped from both inside and outside of each cage and cages were relocated each year. Three cages were randomly located in each seeded pasture, 4 cages in each flat native, and 5 cages in each rolling native pasture. More cages were located in native pastures because of the diversity of vegetation. Forage samples were dried at 60°C and used to calculate end of season standing crop dry matter (DM), and grazed residue per hectare. Forage utilization was calculated as follows: Utilization (%)=[(end of season standing crop DM (within cage samples)-grazed residue DM (outside of cage samples))/end of season standing crop DM (within cage samples)] x 100.

Steers were weighed following an overnight stand without feed or water at the beginning and end of each study and at 21-day intervals during the studies. Trace mineralized salt containing 96-98.5% salt, 0.35% zinc, 0.34% iron, 0.20% manganese, 0.033% copper, 0.007% iodine, and 0.005% cobalt (Akzo Salt, Inc., Clarks Summit, Penn.) was available at all times.

In 1994 steer activities on smooth bromegrass, western wheatgrass, crested wheatgrass, and flat native pastures were observed every 20 minutes from dawn to dusk for 9 days in August and September. All treatments were observed on the same days. Time spent grazing, lying, standing, walking, playing, scratching, salting and drinking were recorded, and the percent of the total daily observation time spent in these activities was calculated. Walking, playing, scratching, salting, and drinking were minor activities which occupied little time and thus were grouped and analyzed as all other activities.

Daily precipitation and ambient minimum and maximum air temperatures were recorded at a weather station located about 3.2 km north of the study site. Monthly precipitation totals and mean monthly temperatures (minimum and maximum) were calculated and compared to historic values (Table 1).

Data were analyzed by analysis of variance according to a completely randomized design. Pasture treatment, stocking rate and pasture treatment x stocking rate were tested using replicate(pasture treatment x stocking rate) as the test term. Year, pasture treatment x year, stocking rate x year, and pasture treatment x stocking rate x year were tested using year x replication (pasture treatment x stocking rate) as the test term. Data were considered significant at P<0.05 unless otherwise indicated.

Results and Discussion

During this 3-year study, western wheatgrass had the highest average end of season standing crop dry matter per hectare and the greatest amount of grazed residue at the end of the grazing season, while smooth bromegrass had the lowest end of season standing crop dry matter and the least amount of grazed residue (Table 2). There were significant (P<0.05) interactions between pasture treatment and year for both ungrazed and grazed end of season standing crop and utilization rates, indicating that forage production and utilization differences among pasture treatments were not entirely consistent over the 3 years. In a previous study on this site (Hofmann et al. 1993), western wheatgrass was also the most productive and had the most grazed residue at the end of the season, but hilly (rolling) native pastures produced the least end of season standing crop and had the least remaining grazed residue. Despite increased stocking rates, forage utilization over both moderate and heavy treatments in the current study was lower than utilization rates for these pastures reported by Hofmann et al. (1993). Utilization in the current study ranged from 19% for flat native to 31% for smooth bromegrass pastures, but differences among pastures were not significant. Utilization rates were probably lower in the current study because precipitation levels were generally above normal (Table 1), while the earlier study included 2 drought years.

Although smooth bromegrass pastures produced the least forage, steers gained similarly on smooth bromegrass and

Table 3. Stocking rate means for end of season standing crop (standing crop), forage utilization, and yearling steer weight gains averaged over pasture treatments and years for 140-day grazing seasons in 1992–1994^{1,2}.

	Standi	Standing Crop		Steer performance		
Stocking rate	Ungrazed	Grazed		Gain steer ⁻¹	ADG	Gain ha ⁻¹
	(kg h	a ⁻¹)	(%)		(kg)	
Moderate	4,223 ^a	3,189 ^a	22 ^b	138 ^a	0.99^{a}	73 ^b
Heavy	3,582 ^b	$2,480^{b}$	30^{a}	128 ^b	0.92^{b}	101 ^a
SE	129	112	2	2.9	0.02	2

¹Moderate and heavy stocking rates were 1.6 and 2.4 AUM ha⁻¹, respectively.

Means within a column with different letters differ (P<0.05).



Fig. 1. Three year (1992–1994) average cumulative yearling steer weight gains by weighing period (± SE) for seeded cool-season and flat and rolling native pastures.

western wheatgrass (Table 2). There were no significant (P>0.20) interactions among pasture treatment, stocking rate, or year with regard to animal performance data. Weight gains were not different among seeded cool-season pastures and the flat native treatment, but weight gains were lower for the rolling native treatment. Hofmann et al. (1993) reported that weight gains for the level (flat) native pastures were significantly higher than gains from the seeded coolseason pastures. Differences between the 2 studies suggest that when precipitation is average or above, cool-season grasses support good animal performance, but with drought conditions weight gains from the well established native grasses may be greater.

Three-year-average cumulative weight gains show that beginning with the second weighing period in late June, steers grazing smooth bromegrass tended to have the highest weight gains while steers grazing rolling native pastures had the lowest (Fig. 1). These weight gain differences continued to increase until the end of the season, but cumulative gain differences among the other grasses changed little after mid-July. Although Sarvis (1941) reported seasonlong average daily gains on smooth bromegrass (0.92 kg) which were comparable to weight gains in this study (Table 2), they sometimes reported large weight losses in August and September which were not encountered in the current study (Fig. 1).

End of season standing crop averaged over all cool-season and native pastures was greater (P<0.05) at the moderate compared to the heavy stocking rate, which suggests the heavier stocking rate may have adversely affected forage production (Table 3). Grazed residue was also greater (P<0.05) on moderately grazed pastures, therefore forage disappearance per hectare through grazing, trampling and deterioration was comparable between moderate and heavy stocking rates at 1,034 and 1,102 kg ha⁻¹, respectively.

Average daily gains were significantly higher (8%) at the moderate compared to the heavy stocking rate, but weight gains per hectare were 39% higher for the heavy stocking rate (Table 3). Cumulative weight gains for moderate and heavy stocking rate treatments averaged over all 3 years did not vary significantly (P<0.11) until mid-July (Fig. 2). From early August until October, steers grazing at the moderate stocking rate had

Table 4. Mean end of year standing crop (standing crop), forage utilization, and yearling steer weight gains averaged over pasture treatment and stocking rates for 140-day grazing seasons in 1992, 1993, and 1994¹.

	Standi	ng Crop	Utilization	S	teer perforn	nance
Year	Ungrazed	Grazed		Gain steer-1	ADG	Gain ha ⁻¹
	(kg ha	⁻¹)	(%)		(kg)	
1992	3,483 ^c	2,544 ^c	27^{a}	135 ^a	0.96 ^a	88^{a}
1993	3,928 ^b	3,136 ^a	20^{b}	139 ^a	0.99^{a}	91 ^a
1994	4,296 ^a	$2,818^{b}$	32 ^a	125 ^b	0.89^{b}	82 ^b
SE	120	81	2	2	0.01	1.2

¹Means within a column with different letters differ (P<0.05).



Fig. 2. Three year (1992–1994) average cumulative yearling steer weight gains by weighing period (± SE) for moderate and heavy stocking rates.

progressively higher weight gains than steers grazing at the heavy stocking rate.

Ungrazed end of season standing crop increased significantly from 1992-1994, but the grazed end of season standing crop was lower in 1994 than 1993 (Table 4). Higher ungrazed end of season standing crop each year may have reflected a gradual recovery from the drought of 1988 and 1989 and carry over water from 1993. Lauenroth and Sala (1992) also reported a lag time between increased precipitation and a response in forage production. Forage utilization was highest in 1994, and lowest in the extremely wet year of 1993. End of season grazed and ungrazed standing crop differences between 1993 and 1994 could have been due to less growing season precipitation in 1994, which would have resulted in less forage regrowth and lower grazed end of season standing crop. The high ungrazed end of season standing crop in 1994 probably occurred early in the summer as a result of stored moisture from 1993. It is unlikely that ungrazed end of season standing crop levels were substantially affected by a build up of the previous year's forage growth, because cages were relocated each year.

Steers on smooth bromegrass pas-

tures spent significantly more time grazing than steers on western wheatgrass, crested wheatgrass, or flat native pastures (Table 5). Time utilized in other activities was similar among pastures, but steers grazing smooth bromegrass tended to spend less time lying, standing, and in all other activities compared to steers on the other pastures. Smooth bromegrass pastures produced the lowest dry matter yield, yet steer weight gains were comparable to the other pastures, therefore grazing time may have been greater because steers were exercising a high degree of diet selectivity or because less available forage necessitated increased grazing time. Hardison et al. (1954), Kirby and Stuth (1982), and many others have reported that cattle graze selectively and that they prefer leaves to stems.

Steers spent significantly less time grazing and more time standing on moderately stocked than on heavily stocked pastures (Table 6). Steers on heavily stocked pastures may have spent more time grazing because lower forage production (Table 3) necessitated increased grazing time for them to reach satiety.

Conclusions

Results of this study show that coolseason seeded grasses can be grazed continuously over a 140-day season in the Northern Great Plains, where precipitation and environmental conditions are similar to central North Dakota, and support yearling steer weight gains comparable to good quality native

Table 5. Percentage of observation time steers were engaged in various activities during dawn to dusk observation for 9 days in August and September 1994¹.

		ACT	TIVITY	
Pasture	Grazing	Lying	Standing	All Other
		(%)		
Smooth bromegrass	64 ^a	26 ^a	7 ^a	3 ^a
Western wheatgrass	57 ^b	31 ^a	9 ^a	4^{a}
Crested wheatgrass	59 ^b	30 ^a	7^{a}	4^{a}
Flat native	58 ^b	28^{a}	$10^{\rm a}$	4^{a}
SE	1.1	1.1	0.7	0.3

¹Means within a column with different letters differ (P<0.05).

Table 6. Effect of stocking rate on the percentage of time steers were engaged in various activities during dawn to dusk observations over 9 days in August and September 1994^{1,2}.

		ACT	TVITY	
Stocking rate	Grazing	Lying	Standing	All Other
Moderate	58 ^b	30 ^a	9 ^a	4^{a}
Heavy	61^{a}	28^{a}	7 ^b	4^{a}
ŠE	0.8	0.8	0.5	0.2

¹Moderate and heavy stocking rates were 1.6 and 2.4 AUM ha⁻¹, respectively.

²Means within a column with different letters differ (P<0.05).

rangelands and better than more typical rolling rangelands. These data agree with results reported by Hofmann et al. (1993), but do not support the popular management philosophy that cool-season grasses should only be used for spring and fall grazing. Data from this study further indicate that it may be possible to graze cool-season grasses season-long at stocking rates as much as 80% higher than USDA-SCS (1984) recommendations for native range. Acceptable stocking rates will vary according to soil type and precipitation amounts. Good quality native rangelands should not be plowed and reseeded to coolseason grasses, but disturbed lands or marginal croplands can be seeded to cool-season grasses for season-long grazing. Introduced cool-season grass seed is less expensive, the grasses are easier to establish, and they can be grazed sooner after seeding compared to native grass mixtures. Planting introduced cool-season grasses also gives producers the additional flexibility of alternating between small grain and perennial grass production.

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Caatinga vegetation dynamics under various grazing intensities by steers in the semi-arid Northeast, Brazil

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Abstract

The effects of cattle grazing were evaluated on range dynamics of the Caatinga which is a deciduous dry woodland, covering most of the semi-arid Brazilian Northeast. Three stocking rates (SR) were studied (heavy, 1 steer 6.7 ha⁻¹; moderate 1 steer 10 ha⁻¹; light, 1 steer 13.3 ha⁻¹), in addition to an ungrazed exclosure (zero stocking). In the first phase (1978-81) each stocking rate was tested under continuous and deferred grazing. In the second phase (1981-84), deferred grazing was eliminated, so that pastures became replications of continous grazing. Six steers per pasture were used, and pasture size was used to vary stocking rate. There was no effect of stocking rate or grazing system period on the frequency of the herbaceous species. They were, however, influenced by rainfall in the period, and could be divided into 3 groups. Sixteen species increased with increasing rainfall during the last months of the rainy season, and reached the highest frequency in 1984. Eleven species also increased with increasing rainfall but reached the highest frequency in 1983. Rainfall had no effect on the frequency of 2 important species, Herissantia crispa (L.) Briz. and Selaginella convoluta Spring. Death rate of 5 shrubs (Lippia microphylla Cham., Croton rhamnifolius (Kunth em.) Mull. Arg. Calliandra depauperata Benth, Cordia leucocephala Moric., and Bauhinia cheilantha (Bong.) Steud.) decreased with decreasing stocking rate, 11.7, 9.3, 7.7, and 4.5%, respectively on heavy, moderate, light, and zero stocking. Death rates were higher in easily broken shrub species, L. microphylla and C. leucocephala. Stocking rate also influenced the height growth rate of the tagged shrubs, being respectively -2.7 and 9.8% for heavy and zero stocking. Mean density of shrubs and trees, determined by the Point-Centered Quarter Method, was respectively 21,109, and 447 plants ha⁻¹ in 1982, and 13,230 and 401 plants in 1984; the main cause of the high shrub death (37.3%) was probably the 1982 drought. Density was not affected by stocking rate. Considering the 7 experimental areas separately, there was no regression between 1982 and 1984 shrub densities. There was, however, regression between 1982 density and the difference between 1982 and 1984 densities.

Key Words: tropical woodlands, stocking rate, native pastures, grazing system, shrubs and trees, herbaceous stratum, frequency.

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Resumo

Estudaram-se 3 taxas de lotação anual (TL) (pesada, 1 boi 6,7 ha⁻¹; média, 1 boi 10,0 ha⁻¹ leve, 1 boi 13,3 ha⁻¹), além de uma exclusão livre de pastejo (zero). Na 1ª etapa (1978-81), cada TL foi estudada sob 2 sistemas de pastejo, contínuo e rotacionalmente deferido com 3 subdivisões. Na 2ª etapa (1981-84), as subdivisões foram eliminadas, passando a ser repetições do pastejo contínuo. Usaram-se 6 bovinos machos por tratamento. Não houve influência nem da TL e nem do curto periodo de pastejo diferido na freqüência (FQ) das espécies (spp) herbáceas. A grande variação na precipitação anual se refletiu na FQ delas, as quais foram divididas em 3 grupos, sendo o principal deles formado por 16 spp muito influenciadas, para as quais houve correlação (P<0,05) entre os 2 parametros. Não houve efeito da precipitação na FQ de duas spp importantes (Herissantia crispa (L.) Briz. e. Selaginella convoluta Spring.). A mortalidade de 5 arbustos etiquetados (Lippia microphylla Cham., Croton rhamnifolius (Kunth em.) Mull. Arg., Calliandra depauperata Benth, Cordia leucocephala Moric. e. Bauhinia cheilantha (Bong.) Steud.) diminuiu com o decréscimo na TL, sendo 11, 7, 9, 3, 7, 7 e 4,5% respectivamente para Pesada Média, Leve e Zero, havendo diferença significativa entre pastejo e exclusão. Houve diferença (P<0,05) entre arbustos, sendo maior naqueles mais fáceis de serem quebrados como L. microphylla e C. leucocephala. A TL também influenciou significativamente no crescimento em altura, sendo respectivamente de -2,7 e 9,8% para Pesada e Zero. A densidade de arbustos e árvores, determinada pelo Método do Ponto Quadrante, foi respectivamente de 21.109 e 447 plantas ha⁻¹ em 1982, e de 13.230 e 401 plantas ha⁻¹ em 1984, sendo a grande mortalidade de arbustos (37,3%) no período 1982-84 provavelmente devido a grande seca de 1982, nao havendo influência da TL. Considerando-se as 7 áreas experimentais isoladamente, não houve regressão entre as densidades de arbustos de 1982 e 1984, havendo contudo regressão entre a densidade de arbustos em 1982 e a diferença entre as densidades de 1982 e 1984.

The Caatinga, a thorny, deciduous, dry woodland that covers most of the Brazilian Northeast, is dominated by woody plants, and may be a range with the highest density of shrubs and trees in the world. Most of the Caatinga types are shrub dominated, although as quoted by Sampaio (1995), some authors have claimed that most of the Caatinga area was orginally covered with trees. Most woody species are deciduous, and leaf litter represents an important source of forage in the dry season (Kirmse et al. 1987). In spite of being less sensitive to overgrazing than pastures dominated by herbaceous

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vegetation, the Caatinga has also been degradated (Vasconcelos Sobrinho 1949, Andrade-Lima 1981). Degradation was probably caused by shifting cultivation and fuel wood harvest because the Caatinga-covered region is densely populated. The paucity of grasses is one of its characteristics (Cole 1960), but there is evidence that the Caatinga invaded some formerly more open areas covered by grasses (Smith 1974), a situation analogous to those in USA and Australia, in which overgrazing resulted in establishment of woody plants (Herbel 1985, Harrington and Hodgkinson 1986).

Annual stocking rate (SR) is the most important factor in maintaining the stability of a native pasture. In Caatinga, a stocking rate of 15 ha head⁻¹ of cattle is usually recommended (Banco do Nordeste do Brasil 1971, Rodrigues and Borges 1979). On most of the properties, however, cattle are associated with goats and sheep. Adjustments in stocking rate may be followed by adjustment in grazing system for range rest (Hickey 1977). Rotationally deferred grazing is designed to help degraded ranges recover (Sampson 1913).

This research was undertaken to study the effect of stocking rate and rotationally deferred grazing by cattle on the Caatinga of the semi-arid region of Pernambuco State, in the Brazilian Northeast.

Materials and Methods

The research was conducted at the Caatinga Experimental Station (CEC) (9°21' S Lat; 370 m altitude) of the Brazilian Agricultural Research Corporation (EMBRAPA)-Agricultural Research Center for Semi-Arid Tropics (CPATSA), in Petrolina municipality. The area has flat topography and redyellow podzolic soils (Burgos and Cavalcanti 1991) with the following characteristics: pH = 5.8; $Ca^{2+} + Mg^{2+} =$ $3.3 \text{ meq}/100 \text{ g}; / \text{Al}^{3+} = 0.7 \text{ meq}/100 \text{ g}; \text{P}$ - 3 ppm. Annual potential evaporation is 2,630 mm, with a mean annual precipitation of 567 mm (Table 1). The vegetation is an arboreous-shrubby Caatinga, with the tree stratum dominated by Mimosa tenuiflora (Wiild.) Poir., and the shrub stratum dominated by Lippia microphylla Cham., Croton rhamnifolius (Kunth em.) Mull. Arg., Calliandra depauperata Benth., Cordia leucocephala Moric, and Bauhinia cheilantha (Bong.) Steud. The last 3 are endemic to the Caatinga (Prado 1991). The distinction between shrubs and trees follows criteria of Walker (1976).

The study was conducted from August 1978 to August 1984, being divided into 2 phases. In the first one (August 1978-August 1981), 3 stocking rates were tested: heavy, H, 1 steer 6.7 ha⁻¹ (40 ha); moderate, M, 1 steer 10 ha^{-1} (60 ha); light, L, 1 steer 13.3 ha⁻¹ (80 ha). These were combined with 2 grazing systems: continuous (C), and rotationally deferred, with 3 sub-divisions (D). A fourth treatment was an ungrazed exclosure of zero stocking (40 ha). None of the 7 experimental units was replicated. In the second phase (August 1981-August 1984), the pastures used for deferred grazing were eliminated, becoming replications of the continuous grazing treatments. Six steers per experimental unit were utilized, resulting in a total area of 400 ha, including the exclosure of 40 ha.

To evaluate the effect of grazing intensity on vegetation, macro plots of 20 x 5 m were located systematically within each experimental unit, with 6 in continuous grazing and in the exclosure, and 12 in deferred grazing (4 in each sub-division). In each macro plot, the following 2 aspects were evaluated: (1) frequency of herbaceous species and density of seedlings (height <0.5) of woody plants, determined annually, in May (in 1979, 1981, 1983, and 1984) or in April (in 1980 and 1982), by using five $1-m^2$ (2 x 0.5 m) quadrats, placed at random; and (2) mortality and growth in height and in canopy cover of 7 aluminum tagged shrub species, including the 5 dominant ones already cited plus *Lantana camara* L. and *Croton sonderianus* Mull. Arg. Measurements were taken biennially, by monitoring up to 10 plants of each shrub species in each macro plot, starting in 1980.

A third aspect was evaluated in the experimental units in 1982 and 1984: the density of trees and shrubs (height > 0.5 m) as determined by the Point-Centered Quarter Method (PQM) (Cottam and Curtis 1956). Our purpose was to measure effect of stocking rate on the woody stratum as a whole. In the areas of 40 ha (1 steer 6.7 ha⁻¹ and exclusion), 60 ha (1 steer 10.0 ha⁻¹) and 80 ha (1 steer 13.3 ha⁻¹), 100, 150, and 200 points were placed respectively. The sampling points were distributed in lines, and in each one, the minimum and maximum distances between sampling points were 21 and 26, m respectively, any distance in this interval being determining by sorting. From each quarter of each sampling point, I measured the distance to the nearest shrub and to the nearest tree. Shrubs were classified into 3 heights (H1 > 0.5 - 1 m; H2 > 1-2; H3 > 2m).

Data were interpreted, taking into account the effect of stocking rate and year on the frequency of herbaceous species, the effect of stocking rate and biennium on the performance of the tagged shrubs, and the effect of the year on the density of shrubs and trees. Data on mortality and changes in height and canopy cover of the tagged shrubs were transformed from percentage to arc sin and evaluated with analysis of variance (Snedecor and Cochran 1976). As treatments were not replicated, the interactions involving stocking rate, biennia, and plant species were used as residual variance.

 Table 1. Rainfall from October 1978—September 1984, and historical mean, October 1963—September 1997.

				Precipitatio	n		
Month	1978–79	1979–80	1980–81	1981–82	1982–83	1983–84	Historical mean
				(mm)			
OctNov.	42.2	52.1	56.0	14.6	0.0	62.8	58.7
Dec.	12.2	54.8	34.0	90.7	82.8	7.2	75.1
Jan.	118.1	186.0	20.3	10.4	60.0	20.5	72.2
Feb.	96.4	201.3	4.8	20.6	166.4	3.9	83.7
Mar.	28.3	44.7	340.3	79.1	205.2	314.2	140.9
Apr.	118.4	10.6	20.5	97.4	0.8	122.9	86.4
May	18.4	1.2	0.5	1.4	0.0	44.6	20.2
Jun.–Sep.	24.0	1.3	8.4	50.2	37.6	29.2	30.3
Total	458.0	552.0	484.8	364.4	552.8	605.3	567.5

Results and Discussion

There were 29 herbaceous species which occurred with average frquency > 4.33%, considering the means calculated over 6 years and 4 treatments. Plant types were distributed as follows: pteridophyte, 1 species; monocotyledonous, 6 species (5 grasses and 1 sedge); and dicotyledonous, 22 species. The lowest limit of 4.33% was chosen arbitrarily.

Grazing system had no effect on either herbaceous species frequencies or on woody seedling densities. This was an expected result because each deferred sub-division was kept free of grazing only once during the rainy season in the first phase. In the review conducted by Gammon (1978), long duration of deferred grazing was necessary to get improvement in pastures. Grazing system effect on the tagged shrubs was not evaluated because measurements were started in 1980 and the deferred system was discontinued in 1981.

Through the years, there was a remarkable variation in frequency of most of the herbaceous species, probably caused by variation in the precipitation. Based on this aspect, the species were divided into 3 groups (Table 2). The frequencies of the first 16 species were strongly infuenced by rainfall, and an association (P<0.01) was detected between rainfall in the period February-April (or Feb.-Mar.) and their mean frequency (Fig. 1). In another Caatinga, Araújo Filho (1985) detected that herbaceous plants reacted more to fluctuation in rainfall than to livestock use. If phytomass had been measured, similar associations would probably have been obtained, confirming that in semi-arid climates, increases in rainfall result in linear increases in primary productivity (Whittaker 1975). In the second group (11 species), the frequencies also varied strongly through the years, but their highest value was in 1983. There was a change of positions between the first 2 groups in 1983 and 1984, i.e. the first group had the highest mean frquency in 1984, while the second group did so in 1983. The third group, made up of 2 very important Caatinga forbs, H. crispa and S. convoluta, was little influenced by rainfall. S. convoluta is a reviviscent pteridophyte that passes the dry season completely desiccated, i.e., in air dried stage with a saturation deficit of up to 72–74% (Morello 1954). On a small ranch near the experimental site, these species pro-

Table 2. Frequency of herbaceous species in 3 groups (Group 1 = very influenced by rainfall but with highest frequency in 1984; Group 2 = Same as Group 1, but with highest frequency in 1983; Group 3 = little influenced by rainfall), in the period 1979–84.

Group/Species Plant 1979 1980 1981 1982 1983 1984 Group 1					Frequ	ency			
	Group/Species	Plant class	1979	1980	1981	1982	1983	1984	
Group 1 Prospalum scutatum Nees ex Trin. Grass 2.14 9.29 7.38 0.71 2.38 4.05 Hypris suaveolens (L.) Poit. Forb 0.00 8.81 11.19 0.00 5.24 10.95 Eragrensis cillaris (L.) R. Br. Grass 4.05 3.10 8.33 0.00 13.33 14.52 Diodia teres Walt. em.) Mull Arg. Forb 0.00 3.81 25.71 0.00 8.10 12.62 Marsypionthes channedrys (Vahl.) Kum Forb 0.00 1.67 3.62 22.38 Borreria cymoides DC. Forb 0.00 0.00 4.29 0.00 1.67 3.62 Vaphea sp. Forb 0.00 3.81 7.14 1.90 19.52 33.33 Mitracaryne frigidas K. Schum. Forb 0.00 3.81 12.14 8.57 17.14 19.05 Turmera pumilica L. Forb 0.67 24.52 38.33 0.00 41.67 61.67 Cyperus uncinulatics Schuad. ex Nees Sedge					(%)				
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Cuphes sp.Forb0.00 3.81 12.14 0.7110.71 31.19 Polygala brizoides St. Hil.Forb0.95 3.81 7.14 1.9019.52 33.33 Mitracarpus frigidus K. Schum.Forb1.19 8.81 32.14 8.57 17.14 19.05Turnera punilea L.Forb0.00 3.81 19.29 12.38 35.48 39.29 Schwenkia americana Roy ex L.Forb 6.67 24.52 38.33 0.00 41.67 61.67 Cyperus uncinulatus Schrad. ex NeesSedge 0.48 17.62 40.48 34.05 39.52 48.57 Gymnopogon rupestris RidleyGrass 29.52 45.78 35.95 17.86 37.38 51.67 Centratherum punctatum Cass.Forb 25.48 54.29 59.05 1.67 54.29 73.81 MeanSchi 15.84 23.22 52.44 23.29 35.13 GroupMacroptilium martii Benth.Forb 0.00 2.86 1.43 0.71 16.67 6.19 Triungleta sp.Forb 0.00 2.38 1.90 20.00 10.48 Croton glandulosus (L. em)Forb 1.67 5.95 2.86 1.90 21.19 14.52 Pornulac an claraca L.Forb 0.00 5.00 9.29 13.10 24.76 16.43 Brachiaria molis (Sw.) L.Paroh 6.67 8.57 0.48 0.95 45.00 9.29 Mul	Borreria ocymoides DC.	Forb	0.00	0.00	4.29	0.00	16.67	37.62	
Polygala brizoides St. Hil. Forb 0.95 3.81 7.14 1.90 19.52 33.33 Mitracarpus frigidus K. Schum. Forb 1.19 8.81 32.14 8.57 17.14 19.05 Turnera pumilea L. Forb 0.00 3.81 19.29 12.38 35.48 39.29 Schwenkia americana Roy ex L. Forb 6.67 24.52 38.33 0.00 41.67 61.67 Cyperus uncinulatus Schrad. ex Nees Sedge 0.48 17.62 40.48 34.05 39.52 48.57 Grunnopogon rupestris Ridley Grass 18.10 49.05 55.48 2.38 58.09 75.71 Centratherum punctatum Cass. Forb 2.5.48 54.29 59.05 1.67 54.29 73.81 Mean 5.61 15.84 23.22 52.24 23.29 35.13 Group Macroppillium martii Benth. Forb 0.00 2.86 1.43 0.71 16.67 6.19 Triumfetta sp. Forb 1.67 5.95 2.86 1.90 21.19 14.52	<i>Cuphea</i> sp.	Forb	0.00	3.81	12.14	0.71	10.71	31.19	
Mitracarpus frigidus K. Schum. Forb 1.19 8.81 32.14 8.57 17.14 19.05 Turmera punilea L. Forb 0.00 3.81 19.29 12.38 35.48 39.29 Schwenkia americana Roy ex L. Forb 6.67 24.52 38.33 0.00 41.67 61.67 Cypnens uncinulatus Schrad. ex Nees Sedge 0.48 17.62 40.48 34.05 39.52 48.57 Gymnopogon rupestris Ridley Grass 29.52 45.78 35.95 17.86 37.38 51.67 Panicum trichoides Sw. Grass 18.10 49.05 55.48 2.38 58.09 75.71 Centratherum punctatum Cass. Forb 25.61 15.84 23.22 5.24 23.29 35.13 Group 40.00 2.86 1.43 0.71 16.67 6.19 Triumfetta sp. Forb 0.00 2.86 1.43 0.71 16.67 6.19 Mull. Arg <td< td=""><td>Polygala brizoides St. Hil.</td><td>Forb</td><td>0.95</td><td>3.81</td><td>7.14</td><td>1.90</td><td>19.52</td><td>33.33</td><td></td></td<>	Polygala brizoides St. Hil.	Forb	0.95	3.81	7.14	1.90	19.52	33.33	
Turnera pumilea L.Forb 0.00 3.81 19.29 12.38 35.48 39.29 Schwenkia americana Roy ex L.Forb 6.67 24.52 38.33 0.00 41.67 61.67 Cyperus uncinulatus Schrad. ex NeesSedeg 0.48 17.62 40.48 34.05 39.52 48.57 Gymnopogon rupestris RidleyGrass 29.52 45.78 35.95 17.86 37.38 51.67 Panicum trichoides Sw.Grass 18.10 49.05 55.48 2.38 58.09 75.71 Centratherum punctatum Cass.Forb 25.48 54.29 59.05 1.67 54.29 73.81 Mean5.61 15.84 23.22 5.24 23.29 35.13 GroupTriunfetta sp.Forb 0.00 2.86 1.43 0.71 16.67 6.19 Croton glandulosus (L. em)Forb 1.43 8.10 5.00 2.38 22.86 2.62 Mull ArgParonia cancellata (L.F.) Cav.Forb 1.67 5.95 2.86 1.90 21.19 14.52 Portulaca oleracea L.Forb 0.00 5.33 7.14 0.00 33.33 16.67 Bernardia sinoides Mull Arg.Forb 0.48 0.48 15.48 1.43 38.81 24.52 Althernanthera brasiliana (L.)Korb 2.86 19.52 29.29 9.55 4.52 45.00 9.29 Microtea scabrida Urb.Forb 0.48 0.48	Mitracarpus frigidus K. Schum.	Forb	1.19	8.81	32.14	8.57	17.14	19.05	
Schwenkia americana Roy ex L. Forb 6.67 24.52 38.33 0.00 41.67 61.67 Cyperus uncinulatus Schrad. ex Nees Sedge 0.48 17.62 40.48 34.05 39.52 48.57 Gynnopogon rupestris Ridley Grass 29.52 45.78 35.95 17.86 37.38 51.67 Panicum trichoides Sw. Grass 18.10 49.05 55.48 2.38 58.09 75.71 Centratherum punctatum Cass. Forb 25.48 54.29 59.05 1.67 54.29 73.81 Mean 5.61 15.84 23.22 5.24 23.29 35.13 Group Macroptilium martii Benth. Forb 0.00 2.86 1.43 0.71 16.67 6.19 Triumfetta sp. Forb 0.00 2.86 1.43 0.71 16.67 6.19 Wall Arg Forb 0.00 3.33 7.14 0.00 3.33 16.67 Portulaca oleracea L Forb 0.00 5.00 9.29 13.10 24.76 1643	Turnera pumilea L.	Forb	0.00	3.81	19.29	12.38	35.48	39.29	
Cyperus uncinulatus Schrad. ex Nees Sedge 0.48 17.62 40.48 34.05 39.52 48.57 Gymnopogon rupestris Ridley Grass 29.52 45.78 35.95 17.86 37.38 51.67 Panicum trichoides Sw. Grass 18.10 49.05 55.48 2.38 58.09 75.71 Centratherum punctatum Cass. Forb 25.48 54.29 59.05 1.67 54.29 73.81 Mean 5.61 15.84 23.22 5.24 23.29 35.13 Group 5.61 15.84 23.22 5.24 23.29 35.13 Macroptilium martii Benth. Forb 0.00 2.86 1.43 0.71 16.67 6.19 Triumfetta sp. Forb 0.00 2.38 1.90 20.00 10.48 Croton glandulosus (L. em) Forb 1.67 5.95 2.86 1.90 21.19 14.52 Portulaca oleracea Llata (LF.) Cav. Forb 0.00 5.00	Schwenkia americana Roy ex L.	Forb	6.67	24.52	38.33	0.00	41.67	61.67	
Gymnopogon rupestris Ridley Grass 29.52 45.78 35.95 17.86 37.38 51.67 Panicum trichoides Sw. Grass 18.10 49.05 55.48 2.38 58.09 75.71 Centratherum punctatum Cass. Forb 25.48 54.29 59.05 1.67 54.29 73.81 Mean 5.61 15.84 23.22 5.24 23.29 35.13 Group Macroptilium martii Benth. Forb 0.00 2.86 1.43 0.71 16.67 6.19 Triumfetta sp. Forb 0.00 2.86 1.43 0.71 16.67 6.19 Triumfetta sp. Forb 0.00 2.38 1.90 20.00 10.48 Croton glandulosus (L. em) Forb 1.43 8.10 5.00 2.38 22.86 2.62 Mull. Arg Portulaca oleracea L. Forb 0.00 3.33 7.14 0.00 33.33 16.67 Bernardia sinoides Mull Arg. Forb<	Cyperus uncinulatus Schrad. ex Nees	Sedge	0.48	17.62	40.48	34.05	39.52	48.57	
Panicum trichoides Sw. Grass 18.10 49.05 55.48 2.38 58.09 75.71 Centratherum punctatum Cass. Forb 25.48 54.29 59.05 1.67 54.29 73.81 Mean 5.61 15.84 23.22 5.24 23.29 35.13 Group Macroptilium martii Benth. Forb 0.00 2.86 1.43 0.71 16.67 6.19 Mull. Arg Forb 0.00 0.00 2.38 1.90 20.00 10.48 Pavonia cacellata (L.F.) Cav. Forb 1.43 8.10 5.00 2.38 22.86 2.62 Mull. Arg Porb 0.00 3.33 7.14 0.00 33.33 16.67 Pavonia cacellata (L.F.) Cav. Forb 0.00 5.00 9.29 13.10 24.76 16.43 Brachiaria molis (Sw.) L. Parodi Grass 6.67 8.57 0.48 0.95 45.00 9.29 Schulze Forb 7.38 26.90 24.76 1.67 38.81 24.52 Schulze Corchorus argutu	Gymnopogon rupestris Ridley	Grass	29.52	45.78	35.95	17.86	37.38	51.67	
Centratherum punctatum Cass. Forb 25.48 54.29 59.05 1.67 54.29 73.81 Mean 5.61 15.84 23.22 5.24 23.29 35.13 Group Macroptilium martii Benth. Forb 0.00 2.86 1.43 0.71 16.67 6.19 Triumfeita sp. Forb 0.00 0.00 2.38 1.90 20.00 10.48 Croton glandulosus (L. em) Forb 1.43 8.10 5.00 2.38 22.86 2.62 Mull. Arg Pavonia cancellata (L.F.) Cav. Forb 1.67 5.95 2.86 1.90 21.19 14.52 Portulaca oleracea L. Forb 0.00 3.33 7.14 0.00 33.33 16.67 Brachiaria molis (Sw.) L. Parodi Grass 6.67 8.57 0.48 0.95 45.00 9.29 Microtea scabrida Urb. Forb 0.48 0.48 1.43 38.81 24.52 Althermanthera brasiliana (L.) Kuntze Forb <	Panicum trichoides Sw.	Grass	18.10	49.05	55.48	2.38	58.09	75.71	
Mean 5.61 15.84 23.22 5.24 23.29 35.13 Group Macroptilium martii Benth. Forb 0.00 2.86 1.43 0.71 16.67 6.19 Triumfetta sp. Forb 0.00 0.00 2.38 1.90 20.00 10.48 Croton glandulosus (L. em) Forb 1.43 8.10 5.00 2.38 22.86 2.62 Mull. Arg Pavonia cancellata (L.F.) Cav. Forb 1.67 5.95 2.86 1.90 21.19 14.52 Portulaca oleracea L. Forb 0.00 3.33 7.14 0.00 33.33 16.67 Bernardia sinoides Mull Arg. Forb 0.00 5.00 9.29 13.10 24.76 16.43 Brachiaria molis (Sw.) L. Parodi Grass 6.67 8.57 0.48 0.95 45.00 9.29 Microtea scabrida Urb. Forb 0.48 0.48 15.48 1.43 38.81 24.52 Microtea scabrida Urb. Forb 0.48 0.48 15.48 1.43 38.81 24.52	Centratherum punctatum Cass.	Forb	25.48	54.29	59.05	1.67	54.29	73.81	
Group Macroptilium martii Benth. Forb 0.00 2.86 1.43 0.71 16.67 6.19 Triumfetta sp. Forb 0.00 0.00 2.38 1.90 20.00 10.48 Croton glandulosus (L. em) Forb 1.43 8.10 5.00 2.38 22.86 2.62 Mull. Arg Pavonia cancellata (L.F.) Cav. Forb 1.67 5.95 2.86 1.90 21.19 14.52 Portulaca oleracea L. Forb 0.00 3.33 7.14 0.00 33.33 16.67 Bernardia sinoides Mull Arg. Forb 0.00 5.00 9.29 13.10 24.76 16.43 Brachiaria molis (Sw.) L. Parodi Grass 6.67 8.57 0.48 0.95 45.00 9.29 Microtea scabrida Urb. Forb 0.48 0.48 15.48 1.43 38.81 24.52 Mithermanthera brasiliana (L.) Kuntze Forb 7.38 26.90 24.76 1.67 38.81 35.71 Hybanthus calceolaria (L.) Forb 6.90 29.05 21.90 3.10	Mean		5.61	15.84	23.22	5.24	23.29	35.13	
Macropilium martii Benth. Forb 0.00 2.86 1.43 0.71 16.67 6.19 Triumfetta sp. Forb 0.00 0.00 2.38 1.90 20.00 10.48 Croton glandulosus (L. em) Forb 1.43 8.10 5.00 2.38 22.86 2.62 Mull. Arg 14.52 Pavonia cancellata (L.F.) Cav. Forb 1.67 5.95 2.86 1.90 21.19 14.52 Portulaca oleracea L. Forb 0.00 3.33 7.14 0.00 33.33 16.67 Brachiaria molis (Sw.) L. Parodi Grass 6.67 8.57 0.48 0.95 45.00 9.29 Microtea scabrida Urb. Forb 7.38 26.90 24.76 1.67 38.81 24.52 Althermanthera brasiliana (L.) Kuntze Forb 2.86 19.52 29.29 9.05 51.43 24.52 Schulze 2.49	Group								
Triumfetta sp. Forb 0.00 0.00 2.38 1.90 20.00 10.48 Croton glandulosus (L. em) Forb 1.43 8.10 5.00 2.38 22.86 2.62 Mull. Arg Pavonia cancellata (L.F.) Cav. Forb 1.67 5.95 2.86 1.90 21.19 14.52 Portulaca oleracea L. Forb 0.00 3.33 7.14 0.00 33.33 16.67 Bernardia sinoides Mull Arg. Forb 0.00 5.00 9.29 13.10 24.76 16.43 Brachiaria molis (Sw.) L. Parodi Grass 6.67 8.57 0.48 0.95 45.00 9.29 Microtea scabrida Urb. Forb 0.48 0.48 15.48 1.43 38.81 24.52 Althernanthera brasiliana (L.) Kuntze Forb 7.38 26.90 24.76 1.67 38.81 35.71 Hybanthus calceolaria (L.) Forb 2.86 19.52 29.29 9.05 51.43 24.52 Schulze Corchorus argutus H.B.K. Forb 6.90 29.05 21.90 3.10	Macroptilium martii Benth.	Forb	0.00	2.86	1.43	0.71	16.67	6.19	
Croton glandulosus (L. em) Forb 1.43 8.10 5.00 2.38 22.86 2.62 Mull. Arg Pavonia cancellata (L.F.) Cav. Forb 1.67 5.95 2.86 1.90 21.19 14.52 Portulaca oleracea L. Forb 0.00 3.33 7.14 0.00 33.33 16.67 Bernardia sinoides Mull Arg. Forb 0.00 5.00 9.29 13.10 24.76 16.43 Brachiaria molis (Sw.) L. Parodi Grass 6.67 8.57 0.48 0.95 45.00 9.29 Microtea scabrida Urb. Forb 0.48 0.48 15.48 1.43 38.81 24.52 Althernanthera brasiliana (L.) Kuntze Forb 7.38 26.90 24.76 1.67 38.81 35.71 Hybanthus calceolaria (L.) Forb 2.86 19.52 29.29 9.05 51.43 24.52 Schulze Corchorus argutus H.B.K. Forb 6.90 29.05 21.90 3.10 48.33 37.86 Mean 2.49 9.98 10.91 3.29 32.83 <td< td=""><td>Triumfetta sp.</td><td>Forb</td><td>0.00</td><td>0.00</td><td>2.38</td><td>1.90</td><td>20.00</td><td>10.48</td><td></td></td<>	Triumfetta sp.	Forb	0.00	0.00	2.38	1.90	20.00	10.48	
Mull. Arg Pavonia cancellata (L.F.) Cav. Forb 1.67 5.95 2.86 1.90 21.19 14.52 Portulaca oleracea L. Forb 0.00 3.33 7.14 0.00 33.33 16.67 Bernardia sinoides Mull Arg. Forb 0.00 5.00 9.29 13.10 24.76 16.43 Brachiaria molis (Sw.) L. Parodi Grass 6.67 8.57 0.48 0.95 45.00 9.29 Microtea scabrida Urb. Forb 0.48 0.48 15.48 1.43 38.81 24.52 Althernanthera brasiliana (L.) Kuntze Forb 7.38 26.90 24.76 1.67 38.81 35.71 Hybanthus calceolaria (L.) Forb 2.86 19.52 29.29 9.05 51.43 24.52 Schulze Corchorus argutus H.B.K. Forb 6.90 29.05 21.90 3.10 48.33 37.86 Mean 2.49 9.98 10.91 3.29 32.83 18.07 Group 3 Selaginella convoluta Spring Pteridophyte 29.76 26.90 30.00 34.05<	Croton glandulosus (L. em)	Forb	1.43	8.10	5.00	2.38	22.86	2.62	
Pavonia cancellata (L.F.) Cav. Forb 1.67 5.95 2.86 1.90 21.19 14.52 Portulaca oleracea L. Forb 0.00 3.33 7.14 0.00 33.33 16.67 Bernardia sinoides Mull Arg. Forb 0.00 5.00 9.29 13.10 24.76 16.43 Brachiaria molis (Sw.) L. Parodi Grass 6.67 8.57 0.48 0.95 45.00 9.29 Microtea scabrida Urb. Forb 0.48 0.48 15.48 1.43 38.81 24.52 Althernanthera brasiliana (L.) Kuntze Forb 7.38 26.90 24.76 1.67 38.81 35.71 Hybanthus calceolaria (L.) Forb 2.86 19.52 29.29 9.05 51.43 24.52 Schulze Corchorus argutus H.B.K. Forb 6.90 29.05 21.90 3.10 48.33 37.86 Mean 2.49 9.98 10.91 3.29 32.83 18.07 Group 3 Selaginella convoluta Spring Pteridophyte 29.76 26.90 30.00 34.05 30.00	Mull. Arg								
Portulaca oleracae L. Forb 0.00 3.33 7.14 0.00 33.33 16.67 Bernardia sinoides Mull Arg. Forb 0.00 5.00 9.29 13.10 24.76 16.43 Brachiaria molis (Sw.) L. Parodi Grass 6.67 8.57 0.48 0.95 45.00 9.29 Microtea scabrida Urb. Forb 0.48 0.48 15.48 1.43 38.81 24.52 Althernanthera brasiliana (L.) Kuntze Forb 7.38 26.90 24.76 1.67 38.81 35.71 Hybanthus calceolaria (L.) Forb 2.86 19.52 29.29 9.05 51.43 24.52 Schulze Corchorus argutus H.B.K. Forb 6.90 29.05 21.90 3.10 48.33 37.86 Mean 2.49 9.98 10.91 3.29 32.83 18.07 Group 3 Selaginella convoluta Spring Pteridophyte 29.76 26.90 30.00 34.05 30.00 35.48 Herissantia crispa (L.) Briz. Forb 48.81 39.05 42.86 37.86 59.05 <t< td=""><td>Pavonia cancellata (L.F.) Cay.</td><td>Forb</td><td>1.67</td><td>5.95</td><td>2.86</td><td>1.90</td><td>21.19</td><td>14.52</td><td></td></t<>	Pavonia cancellata (L.F.) Cay.	Forb	1.67	5.95	2.86	1.90	21.19	14.52	
Bernardia sinoides Mull Arg. Forb 0.00 5.00 9.29 13.10 24.76 16.43 Brachiaria molis (Sw.) L. Parodi Grass 6.67 8.57 0.48 0.95 45.00 9.29 Microtea scabrida Urb. Forb 0.48 0.48 15.48 1.43 38.81 24.52 Althernanthera brasiliana (L.) Kuntze Forb 7.38 26.90 24.76 1.67 38.81 35.71 Hybanthus calceolaria (L.) Forb 2.86 19.52 29.29 9.05 51.43 24.52 Schulze Corchorus argutus H.B.K. Forb 6.90 29.05 21.90 3.10 48.33 37.86 Mean 2.49 9.98 10.91 3.29 32.83 18.07 Group 3 Selaginella convoluta Spring Pteridophyte 29.76 26.90 30.00 34.05 30.00 35.48 Herissantia crispa (L.) Briz. Forb 48.81 39.05 42.86 37.86 59.05 58.33 Mean 39.28 32.97 36.43 35.95<	Portulaca oleracea L.	Forb	0.00	3.33	7.14	0.00	33.33	16.67	
Brachiaria molis (Sw.) L. Parodi Grass 6.67 8.57 0.48 0.95 45.00 9.29 Microtea scabrida Urb. Forb 0.48 0.48 15.48 1.43 38.81 24.52 Althernanthera brasiliana (L.) Kuntze Forb 7.38 26.90 24.76 1.67 38.81 35.71 Hybanthus calceolaria (L.) Forb 2.86 19.52 29.29 9.05 51.43 24.52 Schulze Corchorus argutus H.B.K. Forb 6.90 29.05 21.90 3.10 48.33 37.86 Mean 2.49 9.98 10.91 3.29 32.83 18.07 Group 3 Selaginella convoluta Spring Pteridophyte 29.76 26.90 30.00 34.05 30.00 35.48 Herissantia crispa (L.) Briz. Forb 48.81 39.05 42.86 37.86 59.05 58.33 Mean 39.28 32.97 36.43 35.95 44.52 46.90	Bernardia sinoides Mull Arg.	Forb	0.00	5.00	9.29	13.10	24.76	16.43	
Microtea scabrida Urb. Forb 0.48 15.48 1.43 38.81 24.52 Althernanthera brasiliana (L.) Kuntze Forb 7.38 26.90 24.76 1.67 38.81 35.71 Hybanthus calceolaria (L.) Forb 2.86 19.52 29.29 9.05 51.43 24.52 Schulze Corchorus argutus H.B.K. Forb 6.90 29.05 21.90 3.10 48.33 37.86 Mean 2.49 9.98 10.91 3.29 32.83 18.07 Group 3 Feridophyte 29.76 26.90 30.00 34.05 30.00 35.48 Herissantia crispa (L.) Briz. Forb 48.81 39.05 42.86 37.86 59.05 58.33 Mean 39.28 32.97 36.43 35.95 44.52 46.90	Brachiaria molis (Sw.) L. Parodi	Grass	6.67	8.57	0.48	0.95	45.00	9.29	
Althernanthera brasiliana (L.) Kuntze Forb 7.38 26.90 24.76 1.67 38.81 35.71 Hybanthus calceolaria (L.) Forb 2.86 19.52 29.29 9.05 51.43 24.52 Schulze Corchorus argutus H.B.K. Forb 6.90 29.05 21.90 3.10 48.33 37.86 Mean 2.49 9.98 10.91 3.29 32.83 18.07 Group 3 Selaginella convoluta Spring Pteridophyte 29.76 26.90 30.00 34.05 30.00 35.48 Herissantia crispa (L.) Briz. Forb 48.81 39.05 42.86 37.86 59.05 58.33 Mean 39.28 32.97 36.43 35.95 44.52 46.90	Microtea scabrida Urb	Forb	0.48	0.48	15.48	1.43	38.81	24.52	
Animatic constraints (Li) familie Forb 1.86 1952 29.29 9.05 51.43 24.52 Schulze Corchorus argutus H.B.K. Forb 6.90 29.05 21.90 3.10 48.33 37.86 Mean 2.49 9.98 10.91 3.29 32.83 18.07 Group 3 Selaginella convoluta Spring Pteridophyte 29.76 26.90 30.00 34.05 30.00 35.48 Herissantia crispa (L.) Briz. Forb 48.81 39.05 42.86 37.86 59.05 58.33 Mean 39.28 32.97 36.43 35.95 44.52 46.90	Althernanthera brasiliana (L.) Kuntze	Forb	7.38	26.90	24.76	1.67	38.81	35.71	
All of the state Schulze Corchorus argutus H.B.K. Forb 6.90 29.05 21.90 3.10 48.33 37.86 Mean 2.49 9.98 10.91 3.29 32.83 18.07 Group 3 Selaginella convoluta Spring Pteridophyte 29.76 26.90 30.00 34.05 30.00 35.48 Herissantia crispa (L.) Briz. Forb 48.81 39.05 42.86 37.86 59.05 58.33 Mean 39.28 32.97 36.43 35.95 44.52 46.90	Hybanthus calceolaria (L.)	Forb	2.86	19.52	29.29	9.05	51.43	24.52	
Corchorus argutus H.B.K. Forb 6.90 29.05 21.90 3.10 48.33 37.86 Mean 2.49 9.98 10.91 3.29 32.83 18.07 Group 3 Selaginella convoluta Spring Pteridophyte 29.76 26.90 30.00 34.05 30.00 35.48 Herissantia crispa (L.) Briz. Forb 48.81 39.05 42.86 37.86 59.05 58.33 Mean 39.28 32.97 36.43 35.95 44.52 46.90	Schulze	1 010	2.00	17102		2100	01110	21102	
Mean 2.49 9.98 10.91 3.29 32.83 18.07 Group 3 Selaginella convoluta Spring Pteridophyte 29.76 26.90 30.00 34.05 30.00 35.48 Herissantia crispa (L.) Briz. Forb 48.81 39.05 42.86 37.86 59.05 58.33 Mean 39.28 32.97 36.43 35.95 44.52 46.90	Corchorus argutus H.B.K.	Forb	6.90	29.05	21.90	3.10	48.33	37.86	
Group 3 Selaginella convoluta Spring Pteridophyte 29.76 26.90 30.00 34.05 30.00 35.48 Herissantia crispa (L.) Briz. Forb 48.81 39.05 42.86 37.86 59.05 58.33 Mean 39.28 32.97 36.43 35.95 44.52 46.90	Mean		2.49	9.98	10.91	3.29	32.83	18.07	
Solution	Group 3								
Herissantia crispa (L.) Briz. Forb 48.81 39.05 42.86 37.86 59.05 58.73 Mean 39.28 32.97 36.43 35.95 44.52 46.90	Selaginella convoluta Spring	Pteridon	nyte 29.76	26.90	30.00	34.05	30.00	35.48	
Mean 39.28 32.97 36.43 35.95 44.52 46.90	Herissantia crispa (L.) Briz	Forh	48.81	39.05	42.86	37.86	59.05	58.33	
	Mean	- 010	39.28	32.97	36.43	35.95	44.52	46.90	



Fig. 1. Relationship between rainfall of last months of rainy season and mean frequency of 16 herbaceous species.

vided 70% of the herbaceous phytomass at the end of the dry season (Leal 1996).

There were so few plants of *L. camara* and *C. sonderianus* tagged in 1980 that neither the effect of biennium nor of stocking rate could be estimated. *L. microphylla* suffered high mortality, so that parameters other than death rate could not be evaluated. There was a significant influence of biennia on mortality rate, which was highest in the second biennium. The influence of the 1981–82 drought could only be detected in 1984. Rainfall in the crop year 1980–81 was not low, but was highly concentrated in March.

There was no apparent effect of stocking rate on frequency of herbaceous species, and differences among treatments were attributed to heterogeneity of the area. Frequency data might not have been sensitive enough to measure effect of stocking rate as in the work of Hacker (1984) in a semi-arid range in Australia. On the other hand, in a dense vegetation with a forage phytomass of ca. 1,000 kg ha⁻¹, distributed equally in both the herbaceous and woody strata (Albuquerque and Bandeira 1995), steer diets were made up of herbs and shrub leaves, decreasing the grazing pressure on the lower stratum. In addition, the high density of *Neoglaziovia variegata* (Arr. Cam.) Mez and other thorny species in the lower stratum could form micro-sites, protecting the herbs from over-use, and providing them the opportunity to set seed. In South Africa, medium sized stone rubble was considered important in protecting grass seedlings from overgrazing by large herbivores (Van der Walt 1980).

Most of the herbaceous species occurred less frequently in the exclosure than in the grazed areas, except *A. brasiliana* and *P. ninuri*, which occurred most frequently in the exclosure. Most research on grazing in range pastures have been done in the USA, where ranges are dominated by grasses and forbs. Dyksterhuis (1949) based his work on such pastures, and recognized that rest in woodlands does not lead to range dominated by herbaceous plants, but to a denser woody vegetation. This is probably the reason that most of our herbaceous species were less abundant in the exclosure. The density of woody species seedlings was not related to stocking rate (Table 3). Friedel (1986) detected influence from sheep and rabbits on woody seedlings, but no effect from cattle. An important point is the trend for the density of woody seedlings to decrease in the exclosure, following the same trend as most of the herbaceous species. The woody canopy of Caatinga in rest trends to become closed, curtailing the space suitable for the herbaceous stratum. Seedling density also decreased under deferred heavy and moderate stockings, but the decrease in the exclosure was more evident. Seedlings of Tabebuia spongiosa Rizzini were not included in Table 3 because in 1983 a great germination of seeds of this tree occurred (mean of 16.4 plants m⁻²), being completely different from other woody species.

Mortality of the tagged shrubs increased with increasing stocking intensity, and grazing treatments were significantly different from the zero grazing (Table 4). This indicates that cattle could cause overgrazing in the shrub stratum as detected by Toutain (1986), and damage can also be caused by trampling (Chesterfield and Parsons 1985). On the other hand, Kelly and Walker (1976) did not detect any harmful influence of cattle and goats on the woody stratum. Mortality was higher for C. leucocephala and L. microphylla, shrubs that can be broken easily. Stocking rate had a significant effect on the height of the 4 shrubs (Fig. 2). Shrubs under heavy stocking always decreased in height in both biennia, although in one of the pastures, heavy stocking under deferred grazing until August 1981 (HD), all shrubs except C.

Table 3. Density of woody species seedlings (height <0.5 m) in the period 1979–84, under 4 stocking intensities [Heavy (H) = 1 steer 6.7 ha⁻¹; Moderate (M) = 1 steer 10 ha⁻¹; Light (L) = 1 steer 13.3 ha⁻¹; Zero = No grazing] and 2 grazing systems (C = Continuous grazing; D = Deferred grazing until 1981).

			Stocking inter	nsity/Grazing syste	em			
Year	HC	HD	MC	MD	LC	LD	Zero	Mean
				- (seedlings m ⁻²)-				
1979	3.03	5.72	2.50	7.68	2.33	0.87	8.67	4.40 ± 3.0
1980	2.47	7.28	2.20	5.77	2.17	2.37	8.63	4.41 ± 2.8
1981	4.03	5.74	2.36	4.65	1.80	1.79	6.50	3.84 ± 1.9
1982	1.40	5.10	1.53	4.35	2.27	1.45	3.60	2.81±1.5
1983	1.83	4.08	5.10	3.95	2.80	1.03	3.57	$\textbf{3.20} \pm \textbf{1.4}$
1984	2.23	3.37	2.53	3.75	2.53	4.14	3.77	3.19 ± 0.7
Mean	2.50 ± 0.9	5.21 ± 1.4	2.71 ±1.2	5.03±1.5	2.32 ± 0.3	1.94 ± 1.2	5.79 ± 2.5	3.64

Table 4. Mortality of 5 tagged shrubs, submitted to 4stocking intensities, in the period 1980–84 (heavy = 1 steer 6.7 ha⁻¹; Moderate = 1 steer 10 ha⁻¹; Light = 1 steer 13.3 ha⁻¹; Zero = No grazing).

			Stocking intens	ity	
Shrub species	Heavy	Moderate	Light	Zero	Mean
			(%)		
		1st bien	nium (1980-82)		
C. leucocephala	10.90	11.38	7.38	0.00	7.41
L. microphylla	22.92	21.31	13.16	0.00	14.35
B. cheilantha	0.00	8.79	6.09	0.00	3.72
C. depauperata	0.90	0.00	1.39	0.00	0.57
C. rhamnifolius	1.55	0.65	0.00	0.00	0.55
Mean	7.25	8.43	5.60	0.00	5.32 A
		2nd bienni	ium (1982–84)		
C. leucocephala	32.25	31.08	17.70	11.43	23.86
L. microphylla	21.62	4.17	9.09	30.00	16.22
B. cheilantha	18.18	7.23	12.04	2.08	9.88
C. depauperata	2.73	4.17	7.04	0.00	3.48
C. rhamnifolius	3.15	4.55	3.61	1.96	3.32
Mean	16.19	10.24	9.90	9.09	11.35 B
		bien	nia mean		
C. leucocephala	23.07	21.23	12.54	5.71	15.64 a
L. microphylla	22.27	12.74	11.12	15.00	15.28 a
B. cheilantha	9.09	8.01	9.06	1.04	6.80 b
C. depauperata	1.81	2.08	4.21	0.00	2.03 b
C. rhamnifolius	2.35	2.60	1.80	0.98	1.93 b
Mean	11.72 a	9.33 a	7.75 a	4.55 b	8.34

*Means with same lower case letters in the same line, in the same column, and with same capital letters in the same column, are not statistically different (Duncan, P>0.05). In spite of the difference between Heavy and Light being higher than between Light and Zero, there is statistical difference between Light and Zero, because of angular transformation.

leucocephala increased in height in the period 1982-84. This increase was probably caused by the good rains in 1983 and 1984 and lack of competition because HD had the lowest shrub density among the 7 experimental units in 1982. Moderate stocking had the opposite effect compared to HD, plants generally grew until 1982, then lost height the following biennium and became shorter than the initial height. Under light and zero grazing, there was a steady increase in growth of all species in the 2 biennia, except for C. leuco*cephala*, which is easily broken and probably reacted to browsing even with the lightest use.

There was no significant influence of stocking rate on mean canopy cover of the 4 shrubs, even though cover tended to increase under light to zero stocking, and decrease under heavier grazing (Fig. 3). Shrub height was generally measured on the central twig in the canopy, which was most likely to be damaged by browsing. Canopy cover was determined by taking 2 perpendicular measures of canopy diameters, and there was always the chance that all 4 twigs were not browsed, mainly when they are tangled with other shrubs. This is probably the reason for the lack of statistically significant effect of stocking rate on canopy cover.

It could be concluded that cattle might cause degradation of the shrub stratum, but even in the heaviest stocking rate in this study, the degradation was lighter than the alteration caused by the 1981-82 drought. Stocking rates are more likely to be determined by animal performance, rather than vegetation response.

Mean density of shrubs was 37.3% lower in 1984 than in 1982, the difference being considered very high (Table 5). Apparently, this was not caused by stocking rate, because in HD as well as in zero stocking, there were increases in shrub densities (Fig. 4). One point that shows the difference very clearly is the correlation between the mortality of the 7 tagged shrubs in 1982-84 and their "mortality" detected by point-centered quatrum method (PQM) (Table 6). The difference in the columns of this table might be attributed to the plant size. Shrubs marked in 1980 had a mean height of 1 m, while shrubs 0.5 m high were included in the PQM measurements, and younger plants of lower stature are more likely to die. Shrubs 0.5-1 m high made up 67.3 and 47.7% of the total in 1982 and 1984, respectively, while shrubs >2 m high made up 9.3 and 21.4% in 1982 and 1984, respectively. The loss of shrubs in the period 1982-84, that was detected by PQM, might have been caused by the 1982 density, i.e. a high density caused high competition for water in 1982. There was no regression (P>0.05)between 1982 and 1984 densities, there being however regression (P<0.01) between 1982 density and the difference between 1982 and 1984. In 2 of the 3 shrub species in which there were no regression between 1982 density and number of plants that disappeared in the

Table 5. Shrub densities in 1982 and 1984, and percent of shrubs with height between 0.5 and 1 m.

Botanical name	Den	isity	Height (0.5–1 m)	
	1982	1984	1982	1984	
	(plants	s ha ⁻¹ ± SD)	(%	ó)	
C. leucocephala	$4,739 \pm 2,585$	2,231 ± 864**	75.6	52.6	
C. depauperata	$2,909 \pm 1,755$	$2,254 \pm 1,415$ ns	84.2	68.5	
C. rhamnifolius	$2,675 \pm 912$	$2,417 \pm 860^{\text{ns}}$	39.2	26.7	
B. cheilantha	$1,545 \pm 1,433$	$1,241 \pm 810*$	77.6	56.6	
L. microphylla	$1,463 \pm 1,142$	$770 \pm 469 **$	47.4	72.3	
L. camara	$1,268 \pm 1,063$	$349 \pm 262^{**}$	89.5	72.3	
C. sonderianus	$953 \pm 1,085$	$942 \pm 1,153$ ^{ns}	21.9	14.5	
C. microphylla ^{1,2}	540 ± 520	$428 \pm 208 **$	97.8	42.9	
M. arenosa ^{1,2}	520 ± 821	$233 \pm 325 **$	98.3	65.1	
M. tenuiflora ¹	258 ± 28	$214 \pm 91*$	87.3	40.2	
Other tree spp ¹	688 ± 282	516 ± 543 ^{ns}	94.8	64.3	
Other shrub spp	$3,550 \pm 3,213$	$1,633 \pm 976*$	68.4	49.8	
Total	$21,109 \pm 6,825$	13,229 ± 3,601**	67.3 ³	47.7 ³	

***, and ns—Refers to regression coefficient (r²) between shrub densities in 1982 and difference between shrub densities in 1982 and 1984, in the 7 experimental areas

Tree species in shrub state.

²Complete botanical names of species appearing for the first time: Caesalpinia microphylla Mart.; Mimosa arenosa (Willd.) Poir. Weighted mean



Fig. 2. Effect of stocking rate on height of C. depauperata, C. leucocephala, B. cheilantha, C. rhamnifolius, and the mean of these 4 shrubs.

period 1982-84, C. rhamnifolius and C. sonderianus, the difference between 1982 and 1984 densities were very low, resembling the performance of trees.

There were increases in shrub density from 1982 to 1984 in heavy deferred and zero grazing, the areas with lowest densities, and the origin of these additional plants can be questioned. It is supposed that competition and browsing determines which plants will die, which ones will stay below 0.5 m height, and which ones will grow. In the zero grazed exclosure, the 4 main shrubs always increased in height from 1982 to 1984,

and this is evidence that some plants passed from lower height to height > 0.5m. Under heavy stocking, C. rhamnifolius increased in height, while C. leucocephala decreased. Although C. depauperata and B. cheilantha decreased in mean height, these 2 shrubs had small increases in height in heavy deferred from 1982 to 1984. C. depauperata, in spite of having a small increase in height in this paddock, decreased in density, together with C. leucocephala. Most of the increase in density in heavy deferred in 1982-84 came from B. cheilantha and C. rhamnifolius, because a number of plants of these 2 species passed from seedling stage to the height >0.5 m stage, and compensated for the number of plants killed by browsing. In addition, the few plants of L. microphylla that escaped mortality increased in height, although this parameter was not evaluated statistically.

ha⁻¹ ha⁻¹

ha⁻¹

ha⁻¹

ha⁻¹

ha⁻¹

ha⁻¹ ha⁻¹ ha⁻¹

Therefore, the high shrub disappearance in the period 1982-84 might be attributed mainly to the drought, and the amount was determined by the density present in 1982, not only by grazing intensity. In the Sahel, the drought of



Fig. 3. Effect of stocking rate on mean canopy cover of 4 shrub species cited in Fig. 2.



Fig. 4. Relationship between shrub density in 1982 and difference between shrub density in 1982 and 1984 [H = heavy grazing (1 steer 6.7 ha⁻¹); M = moderate grazing (1 steer 10.0 ha⁻¹; L = light grazing (1 steer 13.3 ha⁻¹); Zero = no grazing; C = continuous grazing always; D = rotationally deferred grazing until 1981].

1972 caused death of 50% of shrubs (Bille 1978), even though the density was much lower in comparison to our study. Extreme weather fluctuations in almost all semi-arid environments caused changes in ecosystem appear-

Table 6. Mortality of all tagged shrubs independently of treatments from 1982 to 1984, and difference between 1982 and 1984 densities..

Shrub	Mortality	Difference between
	when tagged	1982 and 1984
C. rhamnifolius	3.61 ¹	9.64 ²
C. depauperata	3.67	22.52
C. sonderianus	7.95	1.15
B. cheilantha	10.20	19.74
L. microphylla	13.77	47.37
C. leucocephala	27.36	52.92
L. camara	46.76	72.48
Mean	16.19	32.33

**Correlation coefficient (r) between columns = 0.89 (P<0.01).

ance, and it is difficult to distinguish between temporary and permanent changes (Dodd 1994). Data from both shrub and herb strata prove that Caatinga and African ranges similarly react more to climate than to grazing pressure (Ellis and Swift 1988).

For density of trees, the difference from 1982-84 was only 10.3% there being an association ($r^2 = 0.71$; P<0.05) between both densities (Table 7). The difference might be attributed to normal tree mortality, being aggravated a little by drought. Bille (1978) found tree morality of 20%. This normal rate of tree mortality is illustrated by the fact that in 1982 there was an association (r² = 0.67; P<0.05) between density of trees and density of tree species in shrub stage. In 1984, there was no association (P>0.05) probably due to the high mortality of 30.6% among trees in shrub stage in the period 1982–84.

Table 7. Tree densities in 1982 and 1984.

	Tree densi	ity
Botanical name	1982	1984
	(plants h	a ⁻¹ ± SD)
M. tenuiflora	174.2 ± 94.90	$148.8 \pm 89.20^{**}$
C. microphylla	55.6 ± 41.61	$49.1 \pm 38.76^{**}$
T. spongiosa	54.2 ± 26.66	$55.9\pm21.08*$
M. arenosa	41.7 ± 59.56	$34.1 \pm 40.84 ^{**}$
C. phyllacanthus ¹	30.5 ± 18.75	$22.3 \pm 11.65^{**}$
M. pseudoglaziovii	i^1 24.6 ± 12.35	$25.7 \pm 18.90 *$
B. leptophloeos ¹	19.1 ± 11.52	$16.8 \pm 9.05 **$
C. vitifolius ¹	14.5 ± 12.53	$15.7 \pm 10.60 ^{**}$
A. piauhiensis ¹	10.0 ± 13.04	$11.7 \pm 13.40 ^{**}$
P. obliqua ¹	3.3 ± 2.37	$3.4 \pm 1.98*$
S. tuberosa	1.8 ± 1.87	2.8 ± 2.80^{ns}
Other spp	17.3 ± 7.23	14.7 ± 5.20^{ns}
Total	446.8 ± 94.21	$401.0 \pm 91.93 *$

****, and ns—Refers to regression coefficient (r²) between tree densities in 1982 and 1984, in the 7 experimental areas.

¹Complete botanical names of species appearing for the first time: *Cnidoscollus phyllacanthus* (Pohl) Mull. Arg.; *Manihot pseudoglaziovii* Pax & K. Hoffm.; *Bursera leptophloeos* (Mart.) Engl.; *Cnidoscollus vitifolius* (Mull. Arg.) Pohl; *Acacia piauhiensis* Benth; *Piptadenia obliqua L*. (Pers.).

Among the trees present in the study area, neither seedlings (height<0.5 m) nor shrubs of *Spondias tuberosa* Arr. Cam. were found. The causes are unknown. It is one of the most important Caatinga fruit trees, providing employment for many people during the 2 month fruiting season.

Conclusion

Neither stocking rate nor the short period of rotationally deferred grazing system affected frequency of herbaceous species. Most of them tended to be less abundant under zero grazing, which might have been caused by the trend of woody plants in the Caatinga to become denser when in rest. There was a remarkable increase in the frequency of herbaceous species with an increase in rainfall in the last months of the rainy season. Low precipitation in 1982 probably caused a high mortality of shrubs. Increasing stocking rate significantly increased mortality and decreased growth in height of most shrubs. Cattle can cause degradation in the shrub stratum, but the 1982 drought caused more damage than the heaviest stocking rate of 1 steer 6.7 ha^{-1} .

¹Data based on whole number of tagged plants. ²From Table 5.

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Rangeland cover component quantification using broad (TM) and narrow-band (1.4 NM) spectrometry

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Abstract

Calibrated predictive relationships obtained from simple and multiple regression of thematic mapper or broad-band (BB) and 1.4 nm interval or narrow-band (NB) spectral data were evaluated for quantifying 11 rangeland components (including total vegetation, forb, grass, shrub, litter, and bare soil) and distinguishing among 6 long-term grazing treatments of sagebrush steppe. In general, all 4 data types predicted similar values for each rangeland cover component. Multiple regression models usually had little advantage over simple regression models for predicting cover, particularly for abundant cover components, although this trend was inconsistent among components. Consequently, simple predictive models are recommended for quantifying rangeland indicator components using remotely-sensed data. The use of NB spectral data resulted in lower standard errors of prediction (SEP), although these reductions were inconsistent among rangeland components. Although both data types distinguished among grazing treatments with major plant compositional differences (P < 0.00) using a multivariate analysis of variance (MANOVA), only the NB data distinguished between grazing treatments with minor ecological differences (P < 0.01). These results suggest that in a practical context, NB data are advantageous for quantifying rangeland cover components and distinguishing among grazing treatments under the condition of our study.

Key Words: indicators, long-term grazing, predictability, sagebrush steppe

Remote sensing of western U.S. rangelands has increased the speed and efficiency of gathering information on this extensive resource (Tueller 1989). In addition to collecting baseline inventory data, this technology can be used as a monitoring tool for evaluating the influence of disturbances (e.g.,

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Resumen

Se evaluaron relaciones predictivas calibradas obtenidas a través de regresiones simples y múltiples de datos de mapas temáticos de banda amplia (BA) y banda estrecha (BE) de 1.4 nm de intervalo. El objetivo fue evaluarlas para cuantificar 11 componentes del pastizal (incluyendo vegetación total, hierbas, zacates, arbustos, mantillo y suelo desnudo) y distinguir entre 6 tratamientos de apacentamiento de largo plazo en una estepa de "sagebrush". En general los 4 tipos de datos predijeron valores similares para cada uno de los componentes de cobertura del pastizal. Los modelos de regresión múltiple usualmente tuvieron poca ventaja sobre los modelos de regresión simple para predecir cobertura, especialmente para los componentes de cobertura abundante, aunque esta tendencia fue inconsistente entre componentes. Consecuentemente, para cuantificar los componentes indicadores del pastizal mediante el uso de datos de sensores remotos se recomienda modelos predictivos simples. El uso de datos de espectro de BE produjeron errores estandard de prediccion mas bajos (ESP), aunque estas reducciones fueron inconsistentes entre componentes del pastizal. A pesar de que ambos tipos de datos y utilizando el análisis multivariado (MANO-VA) distinguieron los tratamientos de apacentamiento con mayores diferencias de composición de plantas (P<0.001) solo los datos de BE distinguieron los tratamientos de apacentamiento con diferencias ecológicas menores (P<0.01). Estos resultados sugieren que en un contexto practico y bajo las condiciones de nuestro estudio, los datos de BE son ventajosos para cuantificar los componentes de cobertura del pastizal y distinguir entre tratamientos de apacentamiento.

livestock grazing) on vegetation composition, productivity, and soil degradation (e.g., Bastin et al. 1993, Pickup et al. 1993). In part, remote sensing is viewed as a favorable alternative to the traditional, ground reconnaisance monitoring methods because the latter are slow, laborious, limited to localized areas, and subject to great variation (West and Smith 1997).

Previous remote sensing of rangelands has been particularly successful at monitoring simple biological attributes such as

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total vegetational cover (e.g., Curran 1980, Gamon et al. 1993). The definition and conceptualization of rangeland "health" or condition, however, has changed to include the amount of bare soil, litter, microphytes (algae, lichen, and moss), standing dead vegetation, and various living plant growth forms (e.g., grasses, forbs, and shrubs) as well (National Research Council, 1994). Soil-based information is necessary to protect the long-term sustainability of the ecosystem, such as ensuring that the minimum threshold of vegetational cover on the soil (e.g., Packer 1951) is maintained. Quantitative information on the relative abundances of plant growth forms are particularly important for managing livestock because they are not only indicative of previous grazing activities (e.g., Mueggler 1950, Laycock 1967, Bork et al. 1998a), but also differ in palatability and nutritional value to livestock.

Rangeland assessment using remote sensing has typically been done using small spatial-scale (i.e., coarse-grained, large pixel size) data collected from broad-band (BB) sensors such as Landsat TM and MSS. These data have been effective in classifying and quantifying total vegetational cover and phytomass (e.g., Mouat et al. 1981, Curran and Williamson 1985, Ustin et al. 1986, Lloyd 1990, Paruelo and Lauenroth 1995) and the cover of growth forms such as shrub (Boyd 1986) and grass (Paruelo and Golluscio 1994). More detailed plant community information has also been obtained from coarse spatial resolution, remotely sensed data using spectral unmixing models, which interpolate the amount of contributing surficial sub-components from either BB spectra (Huete 1986, Pech et al. 1986a, 1986b, Ustin et al. 1986) or narrow-band (NB) spectra (Gamon et al. 1993, Mustard 1993, Roberts et al. 1993, Wessman et al. 1997). These models, however, are not without problems. For example, they are often created under simplified, contrived conditions where only one (or a few) primary vegetation component(s) vary for investigational purposes (e.g., Elvidge and Chen 1995). Because rangelands are complex environments with a great diversity of cover components (and thus, component combinations), the accuracy of these models under practical field conditions is often limited (Price 1994). Another problem with mixture models is that non-linear spectral mixing can occur (Roberts et al. 1993, Borel and Gerstl 1994, Ray and Murray 1996), particularly in arid environments.

A possible alternative to the spectral unmixing approach for quantifying rangeland cover components (e.g., plant growth forms) is alternative spectral variables obtained from the increased spectral resolution of NB remotelysensed data. These data are collected over many more, but narrower, spectral bandwidths within each ground resolution element (or pixel) than BB data. Because the accuracy of quantifying individual cover components depends directly on the potential for establishing relationships between the abundance of each component and the spectral information within individual pixels, an increased number of spectral bands may improve the ability to quantify individual surface components. Price et al. (1992) used this technology to establish relationships between NB reflectance and total plant cover and leaf area index in a tall grass prairie. Testing is needed, however, within more structurally complex vegetation types such as the sagebrush steppe, where plant cover is substantially lower. In addition to having less living cover, vegetational features are discontinuous and mixed with varying proportions of litter, rock, and bare ground (Tueller 1987), creating a heterogeneous environment that complicates the use of remotely-sensed data.

This study evaluated the accuracy and reliability of broad-band (BB) and narrow-band (NB) spectra for quantifying indicator cover components, particularly those required to evaluate rangeland "health" (NRC 1994) and biological integrity (EPA 1994, West et al. 1994). A previous investigation indicated that calibrated predictive relationships obtained from NB spectral data may improve the quantification of detailed cover components (i.e., increase R^2) relative to BB spectral data (Bork 1997). The general objective of this study was to examine whether these apparent improvements, when applied to a series of historical grazing treatments, translated into more accurate quantification of rangeland cover components.

The specific objectives of this investigation were to, (1) determine whether the leading BB and NB spectral variables predict similar cover values per component relative to point-based sampling methods, and (2) determine whether the NB spectral variables improved differentiation among grazing treatments compared with BB spectral variables.

Methods

Study Site

This research was conducted over 2 years at the U.S. Sheep Experiment Station, 10 km north of Dubois, Ida. (44°14'44" N. Latitude, 112°12'47" W. Longitude). This rangeland is situated at about 1,650 m elevation in the northeastern portion of the sagebrush steppe ecosystem type (West 1983). The climate is semiarid with cold winters and warm summers. Average annual precipation was 324.6 mm over the past 64 years, including 70 cm of snow, with an average annual temperature of 6.1°C (NOAA 1993). About 44% of the annual precipitation falls from May to August, with peak precipitation in May and June. In the year of this study, precipitation was 30 mm below average, with April and May slightly above average and June through August slightly below.

Data for this study were collected from 6 long-term seasonal grazing treatments, in fenced paddocks varying in size from 4 to 12.5 ha, located near the station headquarters. Vegetation in the area is dominated by three-tip sagebrush (Artemisia tripartita Rydb.), bluebunch wheatgrass (Pseudoroegnaria spicata [Pursh] A Löve), and arrowleaf balsamroot (Balsamorhiza saggitata [Pursh] Nutt.) (Laycock 1963; with currently preferred latin names of Kartesz 1994). All of the grazing treatments were established between 1923 and 1950, resulting in a minimum of 46 consecutive years of treatment. Of the 6 treatments currently in place, one has been annually fall-grazed and one annually springgrazed since 1923. Two others have been fall-grazed and spring-grazed since 1950, respectively, but were previously grazed during the opposite season between 1923 and 1950. These 4 treatments will hereafter be referred to as the old fall, old spring, new fall, and new spring, respectively. The final 2 treatments were exclosures ungrazed by livestock, created in 1940 and 1950, respectively. Prior to establishment, the newer exclosure was spring-grazed, while the

Table 1. Abundance of cover components within each grazing treatment based on 1995 and 1996 cover data (from Bork et al. 1998a).

	Cover (by Grazing Treatment ¹)					
Component	O-Fall	N-Fall	O-Spring	N-Spring	O-Excl.	N-Excl.
Vegetational:			(%	5)		
Live Forb	14.6	11.8	6.4	8.0	13.3	7.1
Live Grass	16.3	17.8	20.0	11.5	13.3	16.0
Total Herb	30.9	29.7	26.4	19.5	26.6	23.0
Live Shrub	17.4	20.5	25.6	28.8	20.5	22.2
Total Veg.	48.3	50.2	52.0	48.3	47.0	45.3
Other:						
Dead Shrub	3.6	6.6	9.2	10.1	7.4	8.5
Lichen	7.1	4.6	3.3	3.2	3.9	3.9
Litter	16.6	15.0	18.3	18.5	17.9	17.0
Moss	1.5	1.1	2.4	1.1	3.3	5.2
Rock	1.1	1.5	1.3	0.8	0.7	0.8
Soil (bare)	21.7	20.9	13.5	17.9	19.6	19.1

¹Treatments are as follows: O-Fall, annually fall-grazed since 1923; N-Fall, annually fall-grazed since 1950 but springgrazed from 1923–1950; O-Spring, annually spring-grazed since 1923; N-Spring, annually spring-grazed since 1950 but fall-grazed from 1923 to 1950; O-Excl, no sheep grazing since 1940 with fall-grazing from 1923 to 1940; N-Excl., no sheep grazing since 1950 with spring-grazing from 1923–1950.

older, fall-grazed. All livestock grazing within the treatments since the start of the long-term study has been by sheep. For a complete history of the timing and stocking rates on each grazing treatment, see Bork et al. (1998a).

Based on a previous study, average cover values within each grazing treatment are summarized in Table 1 for each of the 11 cover components. In general, repeated spring-grazing by sheep has removed the perennial forbs such as balsamroot, resulting in a heavy cover of sagebrush with abundant annual herbs such as cheatgrass. Annual fallgrazing by sheep has maintained the native herbs and removed shrubs, producing a more balanced mixture of perennial grasses, forbs, and shrubs (Mueggler 1950, Laycock 1967, Bork et al. 1998a). The exclosures are intermediate in composition between the falland spring-grazed areas. Additional residual effects are evident within the 3 switchover treatments (i.e., the new exclosure, fall, and spring paddocks). In particular, the new exclosure and new fall-grazed paddock remain greater in shrub cover than their older counterparts (Laycock 1967, Bork et al. 1998a). The significant historical precedent and information available from this grazing trial make it an ideal location to test the effectiveness of BB and NB spectral data for distinguishing among rangelands (i.e., treatments) with distinctly different vegetational compositions.

Soils in the area have been derived from wind-blown loess, residuum, or

alluvium overlying basalt bedrock . All 6 soil types within the study area are Mollisols, with soil characteristics heterogeneous across the landscape because of the variable thickness of unconsolidated parent material (Natural Resources Conservation Service or NRCS, 1995). The mix of soils within pastures, however, is similar (Bork et al. 1998b). Litter, lichen, moss, bare soil, and exposed rock are relatively common.

Spectral Sampling

Repeated, close-range multispectral measurements were made on cloud free days at 30 randomly-positioned circular plots in each of the 6 grazing treatments, during mid June, July, and August of 1996. All plots were clearly marked to facilitate re-sampling. The sampling dates were selected to maximize the phenological separation documented among the major vegetational components within the study area (Blaisdell 1958), and coincided with peak greenness of all growth forms (early to mid June), moderate herb senescence (mid July), and advanced herb senescence (late August), respectively. A Personal Spectrometer II (Analytical Spectral Devices [ASD] Inc., Boulder, Colorado, 1991), mounted on a light-weight, portable aluminum boom, was used to measure each plot between the peak sunshine hours of 1100 hours and 1500 hours MDT (i.e., within 2 hours of solar noon). The spectral receptor had a 25° field of view. It was oriented vertically 3.4 m directly over the center of each

plot at the end of the boom using a water-level and plumb-bob. This produced a circular instantaneous field-ofview (IFOV) with a diameter of 1.51 m and ground surface area of approximately 1.75 m^2 . The observers and frame were consistently positioned on the north side of the plot to avoid shadowing and disturbing the vegetation.

Spectal sampling was preceded by calibration of the spectrometer using a standardized white *SPECTRALON*^{TM1} panel and dark reading adjustment. Integration time per reading was 175 milliseconds. Calibration was redone at least every 30 min. during each sampling session. Each spectral file was recorded as the average of 5 readings over a 2 second period to minimize the impact of plant movement by wind or other factors (e.g., insects) on the readings.

Spectral readings were recorded as the proportion (%) of incident spectral energy reflected, from 380 to 1075 nm wavelength in consecutive 1.4 nm wide bandwidths (i.e., 500 bands). The shortest wavelength measured was 400 nm to eliminate the ultraviolet region. The upper range was set at 960 nm to include the minor water absorption band at this upper limit (Hoffer 1978), but eliminate the noisy bands beyond this range. In addition to the narrow-band (NB) data, the software used with the spectrometer provided simulated broadband (BB) values (i.e., thematic mapper) that were used as a benchmark to which the NB measurements could be compared. Simulated thematic mapper data consisted of the relative percent reflectance over the same waveband intervals as on the Landsat thematic mapper sensor, but as measured by the PS-II, over the intervals 450–520, 520-600, 630-690, and 760-900 nm, respectively (ASD 1991). These data were not adjusted for differences in gains, etc., between instruments, nor to top of atmosphere equivalent.

Cover Component Sampling

Cover data were collected from each of the 180 plots within 48 hours following June spectral sampling. Cover data were measured using a variation of the point sampling method (Floyd and Anderson 1982), with the minimum

¹Registered trademark of Labsphere Inc., North Sutton, N.H. 03260-0070.

number of points determined from a pilot study (Bork 1997). Each plot was sampled with a point-frame containing 164 equally-spaced points, 10.5 cm apart. Two layers of cross wires 20 cm apart were used to facilitate vertical cross-sighting and reduce parallax.

The surface feature immediately below each point was recorded, with the data compiled into average cover values per component per plot. All 11 surface cover components (Table 1, left column) examined were rangeland soil and vegetation indicators that had either been previously linked directly to rangeland condition within the study area (Mueggler 1950, Laycock 1967, Bork et al. 1998a), or were important on the basis of current rangeland condition theory (NRC 1994).

Data Analysis

Previous work (Bork 1997) had analyzed one-third of the study plots, 10 from each grazing treatment (N = 60), with simple and stepwise multiple regression, to determine, within each of the 11 cover components, the potential improvement in predictability from using narrow-band (NB) as compared with broad-band (BB) spectral data. Data analysis evaluated a wide range of spectral variables from each sampling date in each type of spectral data (BB and NB), including isolated spectral reflectances (i.e., simple variables), as

well as composite variables involving more than one reflectance (i.e., complex variables). Examples of the latter included ratio indices such as the Difference Vegetation Index (near infrared [NIR]red), Normalized Difference Vegetation Index ([NIR-red]/[NIR+red]) (Tucker 1979), and the Soil Adjusted Vegetation Index ([NIR-red]*[1+L]/[NIR+red+L]; where L is an adjustment for bare soil effects) (Huete 1988), as well as derivative (i.e., slope-based) indices for the NB data. Multi-date measurements were used to determine the change in each spectral variable between June and July, July and August, and June and August. From these analyses, 4 regressions were established for each cover component, 2 based on the leading simple regression using single spectral variables (one for each data type) and 2 multiple regression models (one for each data type). These regressions are provided in Table 2.

In the present study, the unique history of each grazing treatment allowed evaluation of how well the calibrated spectral data could address the 2 primary management questions that had been identified within the study area (Bork et al. 1998a). The first of these questions examined the impact of seasonal sheep grazing since 1950 (i.e., the general differences among the fall, spring, and exclosed areas). The second question examined the residual impact of the seasonality of sheep grazing prior to 1950 (i.e., rangeland resilience), wherein the original fall, spring, and exclosed areas were compared to the new fall, new spring, and new exclosed treatments, respectively. Note that our objective was not to document the comprehensive differences in cover components among the treatments as that has been done elsewhere (Bork et al. 1998a), but rather to evaluate how the BB and NB spectral data may differentiate among treatments relative to the 2 primary management questions.

To test the regressions for distinguishing among treatments and contrast the calibrations from each data type, spectral data from the plots not used in the initial calibration procedure (N = 119; 20 in each treatment except the new spring paddock, where the marker for 1 plot was lost due to wind) were used to predict the cover of each component using all 4 regressions (i.e., of the variables in Table 2). This was done by inserting the required spectral variable(s) into each regression and calculating the predicted cover in each plot. Predicted cover from each regression (BB simple and multiple, and NB simple and multiple) within each plot was subsequently compared to measured cover to evaluate the accuracy of the calibrations within each cover component. Overall accuracy was determined for each component by computing the adjusted standard error of predicted cover across all 119 validation plots using the formula:

Table 2. Summary of the leading spectral variables used to predict each cover component with broad-band (BB) and narrow-band (NB) data, using simple and multiple regression.

Component:	Broad-	Band ¹	Narrow-Ba	and ¹
	Simple	Multiple	Simple	Multiple
Vegetational:				
Forb	Jn-Aug DVI ²	Jn Green; Jn NIR	Jn-Aug SL32	Jn B769; Jn B784; Aug B755;
				Aug B897
Herb	Jn-Jy SAVI	Aug Blue; Aug Red; Jn Blue; Jn NIR	Jn-Aug SL16	Jn B769; Aug B599; AugB684
Grass	Aug NIR	Aug NIR	Jn-Jy SL8	Aug B954
Shrub	Aug NDVI	Aug Red; Aug NIR	Aug SAVI 698/670	Aug B670; Aug B698; Aug B883
Total Veg.	Jn NDVI*	Jn Blue; Jn NIR	Jn SAVI 698/670*	Jn B542; Jn B613; Jn B698
Other:				
Dead Shrub	Aug Red*	Aug Blue; Aug Red; Jn Green	Aug SLPA*	Jn B585; Aug B514; Aug B670
Lichen	Jn Blue	Jn Blue	Jn B499	Jn B443; Jn B457; Jn 528; Jn B542; Jn B883
Litter	Jn Red	Jn Red	Jn ARred	Jn B641
Moss	Jy G/B NDVI	Jy G/B NDVI	Jy SAVI 570/400	Jy B755
Rock	Jy Blue	Jy Blue	Jy SAVI 698/670*	Jy B400
Soil (bare)	AugNDVI*	Aug Blue	Aug NDVI Max NIR/MinRed*	Aug B514; Aug B570; Aug B954

¹Simple regressions marked with a '*' are 2nd-order, curvilinear functions.

²Spectral variables derived from multi-temporal sampling dates are represented by differences between data on those dates.

$$=\frac{\{[\operatorname{Sum}_{i=1..}N(\operatorname{PC}_{i} - \operatorname{MC}_{i})^{2}] - [(\operatorname{Sum}_{i=1..}N(\operatorname{PC}_{i} - \operatorname{MC}_{i}))^{2}/N]\}}{\operatorname{Sqrt}[N - 1]}$$
(1)

where:

St. Error Prediction Sqrt

- PC = predicted cover,
- MC = measured cover,
- N = total number of plots, and
- i = the ith plot.

To determine whether the spectral data could distinguish among the 6 grazing treatments, a Multivariate Analysis of Variance (MANOVA) using SAS proc GLM (SAS Institute Inc. 1988) was performed on the set of leading BB spectral variables isolated from the simple regressions (Bork 1997). A similar procedure was done on the NB data (Bork 1997). Six single degree-of-freedom contrasts were used within the model to address the management-based questions. Three contrasts examined the data for main grazing treatment differences (i.e., fall vs spring, fall vs exclosed, and spring vs exclosed) and 3 assessed the residual effects of management prior to 1950 (i.e., the original fall, spring, and exclosure vs newer fall, spring, and exclosure, respectively). As a result, the MANOVA tested the ability of each spectral data type (BB and NB) to distinguish significant differences among treatments, both overall and within the specific contrasts (i.e., questions) of interest. Roy's greatest root, a test statistic derived from comparing the among-grazing treatment variation (of spectral variables) to within-treatment variation (of spectral variables), was used to evaluate results of the MANO-VA (Scheiner 1993).

To directly assess whether any of the 4 regressions of spectral data for each cover component had a practical impact on distinguishing among grazing treatments, the same 6 contrasts were done (P<0.10) within each cover component on the BB and NB predicted values from both the simple and multiple regressions. Contrasts among treatments of the measured cover values (P<0.10) provided the benchmark against which



Fig. 1. Mean narrow-band spectral response curves for June (solid line), July (dashed line), and August (dotted line) 1996, for each grazing treatment (n = 30).

Table 3. Mean measured and predicted cover (standard error of prediction [SEP] in parentheses for predicted cover) using the simple and multiple regression calibrations of the broad-band (BB) and narrow-band (NB) data within each of the 11 cover components examined.

Cover Component	Actual Cover $(N = 119)$	F Simple	Predicted Cover Regression	Multipl	e Regression
		BB Data	NB Data	BB Data	NB Data
			(%)		
Vegetational:					
Forb	8.8	8 (5.62)	4.7 (5.80)	8 (4.99)	8.3 (5.84)
Grass	15.6	15.5 (7.59)	15.3 (7.17)	15.6 (7.59)	15.4 (7.75)
Herb	24.2	17.9 (7.62)	23.4 (7.64)	23.6 (7.16)	23.1 (7.14)
Live Shrub	21.7	22.7 (7.87)	21.3 (7.33)	22.8 (7.86)	23.1 (7.14)
Total Vegetation	45.9	46.2 (6.52)	47.2 (6.27)	47.4 (7.14)	47.2 (6.78)
Other / Soil-Based:					
Dead Shrub	7.2	7.4 (4.88)	7.4 (4.81)	7.6 (4.92)	7.6 (4.92)
Lichen	4.7	4.1 (9.02)	4.1 (9.04)	4.1 (9.02)	6.4 (9.03)
Litter	19.2	19.6 (5.91)	19.6 (5.93)	19.5 (5.92)	19.6 (5.89)
Moss	2.7	3.1 (2.91)	2.9 (2.93)	n/a^1 (2.92)	2.9
Rock	1.4	0.8 (2.73)	0.8 (2.64)	0.7 (2.74)	0.7 (2.72)
Soil (bare)	18.9	18.8 (7.09)	19.1 (7.47)	18.5 (7.54)	19.2 (7.20)

¹No BB spectral variables met the minimum significance level for entry using multiple regression.

to check for any practical differences within the 4 calibrated regressions. This procedure evaluated the calibrated regressions at a practical level, and facilitated testing of the NB data for improved predictability of cover components among treatments. For each cover component, we determined, (1) the number of contrasts per calibrated regression that correctly represented measured cover differences, (2) the number of contrasts significant in the measured data that were missed (i.e., found not significant) within the contrasts of predicted data, and (3) the number of non-significant contrasts within the measured data that were found significant in the predicted data. These values represented correct classifications, omission errors, and commission errors, respectively.

Results

The mean narrow-band (NB) spectral response curves from June, July, and August for each grazing treatment are depicted in Fig. 1. Several notable dif-

ferences are apparent, both between main treatment types and within treatment replicates (i.e., old vs new). Among all 6 treatments, the 2 fallgrazed areas had sine wave-like spectral response curves in June, which flattened by July (mid-summer). While the response curve of the old fall treatment flattened out from a drop in the near infrared and increase in red reflectance, the new fall curve changed almost exclusively in visible reflectance (i.e., near infrared was stable). This latter pattern of temporal change was also apparent in the spectral response curves of both spring-grazed treatments. Interestingly, both spring treatments had increased in reflectance in July and declined in August, with the old spring showing greater changes over time. Both exclosures had spectral response curves similar to the old fall treatment, although the magnitude of change was less than that found in the latter.

Average predicted cover values within each cover component were similar to measured cover regardless of regression type (Table 3). Only 3 noticeable exceptions were found. Predicted forb cover was under-estimated using the leading single NB spectral variable while herb cover was under-estimated by the leading single broad-band (BB) spectral variable. In contrast, lichen was overestimated using multiple regression of the NB data.

In general, the standard error of prediction calculated for each of the 4 regression types did not appear to differ within individual cover components (Table 3). In only one case did multiple regression reduce the standard error of prediction by at least 10% relative to simple regression (BB forb, from 5.62 to 4.99). Other decreases in the standard error of prediction from using multiple regression occurred for bare soil (NB), live shrub (NB), and herb (BB and NB) (Table 3). In several situations, the standard error of prediction was greater as a result of using multiple regression. For example, the error for grass using NB data went from 7.17 to 7.75. Other increases in the standard error were evident for bare soil (BB) and total live vegetation (both BB and NB) (Table 3).

Little difference was observed in the standard error of prediction from using NB data (Table 3). Of the differences that did occur, results were mixed regarding the type of spectral data. For example, when NB data were used, the standard error for forb was greater using either simple or multiple regression, but lower for live shrub and total vegetation using each regression strategy (Table 3). While the herb component showed virtually no difference in standard error, grass had a mixed response with only simple regression of NB data resulting in a lower SEP. Among the non-living and soil-based cover components, differences in the SEP from using NB data were minimal, with the only exception being bare soil (Table 3).

Results of the MANOVA showed significant differences between the BB and NB subsets of simple spectral variables among the 6 grazing treatments (Table 4). Furthermore, these significant differences (P<0.001) were apparent in all the main effect contrasts using both data types (Table 4). This trend, however, did not continue into the 3 contrasts addressing the differences among grazing treatments grazed similarly since 1950, but differently before then (i.e., examining residual effects or rangeland resilience). Although all 3 of these contrasts were significant using the NB

Table 4. Results of the overall and contrast-based MANOVA for the broad-band (BB) and narrowband (NB) data.

Test:	<u>BB Spectra (N = 10)</u>		NB Spec	tra (N = 11)
	F - Value ¹	Р	F - Value ¹	Р
Overall Model ²	10.98	p < 0.001	13.72	p < 0.001
Main Effect Contrasts:				
Fall vs Spring	5.83	p < 0.001	9.11	p < 0.001
Fall vs Excl.	5.44	p < 0.001	6.03	p < 0.001
Spring vs Excl.	4.68	p < 0.001	4.69	p < 0.001
Residual Effect Contrasts:				
Old Fall vs New Fall	6.88	p < 0.001	7.3	p < 0.001
Old Spring vs New Spring	1.44	p = 0.18	2.45	p < 0.01
Old Excl. vs New Excl.	1.27	p = 0.26	5.38	p < 0.001

¹F - values are based on Roy's greatest root.

² The overall model tests collective spectral differences among all 6 grazing treatments.

data, when the BB spectral data were used, only the comparison between the old and new fall-grazed treatment was significant (Table 4).

Statistical contrasts among the grazing treatments based on the measured and predicted cover from the 4 regressions were also compared to determine the number of significant contrasts within each type of predicted cover data that were correct, commission errors, and omission errors, relative to the contrasts of measured data (data not shown). In general, the number of correctly predicted significant contrasts were highly variable among the cover components, regardless of data type and regression strategy. Living cover components were particularly poor, with the number of contrasts correctly predicted ranging from 25% (total vegetation) to 75% (forb and shrub). Non-living and soilbased components were not much better, ranging from 50% (litter) to 83% (dead shrub). As might be expected given the low proportion of correct predictions, commission and omission errors were also common among nearly all predicted contrasts for all cover components, with relatively greater errors associated with the vegetational components.

Comparison of the detailed contrasts among grazing treatments using predicted and measured cover values showed that the use of NB data instead of BB data, resulted in an increase in the number of correct contrasts (from 63 to 79% and from 52 to 63% for simple and multiple regression, respectively). A corresponding reduction was evident in the number of commission, and in particular, omission errors, from using NB data (ommission errors changed from 38 to 21%, and 42 to 38%, for simple and multiple regression, respectively).

Discussion

This study is unique in that it simultaneously evaluated both narrow-band (NB) and broad-band (BB) spectral data for quantifying rangeland cover components (e.g., growth forms) through the use of localized plots. The results indicated not only how well these data predict various cover components, but facilitated the subsequent separation of grazing treatments. Although previous remote sensing work has addressed the task of quantifying plant growth forms such as shrubs (e.g., Boyd 1986) and grasses (e.g., Paruelo and Golluscio 1995) on rangelands, these studies have used coarse resolution satellite data and ocular estimates of component cover, making them more difficult to interpret.

The prominent changes in spectral response curves within each of the grazing treatments early in the summer (from June to July) are consistent with the relatively rapid progression of phenologies among most range plants common in the area (Blaisdell 1958). The fall-grazed treatments, particularly the old fall, had the greatest herb cover (Bork et al. 1998a), resulting in these treatments exhibiting the largest degree of temporal change in reflectance within the spectral response curve. Although the exclosures were also high in herb cover, these areas had abundant shrub cover as well. The higher shrub:herb ratio likely produced more shadow and overtopping of the herbaceous understory, reducing green vegetation reflectance (Wilson and Tueller 1987). As a result, the spectral response curves of these treatments varied less throughout the growing season.

The lack of temporal change in the near infrared spectral region of the old spring-, new spring-, and new fallgrazed treatments was somewhat surprising. There are, however, several possible explanations for this observation. These paddocks had the greatest annual herb cover (both forb and grass) (Bork et al. 1998a). Rapid senescence of annuals may have increased the relative reflectance from soil-based components over time, thereby increasing near infrared reflectance. In contrast, the long-term fall-grazed treatment and 2 exclosures, which were dominated by deep-rooted perennial herbs, may have remained green longer into the summer and produced abundant litter in the shrub interspaces that persisted (Comanor and Staffeldt 1979), thus concealing more of the soil surface. Litter from perennial species may also have contributed to a greater organic matter content at the soil surface although this notion has not been independently verified. Finally, surface soil moisture may have played a role, particularly if spectral observations were obtained before the soil surface fully dried following precipitation events during the summer.

Within individual cover components, mean predicted cover was similar to measured cover, regardless of the regression type used. Inspection of the residual differences between predicted and measured cover data at the plot level, however, showed that deviations (i.e., predicted-measured) were highly variable among sampling plots. These differences continue to reflect the inherent "white-noise" of the data within the study area. These results indicate that while the average predictability of components among many plots may be maintained under various regression strategies, caution should be used when trying to extrapolate to the individual plot level. For those cover components where predicted cover and measured cover showed greater discrepancies (e.g., forb, herb, and lichen), the independent spectral variables used to predict cover may be less reliable. In the case of lichen, 5 NBs were selected into the multiple regression model indicating the poor predictability may be due to regression overfitting.

Overall, the standard error of predictions within cover components varied little among the 4 regression types evaluated. The smallest differences occurred within the less abundant cover components (i.e., rock, moss, lichen, and dead shrub) in Table 3. Where differences did occur, the use of multiple regression and NB data did not consistently reduce the standard error, indicating that the ideal type of regression strategy for predicting cover varies among components. Furthermore, changes in standard error appeared to depend on (i.e., interact with) both the mode of regression (simple and multiple) and data type (BB and NB). Multiple regression frequently produced lower standard errors for the more detailed components, particularly plant growth forms (i.e., forb, herb, and shrub). Interestingly, multiple regression within the more general cover components [e.g., total vegetation and bare soil (BB only)] often failed to reduce the standard error of prediction. Hence, it appears that complex predictive models containing multiple spectral variables may only be beneficial for rangeland monitoring when more detailed cover components are of biological interest.

The use of NB data relative to BB data more often than not reduced the standard error of prediction. Unlike the trend for simple and multiple regression, however, NB data were more advantageous for quantifying total living vegetation and other relatively abundant living growth forms. Components that did not have a lower standard error using NB data included those with relatively little cover, such as forb.

Examination of the spectral data using a MANOVA provided a qualitative method to directly examine the grazing treatments for the ecological differences of concern to rangeland managers. Significant differences showed that when either the BB or NB spectral variables from the simple regressions were collectively examined, all of the main effect contrasts among grazing treatments were significant. These results are supportive of the fact that the fall, spring, and exclosed areas have the greatest vegetation compositional differences (Bork et al. 1998a) and hence, are easily separable. However, significant differences among the old and new paddocks within each main treatment were not consistent among the BB and NB data. Using BB data, only the 2 fallgrazed treatments differed. The lack of differences within the 2 exclosed and 2 spring-grazed areas indicated that the BB data were unable to detect the residual effects of management prior to 1950.

Interestingly, of the 3 contrasts evaluating residual effects, the old and new fall-grazed treatments had the most dissimilar cover component compositions (Bork et al. 1998a) due to the slow recovery following spring-grazing prior to 1950 in the latter (Laycock 1967). Unlike the BB data, the MANOVA with NB data showed all 3 contrasts for residual effects were significant. This is despite the 2 spring-grazed treatments both being near-monocultures of shrub and the 2 exclosures being similar stands of spatially mixed shrub and perennial herb. Thus, it appears that while BB and NB spectral data are both useful for qualitatively distinguishing among grazing treatments with prominent compositional differences, the increased spectral resolution associated with NB data may improve the qualitative separability of grazing treatments that are dissimilar with respect to more subtle, but managerially important, ecological characteristics.

The increased number of correct contrasts and decreased number of omission errors as a result of using NB data suggests that despite the lack of differences between BB and NB standard errors of prediction, the NB data may still confer an advantage within practical remote sensing applications designed to quantitatively distinguish among grazing treatments. The extent to which NB data may be beneficial, however, will depend on both the a priori degree of inherent differences among treatments and the required extent of separability during application. The lack of consistent improvements also suggests that to determine whether NB data will be advantageous, a direct comparison between BB and NB data relevant to the problem will be necessary within the area of interest (i.e., on a case study basis).

Conclusion

This study utilized a "bottom-up" framework as an alternative to the traditional "top-down" scientific approach for problem solving in natural resource management (Shrader-Frechette and McCoy 1993). Top-down monitoring of rangelands using remote sensing has typically used coarse resolution spectral data and poorly ground-truthed information on ecosystem characteristics (e.g., Boyd 1986, Paruelo and Golluscio 1995). In contrast, collecting localized data in well-defined plots and correlating it directly with broad-band (BB) and narrow-band (NB) spectral data circumvents the logistical problems associated with coarse-resolution data, such as georectification and ground-truthing. As a result, this study was able to evaluate the potential of NB remotely sensed data for assessing rangeland condition.

This study indicates that NB spectral data offer an advantage over BB data for qualitatively distinguishing among sagebrush steppe rangelands in different vegetational states, particularly when ecologically-induced differences from grazing are subtle. The advantage of NB data for quantitatively predicting rangeland cover components and distinguishing among unique grazing treatments, however, remains questionable due to highly inconsistent results among data types within cover components. Consequently, at present, it is doubtful that NB data can fill the needs of rangeland managers to accurately quantify specific cover components (i.e., growth forms that serve as indicators) (NRC 1994) any better than BB spectral data. Despite this conclusion, further research and testing is clearly needed using both BB and NB data at various spatial scales in order to identify strategies through which remote sensing technology may offer a practical advantage for assessing rangeland condition.

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Defoliation time and intensity of wall barley in the Mediterranean rangeland

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Abstract

Wall barley (Hordeum murinum L.) is the dominant species in northeastern rangeland of Jordan that decreases under grazing. We investigated the responses of wall barley to clipping time and height during 2 growing seasons in the semiarid rangeland of Jordan. A natural stand was utilized to conduct the experiments that were arranged in a randomized complete block design during 1994/95 and 1995/1996 growing seasons. Treatments were combinations of clipping heights (5 or 10 cm above soil surface) and plant growth stages (tillering, jointing, or booting), in addition to unclipped check. Results showed that clipping to 5 and 10 cm stubble height at tillering produced 1,167 and 1,349 kg ha⁻¹ dry matter, respectively, compared to 1,122 kg ha⁻¹ for unclipped check. Clipping to 5 and 10 cm stubble height reduced shoot weight by 28 and 21% at jointing stage and 52 and 38% at booting stage. Defoliation during tillering stage did not impact plant height of regrowth nor seed yield. Weed biomass were higher when plant defoliation was delayed to the jointing and booting stages. Therefore, it is recommended to defoliate wall barley early at tillering stage but before plants reach jointing or reproductive stages.

Key Words: Jordan, *Hordeum murinum* L. clipping, plant height, shoot, seed, annual grass, weeds

Jordanian grassland is located within the 200 to 350 mm rainfall zone of the eastern Mediterranean region. This semiarid rangeland occupies an important part of the country and needs to be well understood to achieve optimum management. Vegetation dynamics and seasonal growth patterns need special attention as many plant communities are exposed to longterm overgrazing. Wall barley (*Hordeum murincum* L.) is an annual native grass that is the key species for many local plant communities in semiarid rangelands. Wall barley withstands the harsh climatic conditions of dry areas by its ability to reproduce readily from seed and to recover quickly from drought events.

Deciding when and to what extent plants should be defoliated are considered the most critical and difficult tasks that a range manager must undertake. Understanding plant responses

Resumen

"Wall barley" (Hordeum murinum L.) es la especie dominante de los pastizales del noreste de Jordania y la cual decrece bajo el apacentamiento. En un pastizal semiárido de Jordania investigamos durante 2 estaciones de crecimiento, 1994/1995 y 1995/ 1996, la respuesta del "wall barley" a la época e intensidad de defoliación. Se utilizó una población natural para conducir los experimentos, los cuales se establecieron bajo un diseño de bloques completos al azar. Los tratamientos fueron combinaciones de alturas de corte (5 o 10 cm arriba de la superficie del suelo) y etapas de crecimiento de la planta (ahijamiento, encañe o embuche), y se tuvo un testigo si cortar. Los resultados mostraron que el corte a los 5 o 10 cm efectuados en el ahijamiento produjeron 1,167 y 1,349 kg ha⁻¹ de materia seca respectivamente, comparado con 1122 kg ha-1 producidos por el testigo sin defoliar. Cortar a 5 o 10 cm de altura del rastrojo remanente redujo el peso de los tallos en 28 y 21 % cuando los cortes se realizaron en la etapa de encañe y en 52 y 38% cuando se efectuaron en la etapa de embuche. La defoliación durante la etapa de ahijamiento no impactó la altura del rebrote ni la producción de semilla. La biomasa de la maleza fue mayor cuando la defoliación fue retrasada hasta los estados de encañe o embuche. Por lo tanto, es recomendable defoliar a "wall barley" en la etapa de ahijamiento, pero antes de que las plantas alcancen el estado de encañe o la etapa reproductiva.

to defoliation allows manager to choose the proper timing for plant use and rest which permits better management of range plant communities (Jameson and Huss 1959). Plant response to green material removal varies greatly among seasons and defoliation intensities. Defoliation timing and frequency affects range grass development (Mullahey et al. 1990). Miller and Donart (1979) reported that forage production and crown diameters of 2 grass species were affected by forage removal season and quantity. The most critical period was during the reproductive stage. Plants become more sensitive to defoliation as reproductive stage is approached (Tarassoum 1982, Moser and Perry 1983). Dual purpose barley (H. spontaneum L) yield was reduced by late clipping (AL-Rawi et al. 1995). The ability of grasses to regrow after defoliation depends on plant genotype and the amount of green leaf tissue remaining in the stubble (Davies 1974). Plant injuries decreased with

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increasing stubble heights after clipping Agropyron spicatum (Sullivan and Sprague 1953, Mclean and Wikeen 1985). Dual purpose barley is becoming more popular in Iraq because it tolerates grazing at the pre-stem elongation stage (AL-Rawi et al. 1995). Grazing barley at pre-stem elongation stage can recover and produce grain equivalent to ungrazed stand (Morey 1961). However, severe defoliation of many semiarid range species was detrimental when defoliated plants relied upon nutrient reserves for regrowth (Trlica and Cook 1971). Therefore, knowledge of defoliation extent and timing is crucial for successful management of annual species such as wall barley range.

Jordanian rangeland is subjected to continuous livestock overgrazing, and thorough understanding of vegetation dynamics is not available. The responses of wall barley to defoliation has not been reported. The objective was to determine the responses of wall barley to clipping time and height in the semiarid rangelands of Jordan.

Materials and Methods

Study Area

Field studies were conducted on the Jordan University of Science and Technology Experimental Station (JUSTES) located 22 km east of Irbid (32° 34' N, 36° 0' E) in the 1994/95 and 1995/96 growing seasons. The site has an altitude of 520 m and is characterized by a flat to gently rolling topography with less than 8% slope. The soil is brown weakly cracked, calcareous, deep silty clay with a pH of 6.8. Natural vegetation at JUSTES is a typical Mediterranean semiarid grassland with the dominating species being Hordeum spp., Avena fatua L. and Trigonella spp. This site was subjected to long term overgrazing and cultivation until 1986, after that it was partially protected from



Fig. 1. Rainfall distribution for 1994/95, 1995/96 growing seasons and long-term precipitation average (LTPA) at JUSTES.

intensive agricultural use. The long-term precipitation average (LTPA) for the site is 230 mm, whereas annual rainfall for the 1994/95 and 1995/96 growing seasons were 275 and 182 mm, respectively (Fig. 1).

Treatment and Statistical Analysis

Field plots of 6 x 5 m were established on a native stand of wall barley. Treatments were combinations of clipping height (5 or 10 cm above soil surface) and timing, that corresponded to plant growth stages of tillering, jointing, and booting. Tillering is the growth stage at which 50% of the plant tillers have 4 leaves per tiller; jointing is the stage at which the second node appear in 50% of the tillers; and booting is the stage that immediately precedes the emergence of the inflorescence from the sheath of the flag leaf in approximately 30% of tillers. Treatment combinations and an unclipped check were replicated

3 times and arranged in a randomized complete block design. All plots were harvested to 5 cm stubble height at seed maturity.

Data collected each year included; plant height (average of 3 vertical measurements from the soil surface to the highest point in the plant and soil surface recorded at physiological seed maturity); total oven-dry forage weight determined by adding the weight of tops removed at the time of defoliation to the total forage weight (vegetative shoot part weight) at time of harvest. Oven dry weight was obtained by heating shoot at 70°C for 48 hours. Seed yield was determined by threshing and cleaning dry heads. Weed biomass was also determined at the end of the season by weighing aboveground weeds after drying at 70°C for 48 hours. All weight measurements were collected for 1 m² quadrats. Analysis of variance (Table 1.) for data combined over the 2 years were performed as outlined for a randomized

Table 1. Mean square and source of variation table showing the effect of defoliation time and height of Hordeum murinum L.

Source of						Mean Square					
Variation	df	Plant height		Forage yield		First cut forage		Seed yield	v	Veed biomas	ss
Year	1	0.46		7817.36		9102.26		11270.10		586.90	
Error (a)	4	4.12		1798.43		229.17		1074.70		725.00	
Treatment	6	788.00	**	436388.80	**	638564.07	**	266279.30	**	53457.30	**
Treatment*Year	6	11.00		11221.47		3476.45	**	699.90		246.20	*
Error (b)	24	5.13		4943.71		3088.52		1182.00		707.04	









Total Forage



complete block design using MSTATC computer program (Michigan State University). Means were separated by Duncan's Multiple Range Test (DMRT) at P<0.01 (Steel and Torrie 1980).

Results and Discussion

Rainfall

Variation in rainfall total and distribution were high between the 2 seasons which is expected for semiarid lands (Noy-Meir and Seligman 1979). In 1994/95, more than 50 % of rain occurred during November, whereas March and April were dry months (Fig. 1). This poor distribution masked the effect of high precipitation on plant growth. Although the precipitation for 1995/96 was lower than LTPA, the distribution was better especially during the period from January to April. This allowed the plant to produce forage yields equivalent to that produced in 1994/95.

Plant Height

Clipping plants during the tillering stage did not affect plant height when measured at physiological maturity (Fig. 2). However, wall barley height was significantly reduced when clipping was performed at the jointing (27 and 29 cm) and boot stage (13 and 18 cm). Clipping height effects were only observed when cutting was practiced at boot. Wall barley height was greatly reduced when plants were clipped 5 cm above soil surface at the boot stage.

Forage Yield

Forage production from the first cut increased with decreasing clipping height (Fig. 3). The greatest forage yield (1349 kg ha⁻¹) was obtained when wall barley plants were clipped to 10 cm above soil surface at tillering stage (Fig. 3). However, clipping wall barley plants to 5 cm above soil surface at tillering lower ed forage yield (1,167 kg ha⁻¹) but was equivalent to unclipped checks. This indicates that clipping heights of 5 and 10 cm at tillering stage did not impede regrowth following clipping in wall barley. Barley herbage at tillering stage has high protein content equivalent to that of forage legumes (Droushiotis and Wilman 1987) which may also improve animal feed quality. Similar results were



Fig. 4. Effect of defoliation time and height on seed yield of *Hordeum murinum* L. Columns with different letters differ significantly according to DMRT at $P \le 0.01$.

obtained where clipping heights of 4 and 10 cm did not affect forage vield of meadow foxtail stand (Smith et al. 1973). However, a 10 cm stubble height clipping improved plant forage yield but this yield was reduced when plants were clipped down to 5 cm stubble height (Leyshon and Campbell 1992). Previous observations indicated that plant responses to defoliation were highly variable among time and intensity of defoliation (Miller and Donart 1979), and the most critical defoliation time was either during the reproductive stage or under unsuitable environmental conditions (Mullahey et al. 1990). In addition, clipping height generally has less influence on forage yield than clipping time (Dovel 1996). This agrees with our result where plant defoliation during jointing or booting stages reduced forage yield. These reductions were more severe when clipping was practiced at lower stubble heights (Fig. 3). Clipping during booting stage coincided with high temperature and low precipitation at the end of the rainy season. This lead to reduction in plant regrowth at booting stage. Italian ryegrass (Lolium multiflorum) regrowth rate and tillering capacity were minimized at high temperature, whereas primary growth rate was at maximum (Hill and Pearson 1985). These results agree with data reported by Kennett et al. (1992) where early season defoliation of bluebunch wheatgrass (Agropyron spicatum) produced higher shoot biomass due to better opportunity to regrow through the growing season.

Seed Yield

Seed yield was low when plants were clipped at jointing or booting stages (Fig. 4). Clipping at booting stage resulted in a severe reduction in seed production. Seed yields at booting stage were 98 and 169 kg ha⁻¹ for clipping height of 5 and 10 cm, respectively. Tiller production was inhibited when the wall barley plants were defoliated at the booting stage therefore seeds produced at the end of the season were from late maturing tillers, due to hot and dry condition during April. Large reductions in H. murinum L. seed production might eliminate this grass from range communities since it depends on soil seed bank for continuity and persistence. Seed production was not adversely affected when clipping occurred at tillering stage regardless of clipping height (594 and 583 kg ha⁻¹ for 10 and 5 cm clipping height, respectively). This indicate that seed reserve will not be depleted if defoliation occurred early in the season. Mowing range grasses early in spring did not affect seed head production, whereas, late spring mowing progressively reduced the density of seed heads (Sims et al. 1971). Day time temperature (Franke et al. 1992), moisture supply (Thakur and Shands 1954), and proper grazing management (Morey 1961), contribute to high forage and seed yields of small grain crops under simulated grazing.

Weed Biomass

The dominating weed species on the site were *Cardaria draba* (L.) Desv., *Sinapis arrensis* L., and *Diplotaxis erucoides* (L.) D.C. Weed interference as detected by weed biomass significantly increased as defoliation was delayed and



Fig. 5. Effect of *Hordeum murinum* L. defoliation time and height on weed biomass. Columns with different letters differ significantly according to DMRT at $P \le 0.01$.

clipping intensity (5 vs 10) increased (Fig. 5). Weed biomass was 201 and 223 kg ha⁻¹ in stands subjected to 10 and 5 cm clipping heights at tillering stage, respectively. Clipping at booting stage reduced wall barley stand and led to increased weed infestation (412 to 426 kg ha⁻¹). Clipping during tillering did not reduce wall barley competing ability and this prevented weed invasion. This negative impact of clipping on competitive ability was stronger when range plants were clipped at later growth stages. Kennett et al. (1992) also reported that spotted knapweed (Centaurea maculosa Lam.) growth and density were influenced by bluebunch wheatgrass defoliation treatments. Weed invasion to any range site is associated with reduction in desirable species range cover and normally reduces the grazing value of that site. Defoliation alters plant competitive ability and influences its role in the community (Maschinski and Whitham 1989).

Conclusion

Maximum forage production was achieved when wall barley was defoliated at either at the early tillering stage or at plant maturity. Adequate soil moisture and temperature will encourage optimal plant regrowth. Defoliation during jointing or booting stages of wall barley reduces forage and seed yield and increases weed interference. Severe reduction in seed yield occurs when plants are defoliated at the booting stage which threatens a possible elimination of the species from the rangeland as a result of heavy unplanned grazing practices. Future studies are needed to determine the optimum number of seeds in the seed bank that are required to maintain a healthy natural wall barley population.

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Plant responses to defoliation and resource supplementation in the Pryor Mountains

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Abstract

Field studies were conducted in 2 types of grasslands in the Pryor Mountain Wild Horse Range of northern Wyoming and southern Montana to examine plant biomass production and nitrogen responses to the separate and combined effects of graminoid defoliation and increased environmental resource (water or nutrients) supply. Short-term plant responses were monitored over 2 years which differed substantially in growing season precipitation. In the arid, low elevation grassland, total grass biomass was significantly lower in the dry year than the wet year in all treatments. Defoliation of the grasses did not reduce their aboveground biomass production in the wet year, but severely reduced it in the dry year, primarily because of a decrease in tiller density. Mass of remaining individual tillers increased with clipping in the dry year, and nitrogen concentrations of the grasses increased with clipping in both years. Irrigation alone increased total belowground biomass compared to the other treatments, but did not increase the aboveground biomass production of any plant functional group. Clipping plus irrigation resulted in greater total aboveground biomass production and higher nitrogen concentrations of the grasses than control or irrigated treatments. Clipping graminoids in the more mesic montane grassland did not decrease their biomass production in either year, but did increase their nitrogen concentrations and increase the collective aboveground biomass production of the other plant functional groups. Fertilization and fertilization plus clipping significantly increased total aboveground biomass production in both years, and total belowground biomass was greatest in fertilized plots.

Key Words: wild horses, Pryor Mountain Wild Horse Range, primary production, nitrogen, *Pseudoroegneria spicata*

Many large ungulate herbivores preferentially consume grasses relative to their proportion in the plant community (Schwartz and Ellis 1981, Vinton et al. 1993). This not only changes the relative ability of grasses to acquire resources, but also alters the competitive interactions within the community

Resumen

Se condujeron estudios de campo en 2 tipos de pastizal en el pastizal Pryor Mountain Wild Horse ubicado en el noreste de Wyoming y sureste de Montana. El objetivo de estos estudios fue examinar los efectos individuales y combinados de la defoliación de gramíneas y el incremento de recursos ambientales (agua o nutrientes). Las respuestas de la planta a corto plazo fueron monitoreadas durante 2 años, los cuales difirieron substancialmente en precipitación durante la estación de crecimiento. En la parte árida, pastizal de baja elevación, la producción total de biomasa de gramíneas en todos los tratamientos fue significativamente menor en el año seco que en el año húmedo. En el año húmedo, la defoliación de los zacates no redujó su producción de biomasa aérea, sin embargo, fue severamente reducida en el año seco, debido principalmente a la disminución de la densidad de hijuelos. Durante el año seco, la biomasa remanente de los hijuelos individuales se incrementó con la defoliación. En ambos años, las concentraciones de nitrógeno de los zacates se incrementó con la defoliación. Comparado con los otros tratamientos, la irrigación sola incrementó la biomasa total subterránea, pero no incrementó la producción de biomasa aérea en ninguno de los grupos funcionales de plantas. La defoliación mas irrigación produjó mayores cantidades de biomasa total aérea y concentraciones de nitrógeno que los tratamientos control o de irrigación. La defoliación de gramíneas en el pastizal montano más mésico no disminuvó su producción de biomasa en ninguno de los años de estudio, pero si incrementó su concentración de nitrógeno e incrementó la producción colectiva de biomasa aérea de los otros grupos funcionales de plantas. En ambos años de estudio, la fertilización y la fertilización mas defoliación incrementaron significativamente la producción total de biomasa aérea y la producción total de biomasa subterránea fue superior en las parcelas fertilizadas.

as plant species or functional groups are differentially affected by the direct and indirect effects of selective herbivory. For example, selective grazing of dominant grasses by bison in tallgrass prairie can increase photosynthesis and growth of neighboring ungrazed plants of the same and other species (Fahnestock and Knapp 1993, 1994).

The ability of grasses to compensate for biomass consumed

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by large herbivores is controlled in part by the availability of environmental resources that can readily be acquired by the plants (Chapin and McNaughton 1989). When resources such as water, light, and mineral nutrients are abundant and readily available to plants, increased aboveground productivity of grasses in response to moderate grazing levels is possible (Archer and Tieszen 1980, McNaughton 1985, Seastedt 1985, Hik and Jeffries 1990, Pandey and Singh 1992, Frank and McNaughton 1993). Conversely, when environmental resources are limited, the ability of grasses to replace tissue lost to grazers is reduced. The persistence of plants in grassland ecosystems, therefore, largely depends on the ability of individuals to cope with complex and dynamic interactions between herbivory and limitations of environmental resources.

The environmental resources that most frequently limit the growth of plants and their ability to recover from grazing and other disturbances often differ with the type of grassland being studied. In arid and semi-arid grasslands, water availability most often limits plant growth (Lauenroth 1979, Sala et al. 1988), while in more humid grasslands, or in wet years, light and nutrients, especially nitrogen availability, are more likely to limit plant growth (Knapp and Seastedt 1986, Burke et al. 1991). The response of plants to grazing may also differ between and within species, depending on the nutrient and water stress tolerance of the species present, and on the type of herbivory and its intensity and frequency (Crawley 1983, Wallace et al. 1984, Coughenour et al. 1985a, 1985b, Polley and Detling 1988).

In the Pryor Mountain Wild Horse Range in southern Montana and northern Wyoming, grasses comprise over 70% of the annual diet of wild horses (Kissell 1996). Little is known, however, about the ability of the grasses in this system to maintain production in response to this potentially substantial grazing pressure, or about the interaction of herbivory with water or nutrient availability in the Pryor Mountains. The principal objective of this research, therefore, was to determine if the dominant grasses in the Pryor Mountain Wild Horse Range could acquire the resources necessary to maintain biomass and nitrogen production in response to selective grass defoliation, or whether there were environmental

resource limitations (i.e., water or nutrient limitations) to growth following defoliation. Because the relative competitive ability of other plants may be differentially affected by selective grass herbivory, we also investigated whether selective defoliation of the grasses would result in increased biomass production or nitrogen content of other plant functional groups, particularly forbs. We hypothesized that biomass production and nitrogen concentrations would increase in plants with additional resource supply, and that the potential negative effects of defoliation on grass growth would be ameliorated with increased resource supply.

Materials and Methods

Site description

The experiments took place during the summers of 1993, a year with above average growing season precipitation, and 1994, a relatively dry year, in the Pryor Mountain Wild Horse Range, an 18,000 ha refuge located 80 km south of Billings, Mont. Elevation ranges from 1,190 m to 2,440 m in the Pryor Mountains, and annual precipitation varies from about 130 mm in some lowland areas to over 500 mm at upper elevations. Our research was carried out in 2 types of grasslands in the Pryor Mountains-a low elevation arid grassland and a more mesic montane grassland-in which plant growth was presumed to be limited, respectively, by water and nutrient availability. To control for grazing, both experiments were established in long-term (>20 years) fenced areas that precluded wild horse use but were similar in botanical composition as those currently grazed by wild horses (Fahnestock 1998).

The first experiment was conducted in an arid lowland community at 1,300 m above sea level that receives only ca. 230 mm of precipitation annually. Precipitation data (1982–1994) for this community were obtained from a weather station located about 1 km south of our study site. Aboveground biomass in this community averages about 128 g m⁻² (Fahnestock 1998) and is dominated by perennial grasses (51% of total plant cover) and forbs (26% of total plant cover), with lesser quantities of cushion plants, dwarf shrubs and succulents. *Pseudoroegneria spicata* (Pursh) A. Löve (bluebunch wheatgrass) is the most abundant plant in these lowland communities, accounting for nearly 50% of the total herbaceous plant cover and over 90% of the total grass cover (Fahnestock 1998). Since water presumably limits plant growth in these lowlands, a grass defoliation and water supplementation experiment was carried out in this community.

The second experiment was conducted in a more mesic, montane meadow at 2,400 m above sea level that receives over 500 mm of precipitation annually. This site is located approximately 4 km north-west of the lowland site and precipitation data for this community were obtained from a weather station located about 1 km north of this site. Vegetation in this community is more abundant than the lowlands, averaging about 177 g m⁻², and consists primarily of grasses and sedges (44% of total plant cover) and forbs (51% of total plant cover). Much of the precipitation at this site comes from frequent summer showers, and thus the availability of nutrients, rather than water, presumably limits plant growth here. We carried out a graminoid (grasses and sedges) defoliation and nutrient supplementation experiment at this site.

Experimental design and treatments

A completely randomized 2 X 2 factorial design with 20 replicate plots was utilized for each experiment. Each experiment was established in a representative area of the upland or lowland grassland community at that site, and plots were selected that were relatively uniform in terms of plant cover and species composition to control for differences within and between plots. Each 3.2 m X 3.2 m plot was subdivided into 4 equal subplots to which a particular treatment was randomly assigned. In the arid lowlands the treatments were grass defoliation (D), irrigation (W), grass defoliation plus irrigation (DW), or untreated control (C). In the more mesic uplands the treatments were graminoid defoliation (D), fertilization (F), graminoid defoliation plus fertilization (DF), or control (C).

Vegetation was sampled in each subplot with 0.25 m^2 circular quadrats that were randomly placed in one of 4 possible locations in each subplot. No vegetation sample was collected within 20 cm of the edge of each subplot to avoid edge effects. To simulate recurrent, selective ungulate herbivory, all graminoid biomass in entire defoliated and defoliated plus irrigated or defoliated plus fertilized subplots of each experiment was clipped to a height of 2 cm once a month in May, June, July, and August of 1993 and 1994, and clipped biomass within the 0.25 m² quadrats of each treatment was retained. This level of defoliation was equivalent to 60–70% utilization of the graminoids over the course of the growing season. Additionally, at the lowland site, tillers of P. spicata were counted in the 0.25 m² quadrats of each plot, and individual tiller mass was quantified by weighing 100 tillers from each treatment in August (i.e., 5 randomly selected tillers from each of the 20 plots).

All aboveground biomass in the 0.25 m² quadrats of each treatment was harvested to ground level in August of both years and oven-dried at 60°C for 48 hours. Because all aboveground biomass was harvested to ground level in 1993, alternate 0.25 m² quadrats within each subplot were sampled in 1994. These alternate plots had received the same treatments except for the ground level harvest in 1993. Biomass and total offtake values for each treatment were sorted by functional group (e.g., live and dead graminoids, forbs, etc.) and weighed. Pooled biomass samples (n=5) of each functional group were ground through an 850 µm (20-mesh) screen in a Wiley mill, subsampled, and nitrogen concentrations were determined by coupled combustion/reduction and gas chromatography (CHN-1000, LECO Corporation, St. Joseph, Mich.). Aboveground N yield was calculated by multiplying the N concentration by the aboveground biomass of each functional group. Root biomass was estimated at the time of final harvest in 1994 by excavating 5 alternate 0.25 m² quadrats to the depth of 30 cm for each treatment. Soils were air-dried and roots and rhizomes were separated from soil by sieving.

In the lowland experiment, irrigated subplots were watered with hand-held sprinklers with water obtained from a nearby well. A 26.6 mm rainfall event was simulated in May, June, and July of each year, approximating a small increase in the number of large rainfall events this lowland area receives during the growing season. A total of 80 mm of water was added to irrigated plots during each growing season, resulting in a near doubling of the long-term average precipitation received at this site in May -July. Each watering event was applied over a 30-hour span so that there was no significant puddling or runoff, and water appeared to uniformly infiltrate the soil to a depth of at least 25 cm (pers. obs. based on excavations). This irrigation scheme appeared to increase the availability of soil water to irrigated plants by nearly 3 weeks during the growing season (i.e., irrigated soils were appreciably more moist at 20 cm than non-irrigated soils for about 1 week following each watering event). In the upland experiment, a moderate level (39 g m⁻²) of slow-release fertilizer (20-10-5 of N-P-

K) was surface-broadcast applied to the appropriate randomly selected subplots once near the beginning (late-May) of the 1993 and 1994 growing seasons. Soils were moist at the time of fertilization and rain fell on the site within 10 days of fertilization. All fertilizer was dissolved into the soil within 4 weeks of application.

Statistical analyses

In each experiment, total biomass (i.e., May-August clipped biomass plus final August harvest biomass) and nitrogen responses to each treatment were compared using the General Linear Models procedure of the Statistical Analysis System (SAS 1989). Models included the main effects of treatment by functional group and the interaction of treatments. Type III sums-of-squares were used for significance (P < 0.05) testing, and least squares methods were used to examine associations between treatments by functional group. We used ttest procedures to compare biomass and nitrogen responses of each functional group to treatments between years.

Results

Biomass responses

Growing season (ca. March–July) precipitation in the lowland site was 202 mm in 1993, well above the long-term average of 143 mm, while in 1994 it was only 101 mm. Live grass biomass and live plus dead grass biomass were significantly lower in all lowland treat-

Table 1. Mean aboveground biomass (g m⁻²) ±1 SE of grasses, forbs, and total biomass in control plots and defoliated, irrigated, and defoliated plus irrigated treatments from arid lowland sites (n = 20 for each functional group x treatment). Values shown are for final harvest in August 1993 and 1994 and include clipped grass biomass from May through August (see text for additional details).

	Control	Defoliated	Irrigated	Defoliated and
				Irrigated
		(g m ⁻	²)	
1993				
Grasses	31.8 ± 1.0^{a} *‡	$33.3 \pm 1.1^{a_{*}}$	$33.4 \pm 1.0^{a_{*}}$	$27.5\pm0.8^{a}{\ast}$
Live	$10.5 \pm 1.1^{a_{*}}$	$13.2 \pm 1.4^{a_{*}}$	12.5 ± 1.4^{a} *	$11.8 \pm 1.2^{a_{*}}$
Dead	21.3 ± 0.8^{a}	$20.1 \pm 3.3^{a_{*}}$	$20.9 \pm 2.8^{a_{*}}$	$15.7\pm2.0^{\mathrm{a}}$
Forbs	$25.8 \pm 2.9^{\mathrm{a}}$	33.3 ± 3.4^{a}	30.0 ± 2.6^{a}	$27.2\pm3.2^{\mathrm{a}}$
Total aboveground biomass	137.2 ± 4.5^a	135.6 ± 4.7^{a}	135.4 ± 4.5^a	126.8 ± 5.2^{aa}
1994				
Grasses	22.7 ± 1.0^{a} *	$8.6 \pm 0.4b^{*}$	$19.0 \pm 0.6^{a_{*}}$	$14.2\pm0.7^{ab}*$
Live	$6.2 \pm 1.1^{a_{*}}$	$3.1 \pm 0.3b^*$	$5.6\pm0.7^{ab}*$	$4.4\pm0.6^{ab}*$
Dead	16.6 ± 3.0^{a}	$5.5 \pm 1.2b^{*}$	$13.4 \pm 1.9^{\mathrm{a}}$	9.8 ± 2.3^{ab}
Forbs	21.0 ± 2.8^{a}	24.4 ± 3.7^a	30.3 ± 4.5^{a}	29.8 ± 3.4^{a}
Total aboveground biomass	119.2 ± 7.2^{a}	123.3 ± 12.2^{a}	134.6 ± 10.2^{ab}	149.5 ± 8.5^{b}

 \ddagger Columns with different letters within a functional group indicate significant differences (P < 0.05) between treatment means. Asterisks indicate significant differences (P < 0.05) between 1993 and 1994 values.



Fig. 1. (a) Individual grass tiller mass (mg tiller⁻¹) and (b) tiller density (no. m⁻²) in 1993, a wet year, and 1994, a dry year, in the lowland experimental site of the PMWHR. Measurements were made on Pseudoroegneria spicata, the dominant grass in these low-lands. Different letters above bars indicate significant (P < 0.05) differences in means between treatments and years. Treatments are control (C), grasses defoliated (D), irrigated (W), and defoliated plus irrigated (DW).

ments in 1994 than 1993 (Table 1). However, forb and total aboveground biomass were not significantly lower in 1994 than 1993 in any treatment. In the lowland experiment, there was not a significant effect of any of the treatments (defoliated, irrigated, or defoliated plus irrigated) on biomass production of any plant functional group in 1993, the wet year (Table 1). This was not the case, however, in 1994, where grass biomass production was much lower in defoliated plots (9 g m⁻²) than in control plots (23 g m⁻²; Table 1).

Much of the lower live grass biomass production in 1994, the dry year, was the result of lower mass of individual live grass tillers. In control plots, mass was 32 mg tiller⁻¹ in 1993 but only 14 mg tiller⁻¹ in 1994 (Fig. 1a). A similar reduction in tiller mass was seen in grasses that were irrigated. In contrast, individual mass of grass tillers that were defoliated (both defoliated and defoliated plus irrigated treatments) were not reduced, but defoliation did reduce tiller density in the dry year (Fig. 1b). Grass tiller density in control plots was about 270 tillers m^{-2} in both years. In defoliated treatments, density averaged 260 tillers m^{-2} in 1993, but only 140 tillers m^{-2} in 1994 (Fig. 1b).

Irrigation did not increase aboveground biomass production of any plant functional group in either year (Table 1). Total belowground biomass, however, was greatest in irrigated plots by the end of the experiment (Fig. 2a). Total belowground biomass in irrigated plots was 158 g m⁻², while that in control, defoliated, and defoliated plus irrigated plots averaged 98 g m⁻² (Fig. 2a). Irrigation apparently also enabled the grasses to compensate, at least in part. for tissue lost to clipping during the dry year; that is, in the dry year defoliation alone reduced live and dead aboveground grass biomass, but biomass of grasses in defoliated plus irrigated plots was not different from that of control plots (Table 1). The combined effects of defoliation and irrigation did not significantly alter aboveground biomass of any individual plant functional groups, but did result in greater total aboveground biomass production than control and defoliated treatments by the end of the experiment in 1994.

In the upland study site, growing season (ca. April–August) precipitation was also lower in 1994 (193 mm) than in 1993 (399 mm). Nevertheless, we found no interannual differences in aboveground biomass production of any plant functional group in control plots (Table

Table 2. Mean aboveground biomass (g m⁻²) ±1 SE of grasses, forbs, and total biomass in control plots and defoliated, fertilized, and defoliated plus fertilized treatments from montane sites (n = 20 for each functional group x treatment). Values shown are for final harvest in August 1993 and 1994 and include clipped graminoid biomass from May through August (see text for additional details).

	Control	Defoliated	Fertilized	Defoliated and Fertilized
		(g	m ⁻²)	
1993				
Graminoids	48.5 ± 6.4^{a} ‡	54.2 ± 5.0^a	$61.7 \pm 7.2^{a_{*}}$	65.4 ± 6.6^a
Live	25.4 ± 2.9^{a}	30.9 ± 2.6^a	$42.0\pm4.8^{b}\ast$	45.2 ± 4.6^b
Dead	23.0 ± 4.2^{a}	23.2 ± 2.7^a	$19.7\pm4.1^{a}{\ast}$	20.1 ± 3.1^a
Forbs	82.0 ± 10.7^{a}	84.0 ± 7.0^{a}	$93.6 \pm 11.3^{a}*$	110.3 ± 17.9^a
Total aboveground biomass	175.6 ± 11.1^{a}	193.1 ± 13.1^{ab}	234.9 ± 17.4^{bc} *	$234.5 \pm 15.2^{bc}*$
1994				
Graminoids	49.7 ± 6.0^{a}	41.2 ± 6.2^a	$105.6 \pm 8.1^{b_{*}}$	59.6 ± 6.5^a
Live	27.8 ± 3.1^{ab}	21.8 ± 2.4^a	$57.5 \pm 4.9^{c}*$	36.1 ± 4.4^{b}
Dead	21.9 ± 3.2^{a}	19.4 ± 3.5^{a}	$48.1 \pm 6.3^{b_{*}}$	23.5 ± 2.5^a
Forbs	90.1 ± 12.0^{a}	101.2 ± 12.8^{ab}	$146.8 \pm 16.8^{\circ}$	137.4 ± 13.7^{bc}
Total aboveground biomass	177.7 ± 18.2^{a}	211.7 ± 22.5^b	$338.3 \pm 19.8^{c} \ast$	$282.8 \pm 17.4^{c} \ast$

Columns with different letters within a functional group indicate significant differences (P < 0.05) between treatment means. Asterisks indicate significant differences (P < 0.05) between 1993 and 1994 values.

2). Selective defoliation of the graminoids also did not significantly reduce their biomass production in either year. However, defoliated plots did have greater total aboveground biomass than control plots by the end of the experiment (Table 2).

Fertilization increased live graminoid biomass in both years, and total live and dead graminoid biomass was highest in fertilized plots by the end of the experiment in 1994. At that time, live (58 g m^{-2}) and dead (48 g m⁻²) graminoid biomass in fertilized plots was more than twice that in control or defoliated plots (Table 2). Aboveground biomass production of all plant functional groups was higher in fertilized plots in 1994 than in 1993 (Table 2). Total belowground biomass in fertilized plots (620 g m⁻²) was greater than that of control (391 g m⁻²) or defoliated (306 g m⁻²) plots by the end of the experiment, but was not significantly different from defoliated plus fertilized plots (453 g m⁻² Fig. 2b). The defoliation plus fertilization treatment increased live graminoid biomass in 1993 compared to control plots, but total grass biomass was not significantly changed by this treatment (Table 2). Additionally, total aboveground biomass was significantly higher in defoliated plus fertilized plots than in control plots in both years.

Nitrogen responses

In the arid lowland grassland, N concentrations of both live and dead grass in defoliated and defoliated plus irrigat-

Table 3. Nitrogen concentrations (%) of live and dead grass and forbs in 1993, a wet year, and 1994, a dry year, from the lowland experimental site (n = 5 for each functional group x treatment).

	Control	Defoliated	Irrigated	Defoliated and Irrigated
		(%	5)	
1993				
Live grass	0.81 ± 0.01^{a}	$1.26 \pm 0.05^{b}*$	$0.85 \pm 0.04^{a}*$	$1.25 \pm 0.03^{b}*$
Dead grass	$0.45 \pm 0.01^{a_{*}}$	$0.62 \pm 0.02^{b}*$	$0.46 \pm 0.02^{a_{*}}$	$0.61 \pm 0.03^{b}*$
Forbs	0.78 ± 0.03^a	0.84 ± 0.03^a	0.82 ± 0.02^{a}	0.95 ± 0.04^a
1994				
Live grass	$0.66 \pm 0.02^{a} \ast$	$0.80 \pm 0.02^{b}*$	$0.62 \pm 0.02^{a_{*}}$	$0.78 \pm 0.02^{b}*$
Dead grass	$0.53 \pm 0.03^{a} \ast$	$0.76 \pm 0.01^{b}*$	$0.55 \pm 0.04^{a}*$	$0.75 \pm 0.01^{b}*$
Forbs	0.80 ± 0.03^{a}	0.95 ± 0.19^a	0.79 ± 0.04^a	0.81 ± 0.03^a

Columns with different letters within a functional group indicate significant differences (P < 0.05) between treatment means. Asterisks indicate significant differences (P < 0.05) between 1993 and 1994 values.

ed plots were higher in both years than those in either control or irrigated plots (Table 3). The N concentration of live grasses was significantly lower in all treatments in 1994, the dry year, than in 1993, the wet year (Table 3). In contrast, the N concentration of dead grasses was higher in all treatments in 1994 than in 1993. The N concentrations of the forbs were not significantly affected by selective grass defoliation in either year.

In the more mesic montane grassland, all treatments (defoliated, fertilized, and defoliated plus fertilized) resulted in increased N concentrations in the live graminoids, and defoliated and defoliated plus fertilized increased the N concentration of the dead graminoids, in both years (Table 4). As at the lowland site, N concentrations of live graminoids were higher in all treatments in 1993 than in 1994, and N concentrations of the forbs were not affected by any treatment in either year.

Total aboveground nitrogen yield (g N m⁻²) of the lowland and upland graminoids was increased by defoliation only in 1993, the wetter year (Fig. 3). Aboveground N yield of all lowland plants combined was increased in the defoliated plus irrigated treatment by the end of the experiment in 1994, and in the upland experiment, fertilization and defoliation and fertilization increased the aboveground N yield of the graminoids and of all plants combined in both years.

Discussion and Conclusions

In the wet year, 1993, selective defoliation of the lowland grasses, primarily P. spicata, had no effect on their aboveground biomass production; that is, the grasses fully compensated for the shoot biomass removed. In the dry year, however, defoliation in the absence of water supplementation severely reduced grass biomass production. Irrigation in that year enabled P. spicata to compensate for shoot biomass lost to clipping. Consistent with our hypothesis, these data suggest that in the arid lowlands of the Pryor Mountain Wild Horse Range, regrowth following grazing is closely linked to water availability.

Similar reductions in grass biomass production in response to the simultaneous pressures of clipping and water stress have also been found in other studies (e.g., Toft et al. 1987, Georgiadis et al. 1989, Simoes and Baruch 1991, Busso and Richards



Fig. 2. Total belowground biomass (g m⁻²) in the (a) lowland and (b) upland experimental sites at the conclusion of the experiment in August, 1994. Columns headed by different letters indicate significant (P < 0.05) differences between treatments. Treatments are control (C), graminoids defoliated (D), irrigation (W) or fertilization (F), and graminoids defoliated plus irrigation (DW) or graminoids defoliated plus fertilization (DF). Note different scales for the 2 sites.



Fig. 3. Aboveground nitrogen yield (g N m^{-2} ; n = 5 for each vertical bar) for graminoids, forbs, and total N yield in the lowland and upland experiments in August, 1993 and August, 1994. Treatments as in Fig. 2. Asterisks denote significantly higher N yields (calculated as N concentration multiplied by aboveground biomass) in treatment than control. Note different scales for each graph.

1995). This response, however, is in contrast to the prediction of Hilbert et al. (1981) that plants which are stressed in some way, and consequently growing slowly compared to their potential rates, are most likely to increase production following grazing. The response of the lowland grasses in the Pryor Mountains was also not consistent with those of McNaughton et al. (1983) and Coughenour et al. (1985 a, 1985b, 1990); in their studies, the effects of water stress and defoliation were found to often act singly and 1 factor could reduce or ameliorate the negative effect of the other. In our study, additional water supply ameliorated the negative effects of defoliation in the dry year. In the semiarid shortgrass steppe, Milchunas et al. (1994) have found that long-term primary production across 50 years of cattle grazing treatments was most sensitive to precipitation and least sensitive to grazing intensity.

In the dry year, decreased live grass biomass in the lowland control plots was the result of lower individual tiller mass, not tiller density. Busso and Richards (1995) similarly found that mass of individual unclipped tillers of *P. spicata* was severely reduced under drought conditions compared to more average precipitation levels. They also found that plants that were irrigated showed lower tiller height, leaf area, and mass compared to plants under more average precipitation conditions. Our levels of irrigation did not increase individual grass tiller mass of *P. spicata* in either the dry or wet year. Why P. spicata failed to increase its aboveground biomass production in response to artificially increased water supply is not known. Although bare ground evaporation was undoubtedly high, soil excavations showed that soil moisture was appreciably higher in irrigated compared to non-irrigated plots for at least 1 week following each watering event. It is possible that the grasses in these arid lowlands are rather insensitive to large pulses of increased water availability, such as those simulated in this study, and that frequent, smaller rainfall events may be more important to their growth (e.g., Sala and Lauenroth 1982, but see Weaver 1985). Additionally, the overall environment in these lowlands was still arid which may have negated the effects of our irrigation treatment. Nevertheless, total root biomass was significantly higher in the lowland irrigated plots than in the other treatments by the end of the experiment, indicating that plant growth responses to our levels of irrigation may have been belowground only.

In the lowland site, the reduction in grass biomass with clipping that was measured in the dry year was the result of a decrease in grass tiller density and not individual tiller mass, which was much higher in clipped than control plots that year. Bluebunch wheatgrass, the dominant grass in these lowlands, has been shown to be a decreaser under increasing grazing pressure (Williams 1963). A decrease in tiller number resulting from grazing has frequently been reported (Branson 1956, Ellison 1960, Caldwell et al. 1981, Carman and Briske 1985, Polley and Detling 1989), although an increase in tiller production (Richards et al. 1988, Zhang and Romo 1995) and

Table 4. Nitrogen concentrations (%) of live and dead graminoids and forbs in 1993, a wet year, and 1994, a dry year, from the montane experimental site (n = 5 for each functional group x treatment).

	Control	Defoliated	Fertilized	Defoliated and
				Fertilized
		(%)	
1993				
Live graminoids	$1.37 \pm 0.04^{a_{\small { \ast } }}$	$1.50 \pm 0.02^{b}*$	$1.72 \pm 0.02^{c_{*}}$	$1.76 \pm 0.06^{c_{*}}$
Dead graminoids	$0.90 \pm 0.03^{a_{\ast}}$	$1.08\pm0.05^{\rm b}$	$1.04 \pm 0.05^{ab}*$	$1.17\pm0.05^{\rm b}$
Forbs	1.47 ± 0.05^a	1.56 ± 0.03^{a}	$1.58\pm0.07^{\rm a}$	1.59 ± 0.06^{a}
1994				
Live graminoids	$1.13 \pm 0.02^{a} * \ddagger$	$1.27 \pm 0.05^{bc}*$	$1.24 \pm 0.02^{b}*$	$1.37 \pm 0.06^{c_{*}}$
Dead graminoids	$0.70 \pm 0.07^{a_{\#}}$	$0.94\pm0.08^{\rm b}$	$0.55 \pm 0.01^{a_{\ast}}$	$1.00\pm0.10^{\rm b}$
Forbs	1.27 ± 0.03^a	1.33 ± 0.08^a	1.35 ± 0.05^a	1.25 ± 0.06^a

Columns with different letters within a functional group indicate significant differences (P < 0.05) between treatment means. Asterisks indicate significant differences (P < 0.05) between 1993 and 1994 values.

increased regrowth of surviving tillers (Branson 1956, Caldwell et al. 1981, McNaughton et al. 1983, Carman and Briske 1985), has also been observed. In this system there appears to be an inverse relationship between tiller size and density, as is generally the case (Risser 1969, Gorham 1979, Christiansen and Svejcar 1988). The simultaneous pressures of clipping and water stress reduced tiller density of *P. spicata*, but increased the mass of the surviving tillers relative to those of unclipped plants. Additions of water to clipped plots in the dry year did not prevent a reduction in tiller density following clipping, providing further evidence to suggest that *P. spicata* is not very responsive to the large, infrequent rainfall events simulated in this shortterm study.

In the upland defoliation-fertilization experiment, the decrease in growing season precipitation in 1994 compared to 1993 did not result in a decrease in aboveground biomass production of any plant functional group, suggesting that water did not limit plant growth at this site during the study. This was not true at all upland sites in the Pryor Mountain Wild Horse Range, however, since decreases in plant cover and biomass were measured at some sites in the dry year (Peterson et al. 1997, Fahnestock 1998). At this site, our finding that defoliation did not reduce live or total graminoid biomass production in either year indicates that the graminoids are apparently able to compensate for biomass lost to grazers without additional resource supply.

Fertilization increased the growth of most plant functional groups such that total above- and belowground biomass production were higher in fertilized only plots than unfertilized plots by the end of the experiment. In individual plants, nutrient limitation is recognized by an increase in growth in response to an addition of the limiting nutrient. The analogous response at the community level is an increase in total community production in response to fertilization (Chapin et al. 1986). In this experiment only, the upland graminoids increased their aboveground biomass production in response to fertilization in the first year, but by the second year all plant functional groups had increased biomass production. These results suggest that species or functional groups differed in their ability to respond to increased nutrient supply or that nutrient limitations were not the same for all

plants (Chapin 1980, Jaramillo and Detling 1992). Fertilization also resulted in defoliated graminoids producing more live, but not dead, biomass in 1993, than unclipped, unfertilized plants. Therefore, the effect of increased nutrient supply on defoliated graminoids in the uplands may be to decrease their rate of senescence, and to increase their belowground biomass production (see above).

Our results suggest that the dominant graminoids in the Pryor Mountains are able to withstand fairly heavy levels of defoliation through compensatory growth. In the uplands, the graminoids are able to compensate for tissue lost to grazers without additional resource supply. In the lowlands, however, their ability to fully regrow following grazing is only possible when water availability is not too low. Increased water availability in the lowlands of the Pryor Mountains will most likely stimulate belowground growth in these plant communities, and will increase the nitrogen concentrations of all plants except perhaps the forbs.

In both the lowland and upland communities, selective graminoid defoliation increased the N concentrations of graminoids in both years, and increased total aboveground N yield of graminoids in the wet year. This may have resulted from increased N uptake by defoliated grasses, increased allocation of N to aboveground plant tissue, or both. Nitrogen uptake, N concentration, and physiological activity are often higher in plants that have been grazed or otherwise defoliated than in plants from ungrazed areas (e.g., Jameson 1963, Detling et al. 1979, McNaughton 1979, Coppock et al. 1983, McNaughton et al. 1983, Ruess et al. 1983, Detling and Painter 1983, Polley and Detling 1988, Jaramillo and Detling 1988). Increased N concentrations in grazed graminoids results in higher quality forage available to herbivores. This may have important consequences for subsequent food preference by herbivores in the Pryor Mountain Wild Horse Range. In addition, the higher N-yield of defoliated graminoids suggests that herbivores may, via their grazing activities, increase not only the quality of their forage but also the quantity of crude protein subsequently available to them when they regraze the same patch. Defoliation of the graminoids did not change the aboveground biomass production or nitrogen concentrations of the

other plant functional groups in the Pryor Mountains, indicating that the relative competitive abilities of plants in the upland and lowland communities are not greatly, or at least rapidly, altered by selective graminoid defoliation.

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Imbibition temperature affects winterfat *(Eurotia lanata (Pursh) Moq.)* seed hydration and cold-hardiness response

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Abstract

Winterfat (Eurotia lanata (Pursh) Moq.) diaspores harvested from 1 Canadian and 2 USA sites were imbibed at 0, 5, 10, and 20°C. It was hypothesized that imbibition temperature affects seed hydration which is related to cold-hardiness of winterfat. Weight gain was measured at 8-hour intervals until full hydration, and embryo water content was determined. Water content of fully hydrated seeds differed among collections and lower imbibition temperatures were always associated with greater seed water content. Differences in water content of seeds imbibed at different temperatures was related to cold-hardiness. When water content of embryos was measured, differences among imbibition temperatures existed, but were reduced. Differences in seed water content among imbibition temperatures were mainly due to endosperm other than the embryo because the embryo hydrated faster than other seed parts. Suggestions were made for modeling seed water relations based on this study.

Key Words: *Krascheninnikovia, Ceratoides*, embryo, threshold water content.

Environmental stress affects plants at all life stages, though dry seeds are most tolerant. As seed water content increases, physiological activities of seeds are increasingly influenced by temperature-water interactions. Many seed studies have dealt with species that are injured by imbibing cold water (Hobbs and Obendorf 1972, Ashworth and Obendorf 1980, Herner 1986). Few have examined basic themes using seeds with unusual tolerance to extremes, such as winterfat (*Eurotia lanata* (Pursh) Moq.), which may be unaffected or even benefited by cool conditions (Booth 1992).

Winterfat seeds can germinate over a wide range of temperatures (Dettori et al. 1984), including 0 or near 0°C (Hilton 1941, Woodmansee and Potter 1971, Dettori et al. 1984, Booth 1987). A recent study indicated that hydrated winterfat seeds were tolerant to cooling as low as -30°C even after the occurrence of the low temperature exotherm; cold-hardiness

Resumen

Semillas de "Winterfat" (Eurotia lanata (Pursh) Moq.) cosechadas de un sitio canadiense y dos de U.S.A fueron imbibidas a 0, 5, 10, y 20°C. Se hipotetizó que la temperatura de imbibición afecta la hidratación de la semilla la cual esta relacionada con la resistencia al frío del "winterfat". La ganancia de peso se midió a intervalos de 8 horas hasta la hidratación total y se determinó el contenido de agua del embrión. El contenido de agua de semillas completamente hidratadas difirió entre colecciones y las bajas temperaturas de imbibición siempre estuvieron asociadas con un mayor contenido de agua de la semilla. La diferencia del contenido de agua de las semillas imbibidas a diferentes temperaturas fue relacionada a la resistencia al frío. Cuando se midió el contenido de agua de los embriones existían diferencias entre las temperaturas de imbibición, pero eran mínimas. Las diferencias en el contenido de agua de las semillas entre temperaturas de imbibición fueron debidas principalmente al endospermo mas que el embrión, esto porque el embrión se hidrató más rápido que otras partes de la semilla. Basado en este estudio se hicieron sugerencias para modelar las relaciones hídricas de la semilla.

measured by seed germination percentage and rate depended on imbibition temperature (Bai et al. 1998). Since seed water relations are also related to cold-hardiness, a closer look at hydration processes of winterfat seeds may provide additional information on its cold-hardiness mechanism.

Seeds must reach a threshold water content before germination starts. Water content at the onset of germination was the same among osmotic conditions (Bradford 1986, Gray et al. 1990) or certain temperatures (Gummerson 1986). On the other hand, if different seed parts imbibe water at different rates, then using the whole seed water content as a pre-condition for seed germination may be questionable. In the study reported here, seed hydration of winterfat was tested at temperatures ranging from 0 to 20°C. Objectives of this study were to determine effects of imbibition temperature on seed water in relation to cold-hardiness and to incipient germination in winterfat.

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Materials and Methods

Seed sources and post-harvest handling

Winterfat diaspores (seed-containing dispersal units) were hand-collected in October 1994 from Matador, Saskatchewan, Sterling, Colo., and Pine Bluffs, Wyo. (Table 1). The first 2 sites are located in Mixed Prairie while the third is located in Shortgrass Prairie (based on a map by Dodd; in Tetlyanova et al. 1990). Harvested diaspores were stored in paper bags at room temperature until February 1995. Dry weight of threshed seeds from Matador and Sterling were 38 and 28% heavier than from Pine Bluffs.

Seed water content as affected by imbibition temperature

We placed diaspores of the 3 collections on moistened germination paper (Anchor Paper Corp., St. Paul, Minn.) over plastic slant-boards, and covered them with 1 layer of cellulose tissue (Jones and Cobb 1963). Slant-boards were then placed in closed germination boxes ($25 \times 40 \times 20 \text{ cm}$), which were filled with distilled water to 3-cm depth. These boxes were placed in incubators at 0, 5, 10, and 20° C in darkness. The experimental design was a randomized complete block with 3 replicates arranged over time.

For each experimental unit (slant board), we retrieved 10 diaspores from incubators at 8-hour intervals until full hydration (1 to 8 days, depending on imbibition temperature). Bracts were removed and surface water of seeds was blotted away with tissue paper. Seeds were then sealed in 0.25 ml tin capsules (Leco Corp., St. Joseph, Mich.) and weighed (Booth and Bai 1998) before being oven dried at 80°C for 24 hours and dry weight determined. Weighing was done with a micro-balance to 0.001 mg and seed water content was expressed on a dry weight basis (%DW). We defined full hydration as the stage 8 hours before germination began.

Comparison of water contents of seeds and embryos at full hydration

The above imbibition procedures were repeated in June 1995 (4 months after the above study), with 4 replicates for



Fig. 1. Water content (mean±SE) of winterfat seeds collected from Matador, Sask., Sterling, Colo., and Pine Bluffs, Wyo. after imbibition at 0, 5, 10, or 20°C. See Table 2 for regression equations.

each collection. At the end of imbibition, embryos of half of the seeds were separated from other seed parts and the water contents of both seeds and embryos were determined as described above.

Data analysis

Data were first analyzed with ANOVA or GLM in a randomized complete block design (Snedecor and Cochran 1980) over the 3 seed collections, and then analyzed within each collection because of the interaction between seed collection and imbibition temperature. Data were further analyzed separately for each imbibition temperature. Statistical significance was assumed at P \leq 0.05 and means were separated using LSD.

Results

Seed water content as affected by imbibition temperature

Initial seed water content was similar among seed collections, averaging 4.8% (Fig. 1). However, the rate of water uptake during imbibition, time required to reach full hydration, and seed water content when fully hydrated depended on seed collection and imbibition temperature. Water content of seeds at the time of germination decreased with increasing imbibition temperatures. As expected, the rate of seed water uptake increased, and time required to reach full hydration decreased with increasing imbibition temperature.

Seeds from Matador required more
Table 1. Descriptions of sources and habitats for winterfat seeds used in the study.

Site	Geographical location	Vegetation and dominant species	Seed weight (g 100 seeds ⁻¹)
Matador	Saskatchewan, Canada 50°42'N, 107°43'W, elev. 685 m	Mixed Prairie Agropyron dasystachyum (Hook.) Scribn Agropyron smithii Rydb. Koeleria cristata Pers. Stipa viridula Trin. Eurotia lanata (Pursh) Moq.	0.25
Sterling	Colorado, USA 40°37'N, 103°13'W, elev. 1181 m	Shortgrass Prairie Bouteloua gracilis (H.B.K.) Lag. Buchloe dactyloides (Nutt.) Engelm.	0.23
Pine Bluffs	Wyoming, USA 1°10'N, 104°09'W, elev. 1554 m	Mixed Prairie Stipa comata Tri. & Rupr. Agropyron smithii Rydb. Bouteloua gracilis (H.B.K.) Lag.	0.18

of Phase II during germination, or 24

time to reach full hydration, particularly at 0 and 5°C, than those from Sterling or Pine Bluffs (Fig. 1). When seeds were imbibed at 0°C, seed water content at full hydration was greater for the Matador collection than the Sterling or Pine Bluffs collections. At 5, 10, and 20°C, seed water content was highest for the Matador collection and lowest for the Sterling collection.

The relationship between seed water content and time after imbibition were described in linear, quadratic and cubic equations (Fig. 1, Table 2). Phases I and II during imbibition (as defined by Ching 1972, 1973) were more distinct for seeds imbibed at lower temperatures than those imbibed at higher temperatures.

Comparison of water contents of seeds and embryos at full hydration

Water content of seeds and embryos at full hydration was similar among collections (P = 0.26 and 0.17 for seeds and embryos, respectively) and data were pooled (Fig. 2). Seed water content again decreased with increasing imbibition temperatures, ranging from 169 to 231%. Water content of embryo decreased between 0 and 10°C imbibition temperatures, but increased at 20°C, with the range from 94 to 114%.

Discussion

The definition of full hydration of seeds has largely depended on researchers and the intervals used for seed water content determination. Keefe and Moore (1981) used the middle point hours before germination started. Others imbibed seeds for given durations regardless of the physiological stage, and simply called them "imbibed" or "hydrated" seeds (Ishikawa and Sakai 1982, Gray and Steckel 1983, Cremer and Mucha 1985). In the present study we defined full hydration as 8 hours before germination started, or the end of Phase II. Seed water content at full hydration varied by seed collection, but was always greater with lower imbibition temperatures. The greater water content at 0°C explains the warmer lowtemperature exotherm for seeds imbibed at lower temperatures than those imbibed at higher temperatures (Bai et al. 1998).

The fact that embryo water content was much lower than whole seed water content indicates that the rate of hydration, and the water holding capacity, vary among seed parts. Faster hydration in the embryo than in the endosperm was found in several species such as corn (Zea mays L.) (Styles 1948, Vertucci 1989). The seed coat of winterfat is membranous and highly permeable (Booth and McDonald 1994), enabling seeds to absorb water quickly and store it in the endosperm. Nevertheless, seed hydration generally increases with increasing temperature (Shull 1920, Allerup 1958) and at warmer temperatures the embryo may hydrate faster than the endosperm. Variation in hydration rate explain the lower whole-seed water content at higher temperatures than at lower temperatures. Therefore, water content of the whole seed may not accurately reflect the true water status related to seed germination. Instead, the water content of an embryo is a better measurement of germination readiness than that of the whole seed, at least for seeds similar to winterfat.

Table 2. Regression equations describing relationships between water content (Y, %DW) and time after imbibition (X, hour) of seeds collected from Matador, Sask., Sterling, Colo., and Pine Bluffs, Wyo. Curves are presented in Fig. 1.

Seed	Imbibition	Regression equation	R^2	P-value
	Temperature			
Matador	0	$Y = 8.58 + 3.49X - 0.0286X^2 + 0.000085X^3$	1.00	0.000
	5	Y=2.96+5.39X-0.0722X ² +0.000364X ³	0.99	0.000
	10	Y=5.94+5.13X-0.0477X ²	0.99	0.000
	20	Y=2.85+8.35X-0.1600X ²	0.99	0.000
Sterling	0	Y=6.66+2.31X-0.0096X ²	0.99	0.000
	5	Y=3.75+3.03X-0.0201X ²	0.99	0.000
	10	Y=7.46+2.56X	1.00	0.001
	20	Y=2.60+5.37X	1.00	0.001
Pine Bluffs	0	Y=5.89+2.36X-0.0105X ²	0.99	0.000
	5	Y=2.45+3.30X-0.0198X ²	0.99	0.000
	10	Y=4.92+4.38X-0.0367X ²	0.99	0.000
	20	Y=2.14+6.29X-0.0958X ²	0.99	0.001



Fig. 2. Water content of seeds and embryos at full hydration at 0, 5, 10, or 20° C imbibition temperature for winterfat seeds collected from Matador, Sask., Sterling, Colo., and Pine Bluffs, Wyo. Data were pooled for collections and means with the same letter within seed or embryo were not significantly different at P \leq 0.05.

The dependence of seed water content at full hydration on imbibition temperature has been observed in seeds of other species (C.W. Walters, personal communication), but has not, to our knowledge, been reported. The finding implies, the critical moisture content concept (Hunter and Erickson 1952) and the hydrothermal time model (Gummerson 1986, Dahal et al. 1993) of seed germination must be modified based on embryo water content, and expanded to a wider temperature range, particularly for temperatures near 0°C. What remains unanswered is the existence of differences in embryo water content among imbibition temperatures. One possibility is that cold cell walls with lower energy level provide greater resistance to cell extension and elongation. Therefore, greater turgor pressure (higher water content) is required for germination to proceed.

In summary, differences in seed water contents were related to cold-hardiness of winterfat. Higher seed water content at full hydration was associated with lower imbibition temperatures, apparently a result of different hydration rates between embryo and endosperm. Further studies using embryos instead of the whole seeds over a wider range of temperatures are needed for modeling water relations for seed germination.

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Grazing steer fecal output dynamics on south Texas shrubland

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Abstract

Combined with other information, fecal output appears to have potential use in models to predict forage intake. Better understanding of fecal output dynamics relative to forage availability could improve model estimates of animal performance. Field trials were conducted during 4 different periods to investigate the relationship between 1) declining forage mass or forage component availability and beef steer fecal output and between 2) browse consumption and available forage mass. Fecal output was estimated using the rare-earth marker ytterbium. Initial fecal output as a percentage of body weight was greatest in March (1.24%) and least in August (0.96%). Regression slopes were negatively correlated (-0.73) with initial forage mass. As indicated by regression slopes, fecal output declined most rapidly in March (slope = (0.57) and slowest in August (slope = (0.13)). Expression of available forage mass as either daily grass allowance or daily grass leaf allowance, both as g dry matter/kg live weight, produced similar regression equation statistics. Development of regressions for individual pastures within trials did, however, improve equation statistics in all trials except August. Browse consumption was <10% until daily grass allowance fell below 50 g/kg live weight then increased to between 53 and 64% below 25 g/kg live weight, but was not adequate to maintain fecal output. Apparent seasonal differences in fecal output suggest lower forage intake (29%) in August compared to March. Fecal output was not affected by daily grass allowance above 100 g. Fecal output declined to below 0.6% of body weight below 100 g daily grass allowance. Data are interpreted to suggest that different fecal output curves and/or adjustment factors may be needed to account for season and initial forage mass.

Key Words: herbage allowance, beef cattle, browse consumption

Grazing animal forage intake is routinely estimated using fecal output-forage indigestibility ratios (Langlands 1975, Cordova et al. 1978). Fecal output can be relatively stable within a physiological stage (McCollum and Gaylean 1985, Ellis et al. 1988) or across a wide range of digestibility (Ellis et al. 1988) but can change with physiological stage (Sprinkle

Resumen

Combinada con otra información, La producción fecal parece tener un uso potencial en los modelos para predecir el consumo de forraje. Un mejor entendimiento de la dinámica de producción fecal relativa a la disponibilidad de forraje podría mejorar las estimaciones de los modelos acerca del comportamiento productivo animal. Se condujeron estudios de campo durante 4 diferentes períodos con el objetivo de investigar la relación entre 1) la disminución de la masa de forraje o la disponibilidad del componente de forraje y el rendimiento fecal de novillos para carne y 2) el consumo de forraje de arbustos y la masa disponible de forraje. La producción fecal fue estimada usando como marcador el Iterbio. La mayor producción fecal inicial, expresada como porcentaje del peso corporal, se obtuvo en marzo (1.24%) y la menor en agosto (0.96%). Las pendientes de regresión fueron negativamente correlacionadas (-0.73) con la masa inicial de forraje. Como indicaron las pendientes de regresión, la producción fecal disminuyó más rápidamente en marzo (pendiente = 0.57) y más despacio en agosto (pendiente = 0.13). La expresión de la masa de forraje disponible ya sea como la asignación diaria de zacate o la asignación diaria del material foliar de zacate, ambas expresadas como g de materia seca/ kg de peso vivo, produjeron ecuaciones de regresión similares. El desarrollo de regresiones para potreros individuales dentro de los ensayos mejoró la ecuación estadística en todos los ensayos excepto en agosto. El consumo de forraje de arbustos fue <10% hasta que la asignación diaria de zacate cayó abajo de 50 g/kg de peso vivo, entonces, abajo de los 25 g/kg de peso vivo, se incrementó entre 53 a 64% pero no fue adecuada para mantener la producción fecal. Las aparente diferencias estacionales en la producción fecal sugieren un bajo consumo de forraje (29%) en agosto comparado con marzo. El rendimiento fecal no fue afectado cuando la asignación de forraje fue arriba de los 100 g. Cuando la asignación diaria de zacate fue menos de 100 g, la producción fecal disminuyó a menos del 0.6% del peso corporal. Los datos son interpretados para sugerir que diferentes curvas de producción fecal y/o factores de ajuste pueden ser necesitados cuando para reportar por estación y masa de forraje inicial.

et al. 1992), gut capacity or forage type (McCollum and Gaylean 1985), and forage availability (McCollum and Gaylean 1985, McKown et al. 1991). Although fecal output and body weight have been used to predict feed or roughage

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intake (Conrad et al. 1964, Forbes 1983), fecal output dynamics with regard to forage availability need further clarification for use in grazing animal models. Rayburn (1986) reported rapidly declining intake for cattle below 2,250 kg/ha forage availability; however, this threshold may vary from <3,000 kg/ha (Allden and Whittaker 1970) to <135 kg/ha (Handl and Rittenhouse 1972). Vegetation characteristics, e.g., leaf and stem proportions, may be more highly correlated to forage intake and fecal output than gross forage mass. In shrublands, these relationships may be affected by a large, diverse supply of browse.

This research was conducted 1) to examine relationships between available forage mass and fecal output and between forage components and fecal output and 2) to determine how browse consumption relates to available forage mass.

Methods

This study was conducted on the La Copita Research Area (27° 40'N, 98° 12'W) in northeastern Tamaulipan Province, about 80 km W of Corpus Christi, Tex. To establish contrasting forage conditions, four 0.4-ha pastures were established on a gray sandy loam site that had been chained 7 years earlier. Two of the 4 pastures (A and B) were chained only while the other 2 (C and D) were also sprayed 3 years before the study with picloram at a rate of 1.0 kg active ingredient/ha to create grazing conditions with high grass production and low available browse.

Four grazing trials were conducted during seasons representing different phenological stages. Trials were conducted in 1) March, 1985; 2) May, 1985; 3) August, 1985; and 4) January, 1986. Two pastures (1 chained only and 1 chained and sprayed) were grazed by 6 Beefmaster steers each for 21 days or until utilization of the grass standing crop was judged to be 90% during each trial. Pastures A (chained only) and C (chained and sprayed) were grazed in March and August while pastures B (chained only) and D (chained and sprayed) were grazed in May and January, allowing 150 to 210 days between trials. Three sets of steers were used during this study. One set was used in the March and May trials, a second set in August, and a third set in January. Within each trial, each group of steers was 9 to 14 months old and weighed 240 to 340 kg.

Dominant grasses in pastures included purple threeawn (Aristida purpurea Nutt.), plains bristlegrass [Setaria leucopila (Scribn. & Merr.) K.Schum.] and Texas bristlegrass (Setaria texana W.H.P. Emery), Texas tridens [Tridens texanus (S. Wats.) Nash], hooded windmillgrass (Chloris cucullata Bisch), buffelgrass (Cenchrus ciliaris L.), fall witchgrass [Leptoloma cognatum (Schult.) Chase var. *cognatum*], Kleberg bluestem (Dichanthium annulatum Stapf) and Hall panicum (Panicum hallii Vasey var. hallii). Common woody plants occurring in pastures were mesquite (Prosopis glandulosa Torr.), spiny hackberry (Celtis pallida), lime pricklyash (Zanthoxylum fagara (L.) Sarg.), coyotillo [Karwinskia humboldtiana (R.& S.) Zucc], desert yaupon (Schaefferia cuneifolia Gray), shrubby blue sage (Salvia ballotaeflora Benth.), and whitebrush [Aloysia gratissima (Gill. & Hook.) Troncoso]. Plant growth initiates in late March with a bimodal peak of grass standing crop in June and October depending on rainfall patterns. Browse standing crop peaks in July and remains stable for most species through early November.

Five sample collections were conducted during each trial except in January when only 4 were possible. Sample collections occurred at the beginning and end of each trial and at 5-day intervals during the trial. Twelve, 1 x 30 m belt transects were established in each paddock to characterize available forage throughout each trial. Available browse standing crop was measured in each belt transect using the browse volumeweight method (Lopes and Stuth 1984). Two, 0.5 x 1 m quadrats were randomly located in each of the 12 belt transects and herbage composition by weight visually estimated and all herbaceous aboveground biomass subsequently clipped to ground level. Standing crop (kg/ha) was determined by species by multiplying estimated species composition by total clipped herbage for each sample collection within each trial.

Four, esophageal fistulated steers (270 kg, 9 months of age) per pasture were allowed to graze for approximately 30

min at the beginning of each sample collection in each trial. Ten total esophageal fistulated steers were available for sampling. Sample collections were staggered by one day for the 2 pastures used within each trial. Between each collection event, collector steers were grazed in pastures adjacent to and with the same vegetation as trial pastures. Collector steers and their mothers were experienced with the vegetation in the region before weaning. Collected extrusa was dried 48 hours at 60°C and subjected to macrohistological analysis to determine steer diet composition by plant group and plant part (Araujo 1985). Diet samples were analyzed for crude protein (CP) content on a dry matter basis by micro-Kjeldahl procedure (AOAC 1960). Digestible organic matter (DOM) was determined by in vitro procedures using a 48-hour fermentation (Tilley and Terry 1963) followed by neutral detergent fiber procedure (Van Soest and Wine 1967).

Grass standing crop components (live leaf, dead leaf, live stem, and dead stem) were estimated using extrusa grass component composition, grass standing crop disappearance, and initial grass standing crop mass. Grass component mass was estimated by multiplying percent grass component in extrusa obtained at each sample collection by the amount of grass disappearance occurring during the interval between that sample collection and the next and summing interval values for each component over the entire trial. These totals were used to calculate initial mass and initial percentage of each grass component and grass component composition of the residual grass throughout the trial. Herbage disappearance between clipping dates was assumed to be equal to consumption. Little or no growth occurred during the 5 days intervals between sampling dates within each trial. Because available grass was so low during the last interval of each trial, composition of the grass standing crop was assumed to be proportional to extrusa sample grass component composition at the beginning of this interval.

To estimate fecal output, non-cannulated steers used to graze pastures were dosed daily with the rare-earth element ytterbium in powdered acetate form via gelatin capsules. Steers were dosed daily beginning 9 days before each trial. During this pre-trial period, these steers

Table 1. Mean and standard error for initial and end of trial forage crude protein (CP, dry matter basis) and digestible organic matter (DOM) for March, May, August, and January trials by pasture.

		CP,				DOM, %			
	Pasture	e A or B ¹	Pasture	$C \text{ or } D^2$	Pasture	A or B	Pasture	e C or D	
Trial	Initial	Ending	Initial	Ending	Initial	Ending	Initial	Ending	
		(%)			(%	ó)		
Mar.	16.6±0.2	12.1±0.5	17.0±0.3	10.5±0.2	65.2±1.2	34.0±1.3	67.5±1.2	36.0±3.0	
May	12.1±0.2	12.4±0.4	11.5±0.2	9.9±0.3	74.8±0.5	46.0±1.2	71.8±0.5	45.0±2.5	
Aug.	9.8±0.2	9.2±0.4	9.3±0.2	7.6±0.3	74.8±0.5	44.0±1.2	71.4±1.1	46.0±2.5	
Jan.	11.6±0.2	10.2 ± 0.8	11.5±0.3	8.9±0.1	70.6±2.5	38.0±5.0	69.7±0.5	34.0±2.0	

Pastures A & B were chained 7 years before this study.

²Pastures C & D were chained and then sprayed with picloram at 7 and 3 years, respectively, before this study.

n=4

were grazed in pastures adjacent to and with the same vegetation as trial pastures. Because vegetation was the same in these adjacent pre-trial and trial pastures, fecal output estimates should not have been affected. Each trial pasture was grazed by 6 steers. Fecal samples were collected from each steer 24 hours after each diet collection and analyzed for ytterbium concentration using atomic absorption spectroscopy (Ellis et al. 1982). Galyeanet et al. (1986) reported that over a variety of experimental conditions, average continuous-dose marker estimates of fecal output using ytterbium were 104% of total fecal collection with a range of 86 to 144%. Musimba et al. (1987) suggested that this technique is most useful for relative comparisons. Because marker recovery was not determined, results are valuable because they may indicate general relationships and areas for future investigation. Steers were weighed at the beginning of each trial at 0600 hours after penning at 2000 hours the previous evening to determine fecal output on a percent body weight basis.

Regression and correlation analyses (SAS 1988) were performed across and within trials to determine the relationship between available forage, diet composition, and dietary browse consumption and fecal output on a dry matter basis as a percentage of body weight. Non-log functions were tested first in regressions. Log functions were then used in regressions because of the apparent visual trends in the data.

Results and Discussion

Diet Quality

In general both CP and DOM declined during each trial as quantity of forage decreased. Highest CP levels occurred in March and lowest levels in August (Table 1). Initial CP levels were similar between pastures within trials. Ending CP levels tended to be higher in pastures A and B (chained only) with more available brush. Initial and ending DOM levels were relatively similar between pastures within trials, but varied among trials. Generally, DOM levels declined more drastically than CP levels. These dietary trends reflect a shift toward browse as available grass declined.

Daily Grass or Grass Leaf Allowance and Fecal Output

Initial fecal output was associated with a range of ungrazed grass standing crop of 1500 to 3000 kg/ha with lowest herbage mass in March and highest in August (Table 2). Initial fecal output as a percent of body weight differed among trials (P<0.10) from a high in March (1.24%), to a low in August (0.96%), with May (1.09%) and January (1.08%) between these extremes. Initial fecal output in May, January, and August was 88, 87, and 77% of initial March fecal output, respectively.

Using stepwise regression, the log function of grass standing crop explained 74 to 94% of the variation in fecal output for individual trials (Table 3). Except for January, the log of grass standing crop was the only variable

Table 2. Initial standing crop (kg/ha ± standard error) of grass, forbs, and browse and initial percent grass standing crop component by trial and pastures.

				Initial Standing (ron				
Trial	Pasture	Grass	Forbs	Browse	Pasture	Grass	Forbs	E	Browse
-				(kg/	'ha ⁻¹)				
Mar.	A^1	1040±87	163±22	1976±28	C^2	1850±114	101±15	e	532±15
May	\mathbf{B}^1	1512±183	700±107	2200±36	D^2	2788±395	164±20	13	305±29
Aug.	А	1256±113	664±131	2986±46	С	3005±413	356±149	18	308±38
Jan.	В	765±100	239±43	839±16	D	1578±179	71±27	7	769±19
			Initia	al Grass Standing (Crop Componen	t			
		Live	leaf	Dead	l leaf	Live	stem	Dead s	stem
		A/B	C/D	A/B	C/D	A/B	C/D	A/B	C/D
					- (%)				
Mar.		68	34	13	15	7	8	12	43
May		43	53	15	9	16	18	26	20
Aug.		31	28	24	27	25	9	20	36
Jan.		9	10	47	26	6	26	38	38

Pastures A & B were chained 7 years before this study

²Pastures C & D were chained and then sprayed with picloram at 7 and 3 years, respectively, before this study.



Fig. 1. Influence of daily grass allowance, g dry matter (DM)/kg live weight (LW) on marker-estimated fecal output of steers. Predictive equations are based on the log of daily grass allowance with pastures A and C or B and D combined for March, May, August, and January. Pastures A & B were chained 7 years before this study. Pastures C & D were chained and then sprayed with picloram at 7 and 3 years, respectively, before this study. Endpoints of lines for each trial indicate the grass allowance range.

selected. The strongest regression relationships between grass standing crop and fecal output occurred in March and August (Table 3).

The relationship between grass standing crop and fecal output does not integrate pasture size, animal number, and animal size; therefore, the relationship between fecal output and daily grass allowance, g dry matter/kg live weight, was examined for each trial using the log function of grass allowance. Across trials, initial fecal output corresponded to daily grass allowances of 100 to 200 g/kg live weight (Fig. 1) with lower levels occurring in January and accompanied by a fecal output decline in pasture B (chained only) almost twice that in pasture D (chained and sprayed, Table 4). As indicated by slopes of the regression functions (Fig. 1), daily grass allowance had the least impact on fecal output in August and the greatest impact in March. Perhaps this difference in regression slopes indicates either differences in marker recovery, diet quality differences or an unwillingness of animals to shift from highly desirable but minimally occurring and rapidly declining forage components, e.g., live leaf in March. August live:dead leaf ratio was about 1:1 compared to >2:1 in March and May, and < 1:2 in January. Mnene et al. (1996) noted reduced fecal output when cattle diets predominated by dead leaf shifted to diets predominated by live leaf available at low levels.

Pastures C and D (chaining plus picloram) had a higher initial grass standing crop and daily grass allowance than pastures A and B (chained only) in all trials (Table 2, Fig. 1). In all trials except August, analysis of daily grass allowance-fecal output relationships by individual pastures improved regression equation statistics for one or both pastures (Table 4). Initial daily grass allowance was negatively correlated (-0.73) with regression equation slopes. In all trials except March, regression equation slopes for pastures A and B were greater than those for pastures C and D indicating a more rapid decline in

Table 3. Stepwise regression analysis of log functions of kg grass (LGKG), forb (LFKG), and browse (LBKG) standing crops and fecal output as a percent of body weight.

Trial	Variable	Partial R ²	Model R ²	Probability	
Mar.	LGKG	0.94	0.94	0.0001	
May	LGKG	0.75	0.75	0.0055	
Aug.	LGKG	0.84	0.84	0.0002	
Jan.	LGKG	0.74	0.74	0.0060	
	LFKG	0.16	0.90	0.0391	
	LBKG	0.06	0.96	0.0640	



Fig. 2. Effect of daily grass allowance, g dry matter (DM)/kg live weight (LW) on dietary browse content. Predictive equations are based on the log of daily grass allowance with pastures A and C or B and D combined. Pastures A & B were chained 7 years before this study. Pastures C & D were chained and then sprayed with picloram at 7 and 3 years, respectively, before this study.

fecal output in pastures A and B with lower initial grass allowances. These lower initial grass allowances probably resulted in an inability to maintain rumen fill. Although not consistent across trials, McCollum and Galyean (1985) reported greater fecal output in conjunction with increased undigested fill, which was attributed to either expanded gut capacity or the forb component of the diet.

In the present study, the greatest decline in fecal output appears to have occurred below 100 g of daily grass allowance. Ellis et al. (1984) reported that a progressive reduction in daily herbage allowance of ryegrass from 700 to 100 g dry matter/kg body weight had no significant effect on daily fecal output. The NRC (1987) intake function suggests that 100% forage intake is achieved above 200 g daily dry matter forage allowance/kg body weight. On wheat pastures, steers have exhibited increased gain with increasing daily forage allowance up to 250 g (Pinchak

unpublished data). Redmon et al. (1995) suggested similar plateau levels for daily forage allowance on wheat.

Regression of the log of daily grass leaf allowance, g dry matter/kg live weight and fecal output by trial and by pasture within trials resulted in little or no improvement in equation statistics over grass allowance equations (Table 4). Initial fecal output was associated with daily grass leaf allowances of 30 to 120 g.

One potential explanation for lower initial fecal output in August is the influence of high environmental temperatures. Average maximum temperature was 26°C in March, 32°C in May, 38°C in August, and 22°C in January. Depressions in forage intake have been associated with high environmental temperatures (NRC 1987). It seems logical that, like depressed fecal output associated with low forage availability (McCollum and Galyean 1985, McKown et al. 1991), depressed fecal output could be expected if forage intake were depressed by high environmental temperatures. Apparent lower initial fecal output in May could also be related to high environmental temperatures. Because animals were in the thermoneutral zone during the January trial, fecal output values were affected by factors other than temperature.

Differential preferences among forages with contrasting phenologies may also account for the apparent lower initial fecal output levels in May, August, and January. If steers consumed less forage and less indigestible fill, fecal output could be depressed. Estimated dead leaf in the initial forage mass increased almost 2 to 3 fold in August and January, respectively, compared to March and May (Table 2).

Diet quality, specifically with regard to protein, is also a potential explanation for some of the apparent differences in fecal output observed in this study. Milford and Minson (1965) reported depressed intake in relation to CP levels below 7%. In the present study, no CP levels were below this threshold (Table

Table 4. Regression comparisons for fecal output as a percent of body weight and daily grass allowance (GA, g dry matter/kg live weight), daily grass leaf allowance (GL, g dry matter/kg live weight) and most highly correlated single grass species across pastures and by pastures.

	Across Pastures	G	A	GI		Spe	ecies
Trial	GL	A/B^1	C/D^2	A/B	C/D	A/B	C/D
Mar.							
r ²	0.71	0.84	0.99	0.87	0.96	0.97	0.99
SEy	0.13	0.10	0.03	0.09	0.05	0.05	0.004
Slope	0.46	0.54	0.54	0.61	0.46	0.74	0.60
Int^3	0.32	0.006	0.11	0.004	0.41	0.19	0.42
RT^4	log	log	log	log	log	log	log
May							
r^2	0.76	0.65	0.98	0.71	0.98	0.91	0.99
SEy	0.07	0.10	0.007	0.09	0.007	0.05	0.0005
Slope	0.27	0.35	0.13	0.28	0.09	0.33	0.01
Int	0.52	0.29	0.75	0.50	0.85	0.69	0.98
RT	log	log	log	log	log	log	linear
Aug.							
r^2	0.86	0.88	0.87	0.89	0.85	0.86	0.90
SEy	0.04	0.05	0.03	0.05	0.03	0.06	0.03
Slope	0.15	0.21	0.13	0.18	0.12	0.20	0.12
Int	0.63	0.50	0.62	0.61	0.66	0.67	0.75
RT	log	log	log	log	log	log	log
Jan.							
r^2	0.80	0.99	0.91	0.99	0.80	0.99	0.99
SEy	0.08	0.02	0.05	0.02	0.07	0.03	0.002
Slope	0.25	0.54	0.30	0.35	0.17	0.06	0.40
Int	0.61	0.12	0.32	0.59	0.67	0.58	0.95
RT	log	log	log	log	log	linear	log

¹Pastures A & B were chained 7 years before this study.

²Pastures C & D were chained and then sprayed with picloram at 7 and 3 years, respectively, before this study.

³Int = intercept

⁴RT = regression type

1). McCollum (1995) suggested that forages below 10% CP may be deficient in ruminally degradable protein. Improved intake has been reported in relation to ruminally degradable protein (Hannah et al. 1991, Lintzenich et al. 1995, Köster et al. 1996). Initial dietary CP was below 10% in the August trial. It is conceivable that a lack of ruminally degradable protein may have contributed to a depressed intake and the apparent depression in initial fecal output in August. Escape protein (Donaldson et al. 1991) and amino acid profile (Hill and Ellis 1991) have also been reported to function in intake control. The potential influence of these factors should not be overlooked. Although ending dietary CP was above 10% in all trials except August, these values were influenced by dietary browse (Fig. 2). South Texas browse species CP levels are reported in the 10 to 30% range (Taylor et al. 1997). However, recent evidence suggests (Barnes et al. 1991) that crude protein values overestimate the nutritional value of these species. Therefore, it is possible that crude protein, ruminally degradable protein, escape protein, and/or amino acids were deficient toward the end of the trials.

Individual Grass Species and Fecal Output

Within each trial and pasture, correlations were calculated between grass standing crop of each species and fecal output. Standing crop of the single grass species most highly correlated with fecal output was used to develop log or linear regression equations. Except for August, where no improvement was observed, single species equation standard error of estimate was reduced by half to an order of magnitude compared to equations using grass allowance or grass leaf allowance (Table 4). Only in the March chained pasture did the single species used in these regressions rank first in standing crop. In most cases, these species ranked second or third in standing crop and in 2 instances they

were minor components of the standing crop. Although these observations may not have general application, we believe they indicate that partitioning the total grass standing crop can provide greater understanding of fecal output and intake dynamics. The tradeoff between diet selection and acquisition of dry matter can be seen from these analyses.

Dietary Components and Fecal Output

Correlation analysis of fecal output and dietary components indicated differences among trials (Table 5). During March, fecal output was positively correlated (0.67) with live grass stem and negatively correlated (-0.60) with live browse stem. May fecal output was positively correlated with live grass leaf (0.87) and negatively correlated with live forb leaf (-0.76), live forb stem (-0.91), and live browse leaf (-0.63). August fecal output was correlated (0.78) with live grass leaf. In January, dead grass leaf was the only dietary component correlated (0.89) with fecal output. Penning et al. (1994) reported that bite mass was more highly correlated (0.82) with green leaf mass than any other sward measurement. Only in the March trial was grass leaf, live or dead, not correlated with fecal output. In this trial, dietary live leaf content tended to remain high despite declining forage availability. This relatively high level of live leaf is probably an indication of animal drive to consume leaf over stem and live over dead tissue relative to quantity of leaf available per tiller.

For the 3 trials in which grass leaf, live or dead, was correlated with fecal output, maximum observed fecal output was achieved when leaf made up 50 to 70% or more of the diet. However, when grass leaf fell below 10% in the diet, fecal output was depressed by 25 to 40%. In all trials, maximum observed fecal output was attained only when total dietary grass content (leaf and stem) was near 100%.

Table 5. Correlation of diet composition (%) of total grass (TG); live leaf (GLL), dead leaf (GDL) and live stem (GLS); forb live leaf (FLL) and live stem (FLS); and browse live leaf (BLL) and live stem (BLS) to fecal output as a percent of body weight.

Trial	TG	GLL	GDL	GLS	FLL	FLS	BLL	BLS	
Mar.	0.68	0.10	0.50	0.67	0.06	0.25	-0.45	-0.60	
May	0.94	0.87	0.48	0.24	-0.76	-0.91	-0.63	-0.58	
Aug.	0.64	0.78	0.34	0.16	-0.36	-0.21	-0.22	-0.22	
Jan.	0.74	0.17	0.89	0.48	-0.26	-0.54	-0.55	-0.27	

Table 6. Correlation of grass standing crop (GSC; kg/ha) and fecal output as a percent of body weight (FO) or dietary browse content (DBC; %) by trial.

	Correlation (r) by Trial					
Relationship	Mar.	May	Aug.	Jan.		
GSC vs FO	0.91	0.81	0.79	0.84		
GSC vs DBC	-0.71	-0.76	-0.50	-0.51		
FO vs DBC	-0.70	-0.92	-0.75	-0.43		

Dietary Browse, Fecal Output, and Daily Grass Allowance

Both grass standing crop and fecal output were negatively correlated with dietary browse content (Table 6). Daily grass allowance levels at which dietary browse levels increased corresponded to where declining fecal output was observed (Fig. 1 and Fig. 2). These relationships indicate that 1) cattle selected browse in significant amounts only when grass standing crop became limiting and 2) browse consumption was not adequate to maintain fecal output. Seasonal differences in the correlations between grass standing crop and fecal output suggest that forage characteristics other than simply grass standing crop warrant study to gain a clearer understanding of factors influencing fecal output.

To better understand these relationships in shrubland situations, daily grass allowance was compared to dietary browse content (Fig. 2) using the log of daily grass allowance. Browse comprised less than 10% of steer diets until daily grass allowance fell below about 50 g/kg live weight. Prediction equations showed an exponential increase in browse consumption rising to nearly 60% of steer diets as daily grass allowance dropped below 25 g/kg live weight. Highest actual browse consumption was 64% in January, followed by 58, 57, and 53% in March, May, and August, respectively. These browse levels occurred at actual daily grass allowance levels less than 25 g/kg live weight and mostly in pastures A and B (chained only). When contrasted by trial, browse consumption had the strongest relationship with daily grass allowance in May followed by March, January and August in that order (Fig. 2). The shift to browse occurred earliest in May and latest in August, probably because May browse offered a reasonable alternative food, but August offered less alternative forage because of leaf drop.

Conclusions

Whether due to environmental conditions, differential forage quality, or differential forage preferences, apparent differences in fecal output among seasons found in this study could reflect important differences in forage intake. Assuming equal dry matter digestibility and using March and August fecal outputs, forage intake for a 300 kg steer would be 29%, 29%, and 16% lower in August than March at 1) initial fecal output levels, 2) 100 g, and 3) 50 g daily grass allowance/kg live weight, respectively. In reality, forage quality would be expected to decline with rapidly declining forage availability, further diminishing forage intake and animal nutritional status. Although potentially important, the rapid declines in fecal output that occurred below 100 g daily grass allowance would most likely only be observed under extremely high stock densities. Rapid declines in fecal output associated with lower initial daily grass allowance emphasize the need for lower stock densities under these conditions. It appears that, if stock density is maintained so that daily grass allowances are above 100 g dry matter/kg live weight, forage availability will have minimal effect on fecal output and on forage intake. Using the dry matter digestibility assumptions above, estimated forage intake depressions at about 100 g daily grass allowance were 3 to 8% below that calculated using initial fecal output. We interpret the data to indicate that different fecal output curves or adjustment factors may be needed to characterize fecal output relative to 1) seasonal differences and 2) different initial grass standing crops and grazing pressure.

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Cattle use affects forage quality in a montane riparian ecosystem

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Abstract

Forage nitrogen (N) and phosphorous (P) concentrations and in-vitro dry-matter digestibility (IVDMD) were measured in 2 important riparian species the year following short-term, high-intensity cattle grazing treatments in a montane riparian ecosystem in northcentral Colorado. Current year's growth of water sedge (Carex aquatilus Wahlenb.) and planeleaf willow (Salix planifolia Pursh.) was collected monthly from May to September 1996. The effects of grazing and season of grazing in 1995 on forage quality the following growing season was determined. Season of grazing (i.e., latespring, early-summer, late-summer, and fall) the previous year did not differentially affect forage quality in either species. However, grazing by cattle the previous year did increase forage quality of water sedge as compared with plants that were not previously grazed. Grazed water sedge plants had higher concentrations of N and P and greater IVDMD than ungrazed controls. Nitrogen and P concentrations of browsed planeleaf willow were not different from controls, but current year's growth collected in the fall from previously browsed plants was 11% more digestible than current year's growth from non-browsed willow. The 2 species responded uniquely to cattle use, which suggested that these 2 life forms differ in response to herbivory. This study supported the hypothesis that grazing by cattle would improve forage quality in a riparian ecosystem, although results varied with life form.

Key Words: Water sedge, *Carex aquatilus*, planeleaf willow, *Salix planifolia*, nitrogen, phosphorous, in-vitro dry-matter digestibility

Previous studies have shown that large herbivores utilize riparian areas disproportionately heavy relative to upland areas (Roath and Krueger 1982, Platts and Nelson 1985). Heavy grazing might change plant species composition, production, stand density, vigor, and seed production (Ryder

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Resumen

Se midió la concentración de nitrógeno (N) y fósforo (P) del forraje y la digestibilidad in vitro de la materia seca (DIVMS) de 2 importantes especies ribereñas. Las mediciones fueron hechas al año siguiente de aplicar con ganado los tratamientos de apacentamiento de corta duración y alta intensidad en un ecosistema ribereño de montaña de la región norcentral de Colorado. El crecimiento de "water sedge" (Carex aquatilus Wahlenb.) y "planeleaf willow" (Salix planifolia Pursh.)se registró mensualmente de mayo a septiembre de 1996. Se determinaron los efectos que el apacentamiento y la época de apacentamiento de 1995 tuvieron en la calidad del forraje de la siguiente estación de crecimiento. La época de apacentamiento (por ejemplo, fin de primavera, inicio de verano, fin de verano y otoño) del año anterior no afecto la calidad de forraje de ninguna de las especies. Sin embargo, el apacentamiento con ganado en el año anterior incrementó la calidad del forraje de "water sedge" ya que fue superior a la de plantas que no fueron apacentadas anteriormente. Las plantas apacentadas de "water sedge" tuvieron mayores concentraciones de nitrógeno y fósforo y mayor DIVMS que las plantas control sin apacentamiento. La concentración de N y P de plantas ramoneadas de "planeleaf willow" fueron similares a las de las plantas control, pero el forraje colectado en otoño de plantas anteriormente ramoneadas fue 11% más digestible en comparación del forraje producido en la misma época por plantas intactas de "planeleaf willow". Las 2 especies respondieron en forma única al uso por el ganado, lo cual sugiere que estas dos formas de vida responden en forma diferente a la herbívora. Este estudio soporta la hipótesis de que el apacentamiento por ganado podría mejorar la calidad del forraje de los ecosistemas ribereños, aunque los resultados varían con la forma de vida.

1980), and several investigators have observed changes in riparian vegetation biomass, height, composition, and cover in response to specific grazing regimes (Kauffman et al. 1983, Schulz and Leininger 1990, Popolizio et al. 1994, Clary 1995). Nutritive quality of forage species following grazing has not been determined for montane riparian ecosystems, and data that indicate how livestock grazing affects forage quantity in riparian ecosystems are needed for better management of riparian grazing (Platts 1986).

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Two common montane riparian species, water sedge (Carex aquatilus Wahlenb.) and planeleaf willow (Salix planifolia Pursh.), were evaluated to determine how previous cattle use affected forage N and P concentrations and IVDMD. Plants were evaluated at 4 phenological stages of plant development following 1 year of short-term, high intensity grazing treatments in an area that had been excluded from cattle grazing for 40 years. It was hypothesized that water sedge and planeleaf willow would have increased N concentration in current year's growth after grazing, along with concomitant levels of increased P and digestibility. Other researchers have reported elevated N concentrations for upland graminoid species from 4 weeks to 6 months after defoliation (Jaramillo and Detling 1988, Polley and Detling 1988, Rhodes and Sharrow 1990). This study, however, was conducted 8-12 months following cattle use treatments, and riparian rather than upland species were evaluated.

Materials and Methods

Study Site

The Sheep Creek Allotment is located in north central Colorado, 80 km northwest of Fort Collins, within the Roosevelt National Forest at an elevation of approximately 2,500 m. The Allotment consists of 5,340 ha with 1,050 ha classified as grazeable range. The riparian area was heavily grazed from the 1890's to the mid-1950's. Three exclosures comprising a total of 40 ha and 2.5 km of stream and adjacent riparian meadows were constructed in 1956 to exclude cattle use (Schulz and Leininger 1990, Popolizio et al. 1994). The study plots (paddocks), located within these exclosures, had been protected for 40 years.

The nearest weather station to Sheep Creek is located at Red Feather Lakes, 15 km southeast of the study site at an elevation of 2,542 m. Average annual precipitation at Red Feather Lakes is 406 mm, while average precipitation for the growing season (May–September) is 236 mm. Average daily temperatures range from -11° C in January to 25°C in July, and average daily temperatures during the growing season range from 0° to 25°C (National Climatic Data

Center 1948–1990). For the study period, average growing season precipitation at the Red Feather Lakes weather station was 285 mm, and temperatures ranged from 4°to 16°C (NOAA 1995-1996).

The Naz soil series dominates the Sheep Creek region. These are deep, well drained soils formed from granitic parent material. Soils in the riparian study areas are primarily Naz 70, with 1 to 3% slopes. Texture of the soil is a clay loam and is classified as coarse loamy pachic cryoborol. The A horizon has high organic matter (4–17%) and is from 20 to 80 cm thick (USDA 1980).

Overstory vegetation at the study site was dominated by planeleaf willow, Geyer willow (S. geyeriana Anderss.), and yellow willow (S. lutea Nutt.). Understory herbaceous vegetation consisted of Kentucky bluegrass (Poa pratensis L.), fowl bluegrass (Poa pratensis L.), fowl bluegrass (P. palustris L.), water sedge, Nebraska sedge (C. nebraskensis Dewey), beaked sedge (C. rostrata Stokes), tufted hairgrass (Deschampsia caespitosa L.), bluejoint reedgrass (Calamagrostis canadensis Michx.), and dandelion (Taxaxacum officinale Wiggers) (Schulz and Leininger 1991, Popolizio et al. 1994).

Methods

Small (0.25 ha) paddocks utilized in this study were randomly located within the exclosures. Short-duration, highintensity, seasonal grazing treatments with steers were applied in these paddocks in 1995. A set of 3 replicated paddocks that represented each of 5 grazing treatments; late-spring, early-summer, late-summer, fall, and control (not grazed) were assigned at random to the paddocks. Five steers were placed in the designated paddocks at the beginning of each season and allowed to graze until herbaceous utilization reached approximately 65% (Pelster 1998). The average time to reach this level of utilization was approximately 4 days. According to the stubble-height measurement technique (Kinney and Clary 1994), 65% percent of the herbaceous biomass was utilized, and utilization of individual plants within a paddock was fairly consistent. All willow plants within each paddock were browsed to a height of 2 m, although the proportion of willow in cattle diets gradually increased from late-spring to fall 1995 (Pelster 1998). The forage quality

in the 2 contrasting species was determined the year following grazing.

Random samples were taken for both species within each paddock 4 times during the 1996 growing season. Initial forage samples were gathered from all paddocks 1 June, representing earlyspring growth. Early-summer, late-summer, and fall samples were taken at the beginning of each successive month thereafter. These collection times corresponded to the periods of the 1995 grazing treatments: late-spring, early-summer, late-summer, and fall. Grab samples of water sedge leaves and culms were clipped, while leaves and stem tips of current year's growth were removed by hand from planeleaf willow throughout each paddock. Forage samples for willows were taken only to a height of 2 m to insure that samples represented previously-browsed regrowth. Leaf and stem tissue of water sedge was clipped at ground level within each paddock and bagged as a sample. A total of 60 samples for each species, (5 grazing treatments x 4 dates of collection x 3 paddocks) were collected.

Forage samples were placed in paper bags, oven-dried at 50° C, weighed, and ground through a 1-mm mesh screen. Each homogenized sample represented a species within a paddock at a particular time for a grazing treatment. Carbon and nitrogen contents were determined using a LECO CHN-1000 instrument (LECO Corp. 1993). An acid digest was performed after samples were ashed in a muffle furnace at 500° C. The digest was analyzed for P content with an inductively coupled plasma atomic emissions spectrometer (Baker et al. 1964). The IVDMD was determined following the procedure of Tilley and Terry (1963), as modified by Pearson (1970). Each sample was inoculated with ruminal fluid obtained from a fistulated steer on an alfalfa hay diet and allowed to digest for 48 hours at 39° C. This was followed by an acid pepsin digest for an additional 48 hours to simulate digestion of material leaving the rumen.

All data were analyzed using analysis of variance techniques for a completely randomized block design with a factorial arrangement of treatments. Data for each species were analyzed separately and collectively using the SAS (1996) general linear models procedure. A repeated measures procedure was used to determine significant effects (p<0.10) of collection time, species, grazing treatment, and interactions. Differences between grazed plants (all seasonal treatments combined) versus those that were not grazed (control) were compared using a linear contrast statement (SAS 1996). Five models tested the main factors of interest: a) a multivariate repeated measures analysis of variance that included grazing treatments and both species to determine species-level differences and three-way interactions, b) 2 multivariate repeated measures models, 1 for each species, where the variance among all treatments at each collection time was determined, and c) 2 univariate models, 1 for each species, that contrasted the grazed (all 4 seasonal treatments combined) plants with those that were not used by cattle (control).

Results and Discussion

A multivariate repeated measures analysis of variance revealed that collection time was a significant factor for both species (p<0.01) for levels of N, P, and IVDMD ($\underline{F}_{3,61} = 303.4, 255.8,$ 40.97, respectively). Nitrogen and P concentrations and IVDMD, including all grazing treatments plus controls, decreased in both water sedge and planeleaf willow as phenological development continued from young leaves and shoots to senescence (Fig. 1, 2, 3).

Water Sedge

Average N concentration in water sedge of all treatments and controls was 2.5% on 1 June. Average N declined approximately 20% each successive month, to 1.3% N on 1 September (Fig. 1). Phosphorous decreased each month from a high of 0.34% on 1 June to a low of 0.11% on 1 September (Fig. 2). The IVDMD for water sedge, however, did not steadily decline over the growing season (Fig. 3). Average IVDMD for water sedge ranged from 68% in earlyspring to 54% in the fall. Sharp declines in IVDMD were found between latespring and early-summer samples (7%) and between late-summer and fall samples (12%). The decline in water sedge IVDMD between early-summer and late-summer, however, was only 1.6%. Digestibility values between early- and late-summer remained about 63%, which contrasts with the progressive



Collection Times

Fig. 1. Nitrogen concentration in current year's growth for grazed and ungrazed plants of 2 riparian species, water sedge (*Carex aquatilus*) and planeleaf willow (*Salix planifolia*). Data points represent means (± standard error) for the dates that samples were collected. Collection times correspond with the following seasons: late-spring (1 June), early-summer (July 1), late-summer (1 Aug.), and fall (1 Sept.).

decline found for N and P over the summer. Nitrogen and P were not good predictors of digestibility, and differences in the seasonal patterns of N and P as compared with IVDMD indicated that other factors, such as fiber or secondary chemicals, influenced digestibility.

Water sedge nutritive characteristics varied seasonally, and comparative research that includes riparian forage quality data throughout an entire growing season is lacking. Coppock et al. (1983) reported N concentrations of 1.0 to 1.7% and IVDMD values from 52 to 63% over the growing season from May to October for Carex spp. in a mixedgrass prairie. At the Central Plains Experimental Range, N concentration and IVDMD for Bouteloua gracilis (H.B.K.) at peak standing crop (September 1) contained about 1.8% N and was 60-65% digestible (Milchunas et al. 1995). A native sedge of Serengeti National Park in Tanzania, Kyllinga nervosa (Steud.), had N concentrations of 2-3% and P concentrations of 0.2% during the growing season (McNaughton and Chapin 1985). All these data are within the range reported for water sedge in the present study.

The comparable changes in N and P concentrations and IVDMD in water sedge between grazed and control plants with season of cattle use showed no significant collection time by grazing treatment interactions. Therefore, a simple effect of grazing was determined with a linear contrast statement (SAS 1996). This analysis combined the 4 seasonal grazing treatments and compared the forage quality with ungrazed plants. Results showed that grazed water sedge N and P concentrations and IVDMD were greater (p<0.10) compared with plants that were not previously grazed, $(\underline{F}_{3,30} = 3.21, 6.14, 17.97, respectively).$ Nitrogen in grazed water sedge was 5 to 10% higher than in comparable ungrazed plants (Fig. 1). Grazed water sedge plants remained higher in N than ungrazed plants throughout the entire growing season. Phosphorous concentrations were also higher in grazed water sedge (Fig. 2). At the beginning of the growing season, grazed plants were 14% higher in P than ungrazed plants. This differential declined from about 12% in July and August to <1% in September. Thus, the effect of grazing on water



Fig. 2. Phosphorous concentration in current year's growth for grazed and ungrazed plants of 2 riparian species, water sedge (*Carex aquatilus*) and planeleaf willow (*Salix planifolia*). Data points represent means (± standard error) for the dates that samples were collected. Collection times correspond with the following seasons: late-spring (1 June), early-summer (July 1), late-sumer (1 Aug.), and fall (1 Sept.).

sedge leaf and stem P concentration diminished by the end of the growing season. Digestibility of grazed water sedge was also greater than in plants that were not previously grazed (Fig. 3). Differences in IVDMD from 2.9 to 6.3% were found between grazed and ungrazed water sedge, and grazed plants had consistently higher digestibility at each collection time than did ungrazed plants.

The higher forage quality found in grazed water sedge as compared with ungrazed control plants is in agreement with several greenhouse and field experiments where other defoliated graminoids have been studied (Ruess and McNaughton 1984, McNaughton and Chapin 1985, Jaramillo and Detling 1988, Polley and Detling 1988). In these studies the samples were collected within the same season of treatment and imply that intensive grazing or clipping removes older growth and facilitates the subsequent replacement by younger tissue with lower C:N ratios (Jameson 1963). In this study samples were gathered the year following cattle use, and represented current year's growth that was not grazed the year of collection. Additionally, there was significantly higher production of sedges in previously grazed paddocks as compared with ungrazed controls (Schenck 1996, pers. comm.), thereby repudiating the probability that nutrients in the ungrazed standing-crop were diluted by greater aboveground biomass. Other comparable results are not available, so we suggest that these protracted responses may be attributed to water sedge nutrient storage strategies, accelerated mineralization in soils of grazed paddocks and increased nutrient availability, or altered riparian nutrient-cycling dynamics in grazed paddocks as compared with controls.

Planeleaf Willow

Data analysis for N and P concentrations in planeleaf willow indicated that these nutrients were not affected (p>0.10) by the season of cattle use 1 year after plants were browsed. Also, there were no significant collection times by grazing treatment interactions for N and P (Fig. 1 and 2). However, there was a significant (p<0.01) collection time by browsing treatment interaction for IVDMD of planeleaf willow $(\underline{F}_{12,22} = 7.53)$. Browsed willow had greater digestibility during early growth and senescence than during the middle of the growing season (Fig. 3). Digestibility of browsed willow remained the same between late-summer and fall, while IVDMD of unbrowsed willow dropped substantially over the same period of time. The disparate effects of time describe this interaction and illustrate how seasonal nutritive trends may change as a result of cattle use the previous year. The simple effect of treatment varied between browsed and unbrowsed willow IVDMD in the fall. Browsed willow was higher (p<0.10) in IVDMD than unbrowsed willow at this time ($\underline{F}_{4,10} = 4.6$).

Data for planeleaf willow nutritive characteristics with time in the literature are lacking. Nitrogen concentration and digestibility among browse species have been reported under natural and simulated browsing, but these data represent individual points in time with browsing treatments that varied considerably from those in this present study. Nonetheless, previous research does provide a framework for comparison. For example, nitrogen concentrations in forage for Betula pubescens (Ehrh.) of 1.6 to 2.4% have been reported, along with pepsin/cellulase digestibility values of 48-49% (Danell and Huss-Dannell 1985). Forage quality variables have also been determined for Salix spp. in Yellowstone National Park (Singer et al. 1994). They found nitrogen concentrations of 1-2% and dry-matter digestibility values from 45-53% for several willow species. These IVDMD and N data were collected in August and are comparable to the IVDMD and N data found in August for planeleaf willow in our study.

Data for planeleaf willow N and P concentrations were reported for leaf samples taken at Sheep Creek from July–September 1994 and 1995 by Dernburg (1997). The P concentrations from leaf expansion to senescence were 0.32–0.27% and N concentrations over the same time period ranged from 2.4 to 1.8%. These values are slightly lower than those determined in this study, but year-to-year variation is expected.

A univariate analysis that contrasted browsed planeleaf willow plants with

those that were not browsed showed that N and P concentrations were not different (p>0.10) over all collection times the year after grazing treatments were applied (Fig. 1 and 2). The IVDMD time by treatment interaction precluded the use of this univariate model, but the presence of this interaction indicated differences between browsed and unbrowsed willow through time. Browsed willow collected in the fall was 11% more digestible than unbrowsed willow collected at the same time (Fig. 3).

Forage quality differences have been reported to differ for some woody browse species as affected by defoliation intensities (Bryant 1981, Danell et al. 1985, Danell and Huss-Danell 1985, Singer et al. 1994). Moderate to high levels of browsing have resulted in increased leaf N and dry-matter digestibility (Danell and Huss-Danell 1985), lower IVDMD and tannins (Singer et al. 1994), and increased palatability (Danell et al. 1985) among woody species. Again, these responses were measured during the same growing season as when plants were browsed or were under continuous use. These increases, then, may not be meaningful in comparison with results from this study when plant responses were measured in the growing season after browsing.

Species Comparisons

Water sedge and planeleaf willow N, P, and IVDMD were different (p<0.01) from one another ($\underline{F}_{1,11} = 566.6, 93.3, 246.5$, respectively). Averaged across all grazing treatments and controls, planeleaf willow contained 43% and 52% more forage N and P than did water sedge, while digestibility of water sedge was approximately 25% higher than that of planeleaf willow. Water sedge N and P concentrations were highly correlated (r = 0.91), but this was not the case for planeleaf willow (r = 0.10). The gradual



Fig. 3. In-vitro dry-matter digestibility of current year's growth for grazed and ungrazed plants of 2 riparian species, water sedge (*Carex aquatilus*) and planeleaf willow (*Salix planifolia*). Data points represent means (± standard error) for the dates that samples were collected. collection times correspond with the following seasons: late-spring (1 June), early-summer (1 July), late-summer (1 Aug.), and fall (1 Sept.).

seasonal decline that was noted in water sedge P concentration did not parallel the steep decline that was found in planeleaf willow P concentration (Fig. 2). A grazing treatment x species x time of sampling interaction was found (p<0.01) for phosphorous $(\underline{F}_{12,61} =$ 4.77) and IVDMD ($\underline{F}_{14,81} = 4.77$) in the full model that included both species and treatments. This may be explained by differences in seasonal dynamics between the 2 species that caused the interaction. The decline in P concentration in willow plants between earlysummer and late-summer was greater than that found for water sedge. Also, differences in P between browsed and unbrowsed willow plants during the summer were greater, as compared with grazed and ungrazed water sedge plants. Seasonal differences also contributed similarly to the IVDMD grazing treatment x species x time interaction; for willow IVDMD varied more through time than the gradual changes found in water sedge (Fig. 3). These data reflect distinctive species-level responses among seasons that contributed to the significant 3-way interactions.

Species-level differences were also found as a result of varying effects that previous cattle use had on forage quality. Concentrations of N and P increased along with IVDMD in forage of water sedge as a result of previous grazing, while only fall IVDMD increased in planeleaf willow foliage the year following cattle use. The greatest increase in water sedge digestibility for grazed plants, compared with controls, was found in early-summer, while the greatest difference in willow digestibility was found in the fall. Grazed water sedge N and P concentrations were consistently higher than ungrazed control plants each season, while planeleaf willow N and P concentrations did not change from latespring to fall as a result of browsing the previous year.

The contrasting responses between this riparian sedge and shrub are evidence of variability associated with plant life forms that may represent adaptive strategies unique to each life form. Disparate strategies were demonstrated further by significant differences in N and P concentrations and IVDMD between the 2 species throughout the growing season. Furthermore, although this willow and sedge are commonly associated with western riparian ecosystems (Youngblood et al. 1985), their nutritive responses to previous cattle use were quite different.

Conclusions

Forage quality of water sedge and planeleaf willow was affected the year following short-term, high-intensity cattle grazing in a montane riparian ecosystem, and the disparate responses were indicative of ecophysiological mechanisms unique to each life form. Increased N, P, and IVDMD in water sedge as a result of grazing the previous year may be evidence of increased uptake kinetics, greater nutrient availability, or reallocation of reserves. Greater IVDMD in browsed planeleaf willow in the fall may suggest lowered levels of fiber or secondary compounds, and may help explain greater cattle preference for the willow during later growth stages (Meyers 1989, Kinch 1989, Pelster 1998).

Season of use did not affect forage quality the following year, although season of use can affect other variables such as plant cover, production, and streambank erosion (Kauffman et al. 1983). These data demonstrated how grazing might interact with aboveground biomass production the following year in a riparian area on sites that have been excluded from grazing for an extended time, thereby improving graminoid forage quality in the year following cattle use. Conclusions are based on these one time, short-term, high-intensity cattle use treatments. Other cattle management regimes and other sites that are regularly grazed may not yield similar results. This study did demonstrate, however, that previous cattle use can increase forage quality of a montane riparian community, although substantiation with studies at different spatial and temporal scales and in other riparian areas is recommended.

Further field studies are needed to determine spatial and temporal variations in riparian nutrient dynamics and the extent of graminoid responses to herbivory. Ideally, a long-term study would include data collection prior to defoliation, during regrowth that season, and in new growth the following year. This experiment represents data for 1 growing season that encompassed only a commu-

nity-level spatial scale in a montane riparian ecosystem. Clarification of how compensatory nutrient uptake and allocation patterns operate requires specieslevel, ecophysiological approaches be used that explore mechanisms that affect these response variables in the context of highly interactive soil-plant ecology. Evidence of higher forage quality in grazed water sedge in this study suggests that grazing induced a change in available nutrients and nutrient uptake in water sedge. A quantitative understanding of the underlying, indirect mechanisms will require greater study of the riparian soil-plant nutrient exchange complex.

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Evidence of cell deterioration in winterfat seeds during refrigerated storage

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Abstract

Effective storage of wildland seeds helps alleviate supply shortages and mitigates variable production associated with annual weather patterns. The storage environment is critical for seeds like winterfat [Eurotia lanata (Pursh) Mog.) that rapidly lose viability under ambient conditions. Defining seed response to storage conditions is basic to effective seed storage programs. We used electron micrographs of freshly collected, and of stored winterfat seeds, with vigor tests to compare seedling vigor and to relate seed performance to seed cell biology as influence by; (a) seed age under known storage conditions, and (b) imbibition temperatures. We found that imbibition temperatures had little influence on the vigor of fresh seeds but significantly influenced aged seeds. Mitochondrial deterioration was evident in winterfat seeds stored 5-6 years at 5°C, and in fresh, but incompletely hydrated seeds held at 20°C. We recommend seeds be held at -18°C or colder for long-term storage and that field seedings be done during the cold season to reduce the chance that incompletely hydrated seeds will be exposed to warm temperatures.

Key Words: Seed aging, mitochondria, vigor, imbibition, Eurotia, Ceratoides, Krascheninnikovia

Only in laboratory studies has it been possible precisely to separate effects on germination from effects on subsequent survival.—John L. Harper (1977) in his book, 'Population Biology of Plants'.

Winterfat [*Eurotia lanata* (Pursh) Moq.]¹ and closely related species are important forage plants on the cold deserts of North America and Asia, but seeds of these species rapidly lose viability when stored at ambient conditions (Wilson 1931, Hilton 1941, Springfield 1968, 1974b). Springfield

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Resumen

El almacenamiento efectivo de semillas silvestres avuda aliviar la falta de suministro y mitigar la producción variable asociada con los patrones anuales de clima. El ambiente de almacenamiento es critico para semillas como las de "winter fat [Eurotia lanata (Pursh) Moq.]que rápidamente pierden viabilidad bajo las condiciones ambientales. El definir la respuesta de la semilla a las condiciones de almacenaje es básico para implementar programas efectivos de almacenamiento de semilla. Utilizamos micrográficas del microscopio electrónico de semillas recién cosechadas y semillas de "winter fat" almacenadas. Se utilizaron las micrográficas con pruebas de vigor para comparar el vigor de la plántula y relacionar el comportamiento de la semilla con la biología celular influenciado por: (a) la edad de la semilla bajo condiciones de almacenamiento conocidas y (b) las temperaturas de imbibición. Encontramos que la temperatura de imbibición tiene poca influencia en el vigor de semillas recién cosechadas, pero influencio significativamente el de las semillas envejecidas. La deterioro mitocondrial fue evidente en semillas de "winter fat" almacenadas durante 5-6 años a 5°C y en semillas frescas pero hidratadas incompletamente a 20°C. Para el almacenamiento por largos periodos, recomendamos que las semillas deben ser conservadas a -18°C o temperaturas mas frías y que las siembras de campo sean hechas durante la época fría para reducir la probabilidad de que semillas hidratadas incompletamente sean expuestas a temperaturas calientes.

(1974b) recommended refrigeration for long-term storage and reported little germination from collections held at ambient temperatures for 8 years compared to 68% germination for seeds held at 5°C. Although 5°C storage extends seed viability, its effect on seedling vigor is unknown.

Our objective was to determine if seed aging under 5°Cstorage reduced winterfat seedling vigor. Our hypothesis was developed from studies by Booth (1992), Booth and McDonald (1994), and Agustrina (1995). Booth (1992) reported seedling vigor was reduced by warm imbibition temperatures (Fig. 1). Booth and McDonald (1994) found that rapid

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 $^{^{-1}}$ *Krascheninnikovia* Gueldenstaedt. is the current synonymic favorite, replacing *Ceratoides* J.T. Howell. To call attention to the need to stabilize scientific nomenclature except where new evidence clarifies the phylogeny, we have retained *Eurotia* (Adanson 1763) which was used by most publications between 1840 and 1971.



Figure 1. The effect of imbibition temperature on winterfat seedling vigor from seeds collected in Nevada and Wyoming, and from the released variety 'Hatch', as reported by Booth (1992).

imbibition of winterfat seeds at warm temperatures did not damage seed membranes. Agustrina (1995) found freshly harvested winterfat did not exhibit the imbibition-temperature response evident in the stored seeds used by Booth (1992). Because increases in respiratory activity during germination of other species have been associated with rapid development of mitochondrial ultrastructure, including rehydration of its membrane system (Nawa and Asahi 1973, Solomos et al. 1972), we hypothesized (1) that winterfat seeds stored more than 2 years at 5°C contained mitochondrial-ultrastructure changes that reduced seedling vigor and, (2) that imbibition temperatures affected winterfat seedling vigor by influencing mitochondrial hydration, metabolism and development in seeds stored more than 2 years at 5°C.

Methods and Materials

Plant Material

Winterfat diaspores (seed-containing dispersal units) were collected in October, 1986 (Booth 1992); and from the same stand on the High Plains Grassland Research Station, Cheyenne, Wyo., (elevation of 1,909 m) in 1993 (Agustrina 1995). The diaspores of both collections were stored at room temperature for approximately 2 months, then stored at 5°C (Springfield 1974a). Using the methods described by Booth and Griffith (1984), a portion of the diaspores were threshed and seeds stored at 5°C. The 1986 seeds were tested by Booth in 1989 and 1990. Seeds from diaspores collected in Cheyenne in 1993 were tested about 6 months after collection (Agustrina 1995).

Booth (1992) and Agustrina (1995) report tests for differences in seedling axial length (a measure of seedling vigor) due to imbibition temperature. We used these reports to compare seedling vigor from the 1986 and 1993 seeds by calculating the 95% confidence interval for mean axial lengths of seedlings from the 1986 seeds. We used the MSE from an ANOVA comparing seedling axial length by imbibition temperature for day 10 and for day 12 of incubation (n = 75) (Booth, unpublished 1992 data). Confidence intervals were not calculated for the 1993 data because interactions among the several treatments prevented pooling of experimental units (Agustrina 1995). In their procedures Booth (1992) and Agustrina (1995) divided seeds into groups of 20, weighed the groups to 0.01 g, and humidified the seeds for 3 days at 2°C prior to imbibition to reduce imbibitional injury (Vertucci and Leopold 1984, Vertucci 1989). The seeds were then incubated on slant boards (Jones and Cobb 1963). The slant boards containing humidified seeds were placed in plastic boxes with tight fitting lids; the boxes filled to a depth of 5 cm with distilled water, then placed in incubators for 4 days at treatment temperatures that included 5 and 20°C. All treatments were then incubated in the dark at 20°C. The axial lengths of germinants were measured after 5, 7, 10, and 12 days of incubation using a digitizing tablet (Booth and Griffith 1994).

Mitochondrial Ultrastructure Study

Winterfat diaspores of the 1986 and 1993 Cheyenne collections were used for an electron microscope study of mitochondrial structure. The diaspores were threshed, the seeds weighed, and placed in a humidity chamber at 5 or 20°C until the seed weight reached 1.2 or 1.5 times the dry weight. After humidification, 1 mm was cut from the tip of the embryonic radicle and fixed in 5% glutaraldehyde at room temperature for 4 to 5 hours. For comparison, dry seeds were submerged in 1% glutaraldehyde in 0.1 M sodium cacodylate (pH > 4) for 48 hours, then fixed in 5% glutaraldehyde. Standard methods were used for specimen dehydration and mounting (Hayat 1986). The specimens were trimmed using an LKB ultratome (LKB Instruments, Inc., Rockville, Md.) For light microscopy, the 1.0 micron sections were cut using a Reichert Jung Ultracut (Reichert-Jung Optische Werke Ag, Hernalser Hauptstr, Wien, Austria), stained with 1% toluidine blue, and then observed under the light microscope. Using the light microscope we selected a representative area from the winterfat radicle tip for study by transmission electron microscope (TEM). A section approximately 79 nanometers thick was cut from the chosen area using the Reichert Jung Ultracut, stained with uranyl acetate and lead citrate, and then observed by TEM. A second group of representative cells were chosen from these TEM observations. Micrographs were obtained using an internally mounted camera on the TEM, the magnification was 50,700 x. Samples were cut from 3 different seeds in each treatment and 2-6 micrographs were made from each sample.

Ratio of Mitochondrial Area to Cell Surface Area (MA/CA)

Slides of TEM photos were used to determine the mitochondria number and a ratio of mitochondrial area to cell area (MA/CA). Relative area was measured by tracing projected images on tracing paper. Traced images were cut out, weighed, and the data used to calculate the ratio.

Experimental Design and Statistical Analysis

To compare MA/CA, mitochondrial number, and size of mitochondria we used a random design and the ANOVA procedure in SAS. Comparison of individual treatment means used the Least Significant Difference (LSD) for variables with a significant F-statistic (SAS 1985).

Results

Germination and Growth of 1986 and 1993 Seeds

Seedlings from the 1993 seeds had about twice the axial length of seedlings from the 1986 seeds (Table 1), and axial lengths from 1993 seeds did not fall within the axial-length confidence intervals of seedlings from 1986 seeds. These findings imply a significant dif-

		Mean I by Col	Length lection
Temperature	Days		
	Measured	1986	1993
°C		(mm)	
5	10	48 + 4.8	80
	12	48 + 4.7	78
20	10	25 + 4.8	77
	12	25 + 4.7	76

The seedling axial length means for 1986 seeds were obtained from earlier data (Booth, data on file). Means for 1993 are for seeds, at treatment temperature, without fungicide (Agustrina 1995).

ference in the seedling vigor between the 2 seedlots.

Mitochondrial Ultrastructure

Dry Seeds. Radicle-tip cells of dry seeds from 1986 and 1993 collections contained mitochondria with few cristae and numerous translucent areas in the mitochondria matrix. Hydration reconstituted radicle mitochondria for both 1986 and 1993 seeds.

Hydration at 5°C. When hydrated at 5°C to the 20% moisture level, the mitochondria of 1993 seeds contained, (1) more distinct lipid bilayers of the outer membrane, (2) a greater number of cristae, and (3) a more uniformly dense matrix— typical for normal mitochondria of hydrated cells—than did cells from 1986 seeds (Fig. 2a versus 2b).

When hydrated at 5°C to 50% moisture content, mitochondrial ultrastructure of 1986 and 1993 seeds was similar (data not shown).

Hydration at 20°C. Hydration to 20% moisture at 20°C resulted in 1993 seeds with thinner mitochondrial cristae than were observed in seeds hydrated at 5°C (data not shown); however, the mitochondrial matrix was more uniformly distributed. Hydration to 50% moisture at 20°C produced 1993 seed with the most deteriorated mitochondrial structures seen among all treatments (Fig. 3). The outer membrane and cristae were completely degraded while in the 1986 seeds the outer membrane was partially degraded and the cristae structures could still be observed.

MA/CA

Neither imbibition temperature, collection year, moisture, nor their interactions significantly affected numbers of mitochondria. P values ranged from 0.14 for the temperature x year interaction (Table 2) to 0.84 for moisture x year. However, the MA/CA ratio was affected by an imbibition-temperature x collection-year interaction (P=0.03). The greatest MA/CA ratio was observed from 1993 seeds imbibed at 20°C (Table 2). This was significantly greater (P < 0.05) than for 1986 seeds imbibed at 20°C. The 2 collections did not differ when imbibed at 5°C.

Discussion

Mitochondrial Degradation

Early metabolic activity, which begins near 20% seed moisture, consists of membrane reorganization, glycolysis, repair of organelles, and activation of enzymes in preparation for an increasing respiration rate and subsequent radicle emergence (Bewley and Black 1985). Loss of seedling vigor due to seed aging has been associated with a marked decline in soluble carbohydrate (Bermal-Lugo and Leopold 1992), increases in chromosomal aberration (Dimitrov 1994, Guiterrez et al. 1993), changes in ribosomal protein content (Zalewski 1985, Hallam et al. 1973), and abnormal mitochondrial structures (Hallam et al. 1973, Abu-Shakra and Ching 1967). Aging produces an accumulation of a free fatty acid mixture in

Table 2. Data for Cheyenne seeds collected in 1986 and 1993 showing the effects of temperature and collection year on total surface area of mitochondria per surface area of the cell (MA/CA) and on the number of mitochondria per cell. The temperature x year interaction was significant for MA/CA (P=0.035).

Temperature	Year	Mean MA/CA	Mean number Mitochondria ²
NT (dry) ¹	86	0.268a ²	31.67
NT (dry)	93	0.310ab	33.67
5	86	0.305ab	40.50
5	93	0.299ab	37.34
20	86	0.274a	32.67
20	93	0.373b	50.17

Dry and not treated

²Means with the same letter are not different as determined by $LSD_{0.05}$. There were no differences in mitochondria numbers among treatments (P ranged from 0.14 for temperature x year, to 0.85 for moisture x year).



Fig. 2a





Fig. 2. The organelles of embryonic winterfat radicle cells (50,700 x) of 1986 (a) and 1993 (b) seeds, hydrated at 5°C to 20% moisture. The organelles are represented as follows: (m) mitochondria; (cw) cell wall; (l) lipid body; (N) nucleus; (pd) plastid; (pb) protein body,(R) ribosome, and (er) endoplasmic reticulum.

mitochondrial membranes as a result of activation of phospholipase A_2 (Luzikov et al. 1985; Nachbaur et al. 1972). This accumulation induces uncoupling of oxidative phosphorylation, reduces endogenous ATP levels, and leads to

mitochondrial swelling (Luzikov et al. 1985). The characteristics of early mitochondrial degradation are dilution of the matrix, swelling and subsequent straightening of the folds formed by the inner membrane, rupture of the outer membrane, vacuolarization of the matrix, loss of the matrix content, and total disappearance of cristae (Luzikov et al. 1985); in short, a decrease in respiration capability and efficiency. Thus the lack of mitochondrial ultrastructure correlates with the low vigor of the 1986 seeds (Table 1).

Effects of Seed Moisture and Temperature

There were few differences between dry or hydrated seeds. This agrees with Baird et al. (1979) who also reported no appreciable differences between mitochondria in dry and imbibed radicle tissues.

Seed hydration at low temperature did produce differences in MA/CA between the 1986 and 1993 seeds as evident by the significant temperature x collectionyear interaction. The greater MA/CA for 1993 seeds imbibed at 20°C, compared to that of 1986 seeds imbibed at 20°C. and the lack of difference when these seeds were imbibed at 5°C (Table 2), suggest that early metabolic activity at 5°C, maintained or repaired mitochondria in the 1986 seeds. Thus, these data provide a physiological explanation for Booth's (1992) finding that winterfat seedling vigor decreased with increasing imbibition tempertures (Fig. 1). The same explanation may apply to other chenopods shown to benefit from imbibition at temperatures suboptimal for germination (Haferkamp et al. 1990, Shaw et al. 1994).

Hydration at warm temperatures produced unexpected differences due to moisture content of the 1993 seeds. Why did these seeds show so much mitochondrial degradation at 50% moisture whereas the 1986 seed did not? Bain and Mercer (1966) reported that transportation of hydrolyzed food reserves from cotyledon cells of peas did not occur until the moisture level in the seeds reached more than 93%. This suggests that translocation of hydrolyzed food reserves from winterfat seed-storage tissue may not have occurred at 50% moisture.

Vartepetian et al. (1976) reported that ATP-regeneration was essential in maintaining the integrity of mitochondria in excised seedling tissues. Hodson et al. (1987) hypothesized that a delay in the development of mitochondrial structure may be related to the available energy supply in the seeds. The lack of activity



Fig. 3. The organelles of embryonic winterfat radicle cells (50,700x) in 1993 seed hydrated to 50% moisture at 20° C. See Fig. 2 for organelle labeling information.

in the mitochondria of pea seedlings after their peak activity, was correlated with shrinking of the cotyledons (Malhotra et al. 1970).

So lack of an energy supply may have caused mitochondrial degeneration in the 1993 seed at 50% moisture. Would not this also occur in the 1986 seed? Aging may have reduced active catabolic enzymes in the 1986 seeds. Das and Sen-Mandi (1992) reported a decline in amylase activity of aged seeds. Declines in enzyme activity or in the cellular ability to synthesize proteins could indicate reduced catabolic activity. Thus, the 1986 mitochondria could be more degraded than in the 1993 seed at 20% moisture, then be less degraded at 50% moisture.

Implication of Findings and Related Information

The evidence is that storage at 5°C did not protect winterfat seeds from agerelated degradation. The seeds remained viable, but lost vigor. Other chenopod seeds stored at -12 to -23°C were reported to have little loss of vigor after 22 years (Pack and Owen 1950). Roos (1989) recommended seeds be at -18°C or lower for long term storage. Springfield (1968) compared winterfat seeds which had been stored in a warehouse (13 to 35° C) with refrigerated storage (3 to 6° C), and with freezer storage (-20 to -32° C). He did not directly compare refrigerated and freezer storage

but commented that "subfreezing temperatures appear slightly superior". However, he subsequently (Springfield 1974a) recommended refrigerated storage.

The severe degradation of mitochondria in 6-month-old seeds at 50% moisture and 20°C, suggests that fresh, partially hydrated seeds are at risk during periods of warm weather. We believe that the combination of warm soil temperatures (> 15° C) and incomplete seed hydration could account for the failure of late-spring and summer winterfat seedings.

Judging the Evidence

Micrographs. The micrographs of the 1986 seed were made 3–4 years after the vigor test was conducted, and thus represent a more advanced stage of mitochondrial degradation than was present when the seeds were tested. The fact that the micrographs are of seeds that are older than the vigor test is perhaps fortunate since we may not have detected these gradual structural changes in 2-year-old seeds.

Comparing Seedlots from Different Years. The Coefficients of Variation (Steel and Torrie 1980) for mean monthly temperature and precipitation for June through September, 1986 and 1993 at the High Plains Grasslands Research Station are smaller than the coefficients for the three 1993 seed collections (Cheyenne and Pine Bluffs, Wyo; and

Table 3. Climatological data and Coefficients of Variation for Cheyenne and Pine Bluffs, Wyo., and Sterling ${\rm Colo.}^1$

	Mean Temperature	Mean Precipitation
Cheyenne 1986	(°C)	(mm)
June	18.2	62
July	20.4	26
August	19.6	39
Sept	13.1	63
Cheyenne 1993		
June	15.0	84
July	NA	NA
August	18.4	56
Sept	12.5	80
Pine Bluffs 1993		
June	15.8	66
July	NA	NA
August	19.1	22
Sept	12.5	40
Sterling 1993		
June	19.9	52
July	22.8	41
August	22.5	50
Sept	15.4	30
Coefficients of Variation for:	Temperature	Precipitation
Cheyenne 1986 & 1993	17.7	32.6
Chey., P. B., & Sterl. 1993	20.9	37.7

¹National Oceanic and Atmospheric Administration (1986, 1993). Data for Sterling, Colorado was courtesy of the High Plains Climate Center, University of Nebraska, Lincoln (personal communication).

Sterling, Colo.) tested by Agustrina (1995) (Table 3). Agustrina (1995) detected no significant differences in seedling axil length among the three 1993 seeds collections. This implies that differences in the seeds due to production year are small relative to aging differences, and are unlikely to confound our interpretation of the data.

Extrapolation from 1 Seed Source. We detected differences in basic cell biology that have been observed in seeds of other species. A basic process that occurs across species is not likely to change due to seed source within a species. Further, the 3 seed sources tested by Booth (1992) were all more than 2 years old and had been stored under similar conditions and gave similar responses to imbibition temperature. Finally, though Springfield (1968) did not grasp the importance of the differences between "refrigerated" and "freezer"-stored seeds, his observations add to the evidence that winterfat seed aging during 5°C-storage is an important consideration for all winterfat seeds.

Conclusion and Recommendations

We conclude that storage of winterfat seeds at 5°C resulted in age-related degradation of seed mitochondria and other organelles during storage, and in a significant loss of seedling vigor. Also, that age-related degradation was the physiological reason for the seedlingvigor response to imbibition temperature found by Booth (1992) for 3 separate winterfat seed sources. We now believe that warm imbibition temperatures do not significantly reduce vigor of healthy seeds. However, incomplete hydration (>20% and <90% seed moisture) at warm temperatures (near 20°C) will result in rapid mitochondria degradation and loss of vigor. Also, imbibition at warm temperatures will reduce the vigor of seeds needing mitochondrial repair. For these seeds, cold imbibition reduces inefficient respiration and allows repair to proceed.

We recommend winterfat seeds be held $< -18^{\circ}$ C to protect seed vigor during long term storage and, that the seeds be imbibed at 0 to 5°C as a standard laboratory practice. Cold imbibition does no damage to winterfat seeds and it does protect winterfat seed-vigor potential. For that reason we also recommend winterfat be seeded during the cold season.

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Book Reviews

Landscapes of the Interior. Re-explorations of Nature and the Human Spirit. By Don Gayton. 1996. New Society Publishers, Gabriola Island, British Columbia, Canada. 176p. US\$14.95 paper. Can\$17.95 paper. US ISBN 086571-344-8. Canada ISBN 1-55092-285-8.

Don Gayton is a scientist and range ecologist by training. His in-depth experience of the natural landscapes of western North America has been filled out by a wide variety of unusual jobs which include his being a community developer in Latin America, a hired man on an Okanagan cattle ranch, an agricultural extension agent on Saskatchewan Indian reserves, and a steelyard worker.

Combining his scientific knowledge and practical experience, Gayton has written 17 essays about his journey with the human connection and nature. His stories reach out in original ways, reminding us of how nature can be an intense source of spirituality and renewal.

I enjoyed Gayton's essay about the American cowboy writer and painter Will James. He tells how James created himself as the main character in his own novels: cowboy, painter, writer, western myth and finally, victim. Most allow fiction to penetrate only as far as their bookshelves, stopping it far short of personal identity. James became part of the landscape and that is what interests Gayton.

As a boy, Gayton read *Smoky, the Cow Horse* by James. The story features a lone rebellious figure, bonded to a half-wild horse, working with animals and against the elements, dealing rarely with other men and almost never with women. James portrayed himself as the quintessential American cowboy.

Thirty years after first reading *Smoky*, Gayton stumbles across a reference to Jame's beginnings in Canada. He wanted to learn something from Jame's overwhelming obsession with a certain kind of landscape, and obsession that caused him to bury one identity and create another. Will James was born in 1892 as Ernest Nephtali Dufault, in St-Nazaire, Quebec. He spent most of his spare time sketching horses and devouring dime westerns. He was consumed by the desire to be a cowboy. At the age fifteen he bolted, and took a train west to the Canadian prairies.

After spending 4 years on the Canadian prairies, James saw the first real images of the West and cattle ranching. He shifted his language from French to western English. After studying the life of Will James, Gayton concluded that Jame's obsession was not with the land itself, but land with the human totally and perfectly rooted within it. Landscape with figures.

Another interesting essay concerns Gayton's experiences in Saskatoon, Saskatchewan. He tells of his days as a graduate student at the University and of living in the small village of Sutherland. He tells of his interest in cities, with their corrosive and monstrous qualities. He felt it necessary to look at the artificial/biophysical enterprise—the city. With his interest in natural landscapes he takes a philosophical view of the man made landscapes of the city. This makes for interesting reading.

Landscapes of the Interior is about nature, the environment and land use. Gayton takes the reader on a unique journey with his philosophical views. He has a true love of the land and that love is felt on every page.—Jan Wiedemann, Texas Section, Society for Range Management, Vernon, Texas.

Fields of Grass. Portraits of the Pastoral Landscape and Nomads of the Tibetan Plateau and Himalayas. Text and photographs by Daniel J. Miller. 1998. International Centre for Integrated Mountain Development, GPO Box 3226, Kathmandu, Nepal. 204 p. US\$40.00 paper. ISBN 92-9115-824-0.

The high plateaus, mountainous vistas, and colorful cultures of the Himalayas are the focus of *Fields of Grass* by Daniel J. Miller, a recent effort at verbal and photographic portraiture of the region's nomadic pastoralism. Originally a Minnesotan, and with considerable experience as a Montana cowboy, Mr. Miller has, since 1974, been active in range-livestock development and wildlife conservation in the Himalayan region. This book is largely a photographic survey of his experiences of over 2 decades in Bhutan, China, Tibet, Nepal, Mongolia and Pakistan.

After a brief introduction, Fields of Grass is loosely organized into 6 main sections with the titles *Pastoral Landscape*, Pastoral Production, Livestock, Nomads, Changes, and Future Challenges. Each of these sections contains photographs and text focusing on each topic. The quarter-page to full-page photographs are all in black and white. Captions are usually limited to a statement of the subject, location, and date. The brief sections of text are placed among clusters of photographs. Like the mountain air, the technical content of the text is rarefied; the content is mostly cultural and economic rather than ecological. In the sections entitled Changes and *Future Challenges*, Miller states the urgent need to preserve the colorful cultural values and the often sound, but just as often under-appreciated, ecological practices of the Himalayan nomadic pastoralists. A generous section of acknowledgements, a list of suggested readings, and a map of Miller's travels follow the 6 sections of text and photographs. An appendix on "repeat photography" which ends the book essentially allows the author to utilize several dozen more small photographs of landscapes. Lacking either captions or other documentation, these attractive photographs are more useful aesthetically than analytically.

As it does such places as the high plains of West Texas, the black-and-white photography suits the harsh landscapes and hardy peoples of the Himalayas. Even all the color of the powerful landscapes and regional costumes aren't lost, but rather are reduced to images more elemental. These images are at least as good in black and white as their portraits would be in color, just as on the West Texas plains, a pink Cadillac convertible can look better than pink. Evidently, *Fields of Grass* was envisioned and developed as a broad photographic essay of Himalayan landscapes and pastoralists. Characterized in this way, neither the text nor the photography of the book is strongly thematic. The text of *Fields of Grass* resembles a series of annotated captions, whose collective literary continuity in no way mirrors the timeless continuity of the regional history. As was the case in the author's earlier *Rangelands and Pastoral Development in the Hindu-Kush Himalayas* (reviewed in J. Range Manage., 51:723), the textual editing is shaggy in its repetitiveness. Moreover, the individual sections of text don't stand alone as well as the individual photographs. The book might be judged more favorably as a series of photographic vignettes, but the somewhat purposeful arrangement of topics, and the repetitive observations of the text provide the book with just enough verbal binding to encourage the reader to expect textual continuity, even where little exists. Since the text shows little of the originality, energy, or depth of field of the photography, Miller might have said even less.

With an attractive, appropriate format, and all of that austere photography, Mr. Miller's book comes off well anyway. Powerful images of the past, present, and future of nomadic pastoralism on the Himalayan plateaus are there for the attentive, the imaginative, the visionary reader to see. It's all there, in black in white.—*David L. Scarnecchia*, Washington State University, Pullman, Washington.

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