

Journal of Range Management

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The Trail Boss

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- to assist all who work with range resources to keep abreast of new findings and techniques in the science and art of range management;
- to improve the effectiveness of range management to obtain from range resources the products and values necessary for man's welfare;
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Agricultural land use patterns of native ungulates in southeastern Montana

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Abstract

Mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), and pronghorn antelope (*Antilocapra americana*) use of 6 agricultural land use categories in southeastern Montana were monitored to identify use patterns at specific sites. Alfalfa (*Medicago sativa* L.), bottom rangeland, Conservation Reserve Program (CRP) lands, upland rangeland, wheat (*Triticum aestivum* L.) stubble, and growing wheat were observed during dawn, day, dusk, and night hours over a period of 12 months. Mule deer densities on alfalfa peaked in fall and again in spring. The CRP lands were selected in all seasons. Rangeland sites were most heavily used in winter and summer. White-tailed deer used CRP lands in all seasons except fall. Alfalfa was selected in fall, spring, and summer. Antelope densities on alfalfa were highest in spring and fall, while growing wheat fields were used most in spring. Antelope in the northern study area selected CRP land in all seasons except fall. Densities of animals and patterns of use observed during this study would be unlikely to produce significant impacts on forage or crops at most of our study sites.

Key Words: mule deer, white-tailed deer, pronghorn antelope, habitat use, agriculture

Increasing wildlife populations and demands for greater efficiency in agricultural production have produced conflicts between agricultural and wildlife advocates in the Great Plains (Severson 1981). Both groups perceive damage from wildlife as a problem, but they disagree on its extent and importance (Conover and Decker 1991, Adkins 1991, Lacey et al. 1993, Conover 1994, Wywiałowski 1994, Irby et al. 1996). Attempts to measure damage from wild ungulates have been unsatisfactory because of variability in methodology, sampling intensity, and distribution of ungulates at local and regional scales (Tebaldi 1982, Adkins 1991, Matschke et al. 1984).

This study was initiated to provide quantitative information on wild ungulate use of agricultural lands in southeastern Montana.

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Manuscript accepted 21 Sep. 1996.

Resumen

Los usos por parte del venado burro (*Odocoileus hemionus*), el venado cola blanca (*Odocoileus virginianus*) y el antilope pronghorn (*Antilocapra americana*) de seis categorías de tierras de uso agrícola en el sureste del estado de Montana se examinaron para identificar las tendencias de uso en sitios específicos. Observamos la alfalfa, los terrenos de pasto bajos, las tierras del Programa de Reserva para la Conservación (el CRP), los terrenos de pasto altos, el rastrojo de trigo, y el trigo creciente durante el alba, el día, el crepúsculo y la noche a través de un período de doce meses. Las densidades del venado burro en la alfalfa alcanzaron el máximo en el otoño y otra vez en la primavera. Estos venados seleccionaron las tierras del CRP en todas las estaciones. Utilizaron los sitios de los terrenos de pasto más durante el invierno y el verano. Los venados cola blanca usaron las tierras del CRP en todas las estaciones menos el otoño. Seleccionaron la alfalfa en el otoño, la primavera y el verano. Las densidades del antilope en la alfalfa alcanzaron el máximo en la primavera y en el otoño, mientras se utilizaron los sembrados de trigo creciente más durante la primavera. Los antílopes en el área norteña del estudio seleccionaron las tierras del CRP en todas las estaciones menos el otoño. Es improbable que las densidades de los animales y las tendencias de uso observadas durante este estudio produzcan impactos substanciales en los pastos o en las cosechas de la mayor parte de nuestros sitios estudiados.

Ranchers in Carter and Fallon Counties identified consumption of locally grown hay and forage from native range by wild ungulates as a possible economic threat. Studies sponsored by the Montana Department of Fish, Wildlife, and Parks (MDFWP) in the area (Egan 1957, Campbell 1970, Freeman 1971, Griffiths 1990, Olenicki 1993) did not support this contention, but they focused on the ecology of deer and antelope with agricultural impacts addressed as a secondary objective. This study was designed to focus on animal use patterns in agricultural cover types. The primary objectives were to 1) identify seasonal preferences of wild ungulates for agricultural cover types, and 2) to determine if topographic, physical, and biological characteristics associated with specific sites could be used to predict the abundance of wild ungulates at specific sites.

Materials and Methods

Study Area

The study was conducted on sites selected along 2 routes in Carter County, Montana. Observation sites where animals were counted ranged in size from 10 to 100 ha. Sites were placed along unpaved county roads that were maintained as school bus routes to insure year-round accessibility. The northern route (Ekalaka route) included 42 observation sites that encompassed an area of 1,213 ha. Roads on this route encircled the Ekalaka Hills division of Custer National Forest but were located in open, rolling prairie at distances of 0.5 to 6.4 km from forested areas. Vegetation in prairie areas consisted of sagebrush-grassland communities interspersed with agricultural lands. Dominant species were big sagebrush (*Artemisia tridentata* Nutt.), crested wheatgrass (*Agropyron desertorum* (Fisch.) Schultes), western wheatgrass (*Agropyron smithii* (Rydb.) Gould), prairie junegrass (*Koeleria macrantha* (Ledeb.) Shultes), blue grama (*Bouteloua gracilis* (H.B.K.) Lag. ex Stud.), and needle-and-thread (*Stipa comata* Trin. and Rupr.). The CRP lands contained crested wheatgrass and alfalfa (*Medicago sativa* L.). Important tree and shrub species along streams and coulees were green ash (*Fraxinus pennsylvanica* Marsh.), common snowberry (*Symphoricarpos albus* (L.) Blake), fragrant sumac (*Rhus aromatica* Ait.), and common chokecherry (*Prunus virginiana* L.).

The southern route (Box Elder route) included 14 observation sites totaling 462 ha located along a 21-km reach of Box Elder Creek. This route was characterized by rolling plains dissected by ephemeral creeks. Box Elder Creek frequently is dry during summer but had surface water throughout our study. Dominant species in the area were similar to those on the Ekalaka route except for stands of box elder (*Acer negundo* L.), plains cottonwood (*Populus deltoides* Bartr. ex Marsh.), and silver buffalobery (*Shepherdia argentea* (Pursh) Nutt.) along portions of Box Elder Creek and greasewood (*Sarcobatus vermiculatus* (Hook.) Torrey) communities in some bottom land sites.

Average annual precipitation in the Ekalaka area (39.2 cm) is slightly greater than in the Box Elder area (32.9 cm) (NOAA 1993). Seventy-five percent of precipitation in both areas occurs as rain during April–September (Carter County Conservation District 1976). Precipitation for September 1992 to August 1993 was above average for both study areas with significantly higher rainfall occurring in June and July (NOAA 1993). Long term average temperature is 20°C for July and 7°C for January.

At the time of the study, Carter County was approximately 90% rangeland, 1.7% crops, 1.9% CRP, 4.2% forest, and 2.2% other. Major agricultural crops, in order of abundance, were winter wheat (*Triticum aestivum* L.) (including fallow), alfalfa, barley (*Hordeum vulgare* L.), oats (*Avena sativa* L.), rye (*Secale cereale* L.), and safflower (*Carthamnus tinctorius* L.). Sixty-five percent of the land is deeded, 7% is state land, and the remainder is federally owned. (U.S.D.A., Agricultural Stabilization and Conservation Service, unpubl. data).

Deer and antelope harvest reports (Montana Dep. Fish, Wildlife and Parks, unpubl. data) for 1992 suggested that mule deer populations were at or slightly above the 30-year average. White-tailed deer harvest levels were approximately average, and antelope harvest was slightly above average.

Ungulate Count Procedure

From September 1992 to August 1993, deer and antelope counts were conducted on 56 sites located within 6 major land use categories. These were alfalfa, bottom rangeland, Conservation Reserve Program lands (CRP), upland rangeland, wheat stubble, and growing wheat (Table 1). Seven to 10 observation sites were chosen in each land use category. Travel routes were designed so the direction of travel could be alternated.

At each observation site, presence of livestock, number and species of deer, and number of antelope were recorded (1 deer or 1 antelope = 1 observation). Activity and age were recorded when possible.

Table 1. Land use categories used in wild ungulate surveys. Numbers of sites (n) and number of hectares (ha) for each type are given in the table.

Land Use Type	Characteristics
Alfalfa (n = 10, ha = 235)	Fields with a grass-alfalfa mix containing at least 20% alfalfa canopy coverage prior to first harvest. Harvested for livestock feed (not seed production).
Bottom Rangeland (n = 10, ha = 348)	Native or reseeded rangeland used for livestock grazing in any season. Located in the lowest elevation in relation to surrounding topography. Usually adjacent to perennial or intermittent creeks.
Conservation Reserve Program (CRP) (n = 10, ha = 351)	Lands enrolled in the Conservation Reserve Program. Seedings older than three years containing an average mix of alfalfa (0.45 kg pls (pure live seeds)) and crested wheatgrass (1.8 kg pls). Pubescent (<i>Agropyron trichophorum</i> (Link) Richt.) and intermediate (<i>A. intermedium</i> (Host) Beauv. wheatgrass were often substituted and yellow sweet clover (<i>Melilotus officinalis</i> (L.)) was included occasionally.
Upland Rangeland (n = 10, ha = 319)	Native or reseeded rangeland used principally for livestock grazing in any season. Low relief sites located in high elevations in relation to surrounding topography. Usually elevated 2 or more terrace levels above bottom rangeland sites.
Wheat stubble (n = 9, ha = 231)	Winter wheat that was seeded in the fall of 1991 and harvested in the early fall of 1992. Plants were mature when the study was initiated.
Growing wheat (n = 7, ha = 183)	Winter wheat that was seeded in the fall of 1992 to be harvested in the early fall of 1993. Winter wheat that was planted and matured during the study period.

Counts were conducted on each observation site at 4 time periods: 1) dawn (1/2 hour before to 1/2 hour after sunrise); 2) day (2 hours after sunrise to 2 hours before sunset); 3) dusk (15 minutes before sundown to 45 minutes after sundown); and 4) night (1 hour after sundown until the observation route was complete). Observations were not conducted when fog, snow, or rain impaired visibility. Binoculars were employed to verify species sighted at dawn, day, and dusk. Night observations were aided by a 1.5-million candle power spotlight and binoculars.

To assess observation efficiency, 1 person walked through a set of observation sites after making counts from the road while another observer watched for animals that flushed. The CRP lands were tested in winter and summer. Alfalfa, bottom rangeland, and upland rangeland were tested only in summer.

Seasons were defined as fall (September–November), winter (December–February), spring (March–May), and summer (June–August). Counts were conducted 10 times per season at

each time period giving 40 counts at each observation site per season.

To compensate for unequal observation site sizes, an average ungulate density was determined for each land use category in each month. Monthly data were combined to form seasonal estimates.

The total number of deer and antelope observed in each land use category in each season was compared to availability of land use categories on survey routes (Neu et al. 1974). Results are reported as use less than (-), greater than (+), or equal to (=) availability among all land use categories examined at $P < 0.05$.

Wild Ungulate Associations with Landscape Variables

For all observation sites, distance to the nearest agricultural crop (alfalfa, CRP, and wheat) was measured from topographic maps. Slope and the distance from each observation site to the nearest perennial creek, intermittent creek, hiding cover, forest, and occupied homestead were also measured. Data from both study routes were combined to test for associations between landscape variables and deer and antelope abundance. Seasonal correlations and comparisons were determined by Spearman rank correlations (R_s) and Kruskal-Wallis tests (Conover 1980). We determined if combinations of landscape level variables were useful in predicting ungulates numbers at specific sites using multiple linear regression (Neter et al. 1993). Individual models were developed for each species in each season. Ungulate density (total number of ungulates observed on a site in 40 replicated counts/area of the site) was the dependent variable in all models. The independent variables used in the regression models were distances to landscape features and percent slope.

Wild Ungulate Associations with Vegetation and Livestock

Vegetative composition was estimated for alfalfa, rangeland, and CRP at each observation site in late June and early July. Vegetative cover was estimated by recording the percent of the ground covered by grasses, forbs, shrubs, and mosses within 20 by 50 cm plots at 20 random points at each observation site. The vegetative cover classes were: <1%, 1–5%, >5–25%, >25–50%, >50–75%, >75–95%, and >95%. The mid points of the coverage classes were used to calculate means and Spearman rank (R_s) correlations were used to test for associations between wild ungulates and vegetative characteristics for alfalfa, CRP, upland rangeland and bottom rangeland. Spearman rank correlations were also used to test the strength of association between wild ungulates and livestock numbers at observation sites.

Results

During the study period, 4,687 mule deer, 1,322 white-tailed deer, and 2,767 antelope observations were recorded. Forty-two percent of mule deer, 93% of white-tailed deer, and 66% of antelope observations were made on the Ekalaka route. The dominant observed activity in all seasons was feeding, followed by bedding and traveling.

We did not find major differences in sightability among land use categories. In CRP lands, we observed an average of 85% ($n=10$ tests) of all animals present at night and 80% ($n=13$ tests) of all animals present during the day. All other land use cate-

gories had less hiding cover available to animals and were checked only during the day ($n=28$ tests). More than 90% of the animals present in these types were visible from the road. For all 3 species, the number of observations in land use categories was not proportional to availability of categories in any season (chi-square range = 19.11–3652.83, $P < 0.05$) (Table 2).

Use Patterns of Agricultural Cover Categories

Mule deer. Mule deer densities per land use category in individual months varied from 0.0 to 0.42/ha (Fig. 1). In fall, CRP and alfalfa were selected (use>availability) in sites along both observation routes, and all other types were avoided (use<availability) (Table 2). During winter, CRP was selected on the Ekalaka route and upland range on the Box Elder route. Most other categories were used less than expected. In spring and sum-

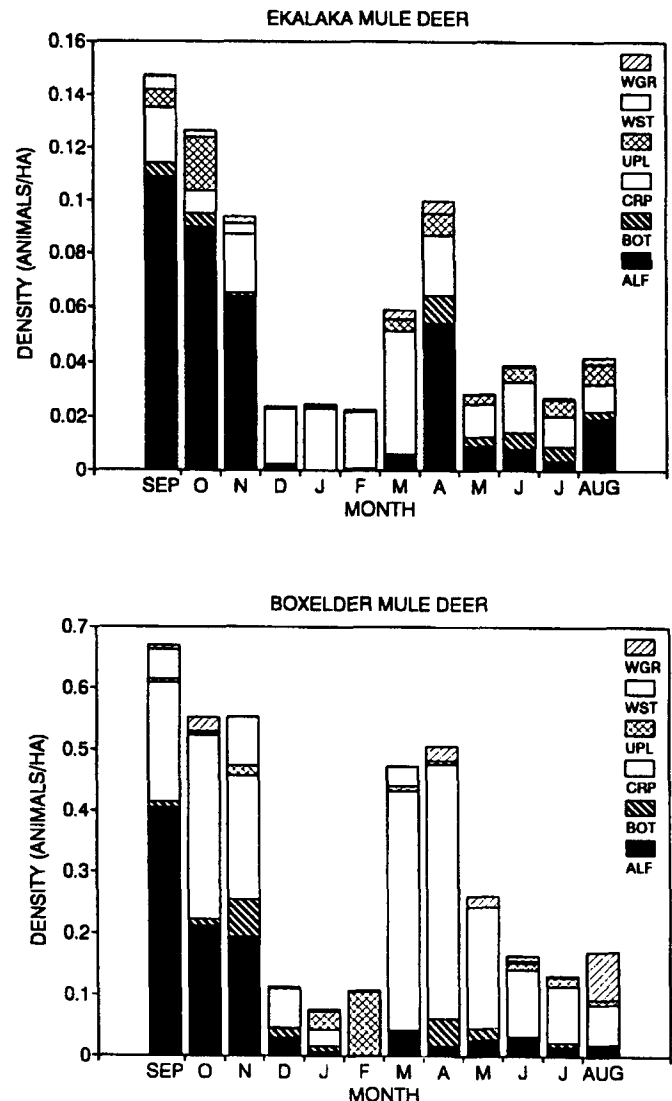


Fig. 1. Average mule deer densities on alfalfa (ALF), bottom rangeland and (BOT), Conservation Reserve Program (CRP), upland rangeland (UPL), wheat stubble (WST), and growing wheat (WGR) observation sites in the Ekalaka and Box Elder study areas from September 1992 to August 1993.

Table 2. Mule deer, white-tailed deer, and antelope use of agricultural land use categories in the Ekalaka and Box Elder study areas.

Area	Use	Season											
		Fall			Winter			Spring			Summer		
		MUL ^a	WTD	ANT	MUL	WTD	ANT	MUL	WTD	ANT	MUL	WTD	ANT
Ekalaka	ALF ^b	+ ^c	+	+	-	-	-	=	+	+	-	+	=
	BOT	-	-	-	-	-	-	-	-	-	=	-	=
	CRP	+	=	=	+	+	+	+	+	+	+	+	+
	UPL	-	-	-	-	-	=	-	-	-	=	-	-
	WST	-	=	-	-	-	-	-	-	-	-	-	-
	WGR	-	=	=	-	-	-	-	-	+	-	-	-
Box Elder	ALF	+	+	-	-	*	-	-	*	=	=	+	=
	BOT	-	=	=	-	*	+	-	*	=	-	-	=
	CRP	+	-	-	=	*	-	+	*	=	+	+	-
	UPL	-	-	-	+	*	-	-	*	=	-	-	=
	WST	-	-	+	-	*	-	-	*	-	-	-	-
	WGR	-	=	=	-	*	-	-	*	=	=	-	-

^aMUL = mule deer; WTD = white-tailed deer; ANT = antelope.

^bALF = alfalfa; BOT = bottom rangeland; CRP = conservation reserve program; UPL = upland rangeland; WST = wheat stubble; WGR = growing wheat.

^c(+) = use greater than availability; (=) = use proportional to availability; (-) = use less than availability; (*) = no test.

mer, CRP was selected along both routes, and most other categories were avoided.

White-tailed deer. White-tailed deer densities ranged from 0.0 to 0.11/ha (Fig. 2). In fall, white-tails selected alfalfa and avoided upland range sites. Use of other types was either proportionate to availability or less than availability, but relationships differed between routes (Table 2). In winter, they selected CRP and avoided all other land use categories. In spring and summer they selected alfalfa fields and CRP and used all other land use categories proportionally less than their availability. During winter and spring, very few white-tailed deer were seen on the Box Elder route so selectivity was based only on sites along the Ekalaka route.

Antelope. Monthly antelope density in land use categories varied from 0.0 to 0.58/ha (Fig. 3). Use patterns along the 2 study routes varied more for antelope than for deer (Table 2). In fall, antelope observed on the Ekalaka route selected alfalfa and avoided wheat stubble. On the Box Elder route, they avoided alfalfa and selected stubble. In winter, antelope observed on the Ekalaka route selected CRP and avoided bottom rangeland. The only antelope seen on the Box Elder route in winter were in bottom rangeland. In spring, antelope on the Ekalaka route selected alfalfa, CRP, and growing wheat and avoided other categories. All categories except wheat stubble were used in proportion to availability along the Box Elder route. In summer most categories were used in a similar manner on both routes except CRP. This category was selected in the Ekalaka area and avoided in the Box Elder area.

Wild Ungulate Associations with Landscape Variables

Mule Deer. Mean numbers of mule deer on the 56 observation sites in each season were negatively correlated with distances to landscape variables in 24 of 36 Spearman Rank Correlations we calculated (Table 3), but only 3 correlations were significant ($P < 0.05$). In winter and spring, deer numbers were negatively associated with distance to CRP. In summer, deer numbers were positively correlated with distance to forest cover.

White-tailed Deer. White-tailed deer observations were negatively correlated with landscape variables in 20 of 36 tests (Table 3). Four correlations were significant. In fall and spring, more white-tailed deer were seen in sites with little or no slope than in steeper terrain. In spring, white-tailed deer numbers were negatively correlated with distance to CRP and forest cover.

Antelope. Negative associations between antelope numbers and landscape variables were calculated for only 8 of 36 tests. There were significant positive associations between antelope numbers and 2 variables, distance to forest cover and occupied homesteads, in spring and summer.

Multiple Regression Models

Twelve multiple regression models, 3 species in 4 seasons, were tested. Only 2 of the 12 models detected marginally significant relationships ($P < 0.10$) between wild ungulates and landscape variables. None of the models explained a substantial amount of the variability ($R^2 < 0.51$) in ungulate observations (Table 4).

Wild Ungulate Associations with Vegetation Coverage and Livestock

The average canopy coverage in bottom rangeland sites was 55% grass, 33% forb, and 8% shrub. Canopy coverage for upland sites averaged 49% grass, 28% forb, and 11% shrub. Alfalfa canopy cover prior to the first cutting was 29%. Canopy coverage of the introduced wheatgrasses used in seeding CRP averaged 43% and alfalfa averaged 6% (for all CRP fields). Other grasses, other forbs, and shrubs combined had a mean canopy coverage of 7%. Of 12 Spearman correlations calculated (3 ungulates species in 4 seasons) for sites with perennial vegetative cover, only 1 was significant ($P < 0.05$). Antelope numbers were negatively associated ($R_s = -0.803$, $P < 0.01$) with alfalfa canopy coverage in summer.

Livestock distribution varied seasonally in the study area. Cattle were grazed on upland and lowland range sites through the year. In winter, there was a tendency for higher use of bottom rangeland to facilitate feeding operations. In summer, cattle tend-

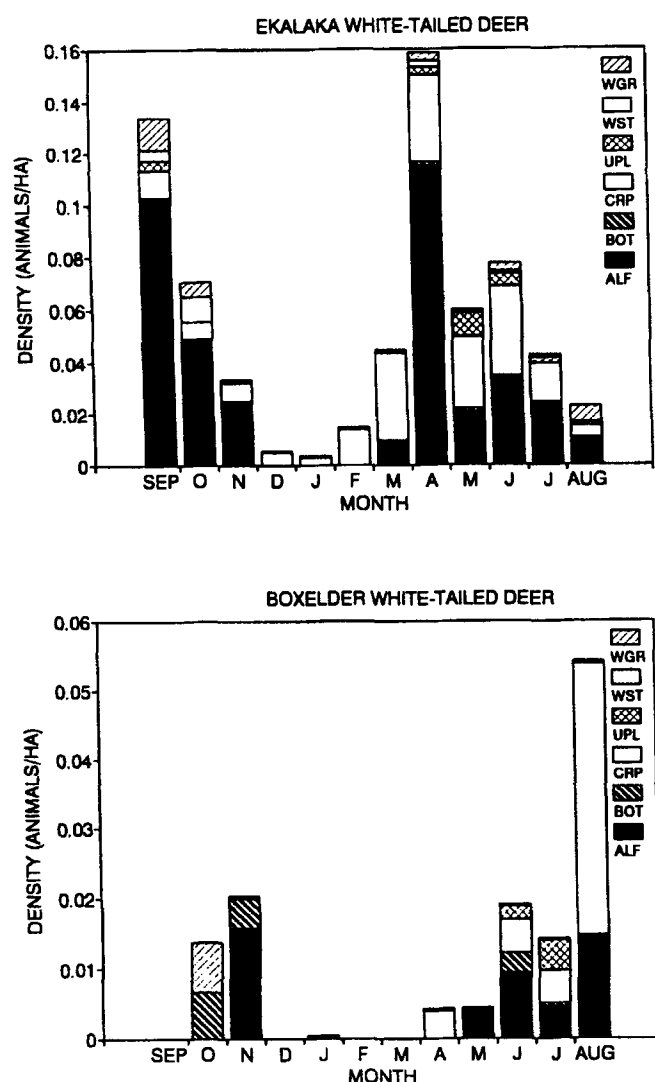


Fig. 2. Average white-tailed deer densities on alfalfa (ALF), bottom rangeland (BOT), Conservation Reserve Program (CRP), upland rangeland (UPL), wheat stubble (WST), and growing wheat (WGR) observation sites in the Ekalaka and Box Elder study areas from September 1992 to August 1993.

ed to be seen in bottom land pastures more than in upland pastures probably in response to shade, water, and/or forage in riparian areas. In winter and early spring, many ranchers allowed their cattle to graze on alfalfa and wheat fields. There were no significant differences (Kruskal-Wallis tests, $P = 0.12$ to 0.40) in number of domestic sheep observed in upland and lowland sites in any season. Most ranchers did not graze sheep on alfalfa or wheat fields. Horses were observed on only one observation site and were not included in the analysis.

Correlations between ungulate numbers and cattle were generally poor. White-tailed deer numbers were negatively correlated with cattle presence in spring ($R_s = -0.386$, $P < 0.01$), and summer ($R_s = -0.369$, $P < 0.01$). There were no significant ($P < 0.05$) associations evident between sheep and wild ungulates.

Discussion

Use of Agricultural Lands

Upland and bottom land range were the most abundant of the agricultural cover categories we sampled and the most common agricultural land use types in eastern Montana (Montana Agricultural Statistics Service 1993). Wild ungulates generally used these types in less than expected proportions. This low relative level of use does not imply that native range is unimportant to wild ungulates in Montana (Pyrah 1987, Wood et al. 1989). It merely indicates that rangeland was so abundant that it was not limiting at current population levels. During 1992–93, forage

Table 3. Seasonal Spearman rank (R_s) correlation coefficients for wild ungulates and landscape variables in all seasons.

		MUL ^a		WTD		ANT	
		R_s^b	P	R_s	P	R_s	P
Fall							
Dist to ^c	ALF	-0.12	0.45	0.10	0.51	-0.01	0.94
	CRP	-0.17	0.27	-0.19	0.21	0.04	0.82
	WHT	0.09	0.57	0.02	0.90	0.12	0.46
	PCK	-0.16	0.23	0.10	0.45	-0.20	0.15
	ICK	-0.22	0.10	-0.08	0.54	0.18	0.19
	COV	-0.18	0.19	0.04	0.78	0.05	0.72
	FOR	-0.08	0.58	-0.20	0.15	0.14	0.31
	HMSD	-0.27	0.05	-0.03	0.82	-0.01	0.97
	SLOPE	-0.02	0.88	-0.35	0.01	0.01	0.93
Winter							
Dist to	ALF	-0.07	0.67	0.13	0.40	0.28	0.07
	CRP	-0.30	0.04	0.09	0.54	0.01	0.94
	WHT	0.15	0.36	0.06	0.74	0.18	0.26
	PCK	-0.19	0.17	0.01	0.96	0.06	0.68
	ICK	0.16	0.24	0.18	0.18	0.27	0.05
	COV	-0.20	0.14	-0.06	0.67	0.08	0.58
	FOR	0.26	0.05	0.11	0.44	0.26	0.06
	HMSD	0.05	0.72	0.18	0.19	0.09	0.50
	SLOPE	0.12	0.38	-0.13	0.34	0.16	0.26
Spring							
Dist to ^c	ALF	-0.18	0.25	0.12	0.43	0.00	0.98
	CRP	-0.31	0.03	-0.40	0.01	-0.02	0.91
	WHT	0.02	0.90	-0.05	0.77	0.03	0.85
	PCK	-0.20	0.14	0.21	0.11	0.08	0.57
	ICK	0.07	0.59	-0.19	0.16	0.11	0.41
	COV	-0.12	0.38	-0.13	0.33	0.11	0.43
	FOR	0.14	0.31	-0.33	0.01	0.03	0.02
	HMSD	-0.24	0.08	0.12	0.40	0.30	0.03
	SLOPE	-0.04	0.78	-0.28	0.04	-0.12	0.40
Summer							
Dist to	ALF	-0.10	0.53	0.06	0.68	0.10	0.51
	CRP	-0.14	0.37	-0.17	0.27	-0.02	0.91
	WHT	-0.07	0.69	-0.04	0.80	-0.07	0.69
	PCK	-0.23	0.10	0.14	0.30	0.05	0.70
	ICK	0.04	0.75	-0.26	0.06	0.18	0.18
	COV	-0.07	0.64	-0.04	0.76	0.22	0.11
	FOR	0.30	0.03	-0.06	0.65	0.27	0.04
	HMSD	-0.26	0.06	-0.11	0.43	0.34	0.01
	SLOPE	0.15	0.28	-0.17	0.21	-0.12	0.39

^aMUL = mule deer; WTD = white-tailed deer; ANT = antelope.

^b R_s = Spearman rank correlation coefficient; P = p-value.

^cDist = distance from observation site to nearest: ALF = alfalfa; CRP = conservation reserve program land; WHT = wheat; PCK = perennial creek; ICK = intermittent creek; COV = hiding cover; FOR = forest; HMSD = occupied homestead. SLOPE = land slope (%).

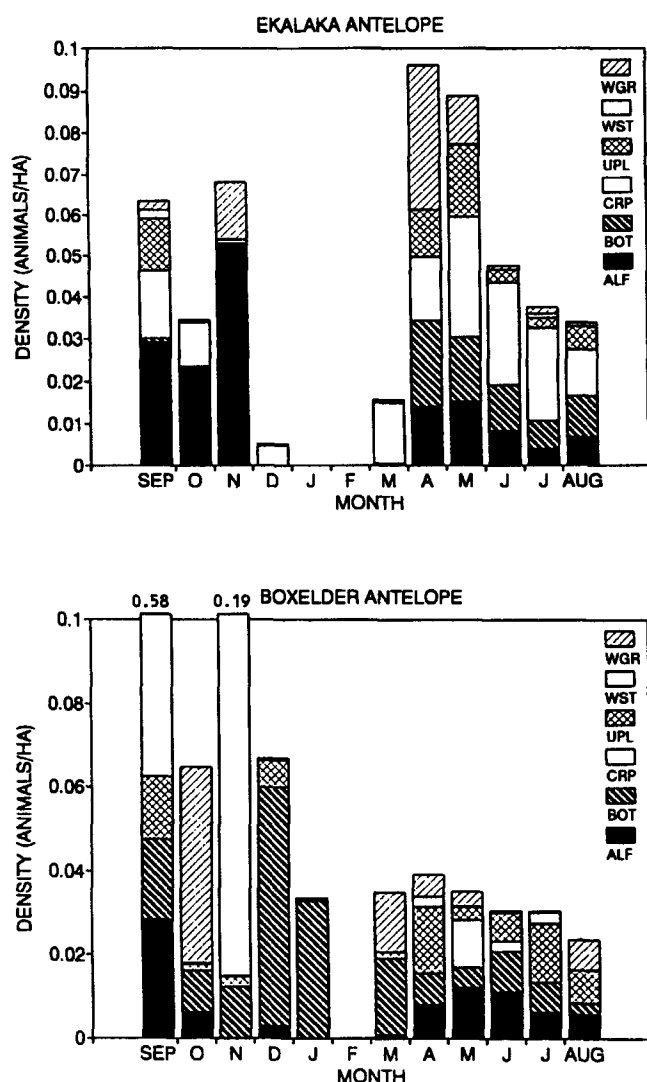


Fig. 3. Average antelope densities on alfalfa (ALF), bottom range-land (BOT), Conservation Reserve Program (CRP), upland range-land (UPL), wheat stubble (WST), and growing wheat (WGR) observation sites in the Ekalaka and Box Elder study areas from September 1992 to August 1993.

consumption by wild ungulates at most range sites in our study was unlikely to be measurable using standard range measurement techniques. The maximum average monthly density (0.1 animals/ha) of wild ungulates (deer plus antelope) occurred in upland range sites during February on the Box Elder route. If AUM equivalency were to be calculated very liberally (i.e. assume the average wild ungulate is equal to 1 domestic sheep and make no allowances for dietary differences), the stocking rate of wild ungulates on native range observation sites (average AUM in each month summed over all months) would have been 0.03 and 0.07 AUM/ha/year in the Ekalaka and Box Elder areas, respectively.

The CRP lands were used in greater than expected proportion in more seasonal tests than any other type. One or more ungulate species favored this type in every season, and all 3 species on the Ekalaka route used it preferentially in winter, spring, and fall. The highest monthly average density was 0.4 animals/ha during

April on the Box Elder route. Even though CRP sites were favored, the annual AUM equivalency (calculated as we did for range sites) was low in 1992–93, 0.1 and 0.4 AUM/ha/year for the Ekalaka and Box Elder areas, respectively.

Gould and Jenkins (1993) noted the importance of CRP to white-tailed deer in South Dakota. Thomas and Irby (1991) demonstrated that perennial grass plantings similar to CRP mixes were used heavily by mule deer in southeastern Idaho. Urness et al. (1983) demonstrated that crested wheatgrass (*A. desertorum*), a major component in CRP plantings, was an important winter forage for mule deer in Utah. They noted that crested wheatgrass often produced greater fall regrowth and earlier spring growth than native grasses. This favorably affected the nutritional plane of wintering mule deer because the green crested wheatgrass had relatively high protein levels compared to dormant native grass and browse species.

Wild ungulates are apparently attracted to CRP in eastern Montana for its forage and cover value. The CRP sites we observed had not been grazed for several years and had dense stands of exotic wheatgrasses. The stands were taller, denser, and had greater standing and ground litter cover than native range sites we measured (Selting 1994). The relatively dense vegetation in CRP trapped snow and retained moisture better than native range sites.

Because the CRP lands were neither grazed nor mowed, they provided better cover than native range or hay fields. Parker and Gillingham (1990) demonstrated that the effects of vegetative structure on temperature, wind speed, and solar radiation benefited wintering mule deer. The CRP lands were evidently comparable in quality for hiding fawns, hiding adults, wind protection in winter, and shade in summer to the topographic features, riparian tree stands, and shrubs ungulates routinely select in the prairies of eastern Montana (Wood et al. 1989, Olenicki 1993).

Alfalfa fields were the most heavily used land type on the Ekalaka route and ranked second on the Box Elder route. White-tailed deer were more closely tied to this land use type than antelope or mule deer, but all 3 species selected alfalfa in at least 1 season. The greatest density of ungulates using alfalfa was 0.4/ha in September on the Box Elder route, but the calculated AUM value for 1992–93 was only 0.2 AUM/ha/yr for both routes.

In eastern Montana, increased use of alfalfa fields during autumn by deer is well documented (Egan 1957, Wood et al. 1989, Griffiths 1990). Most alfalfa fields remain green longer than native forages due to their location in bottom land areas

Table 4. Regression Coefficient of determination (R^2) (P-values in parentheses) from multiple regression models for mule deer, white-tailed deer, and antelope using ungulate density as the dependent variable and landscape variables as independent variables.

Season	Mule deer	White-tailed deer	Antelope
Fall	0.30 (0.08)	0.23 (0.30)	0.09 (0.25)
Winter	0.18 (0.75)	0.50 (<0.01)	0.17 (0.85)
Spring	0.17 (0.90)	0.24 (0.30)	0.17 (0.83)
Summer	0.19 (0.61)	0.20 (0.51)	0.15 (0.91)

where they benefit from runoff and subirrigation. Olenicki (1993) documented the decrease in forage succulence on uplands adjacent to alfalfa bottoms on Box Elder Creek as summer progressed.

The critical time for financial loss of growing alfalfa is between green-up and harvest. Austin and Urness (1993) developed a model to estimate losses to deer based on the average night counts of deer on fields. When we applied this model to dusk and night counts, the average total losses we calculated for April through August were generally low (14.2 kg/ha). The greatest loss we estimated for an individual field over the 5-month growing season was 35.1 kg/ha/mo. Alfalfa consumption in the summer of 1993 was probably lower than average even though ungulate densities were near average. High rainfall, distribution of rain throughout summer, and abundant sweet clover probably delayed and reduced alfalfa use relative to an average or dry summer. The common practice of foregoing a second cut and saving alfalfa for seed harvest during dry years tends to increase depredation problems above that associated with foliage losses.

Wheat stubble was used less than expected in more tests than any other land use type. Sightings of large antelope herds in a few fields along the Box Elder route in September produced the highest monthly average density, 0.6 animals/ha. Annual AUM estimates were <0.1 and 0.2 AUM/ha/year for the Ekalaka and Box Elder areas, respectively. Ungulate densities in growing wheat were even lower. Annual AUM estimates were <0.1 AUM/ha/year for both study areas.

The potential for reductions in wheat yield due to ungulate use of fields was low. Wheat is generally not vulnerable to yield reduction from grazing until the growing point emerges from the ground (Dunphy et al. 1982). In Carter County, wheat growing point emergence occurs around May 15 at the earliest (Bauer et al. 1992, Schafer et al. 1985). Ungulate use of growing wheat peaked in April at 0.04 animals/ha but declined to <0.01 animal/ha by May.

Predicting Use Patterns

The associations between landscape variables and use of specific sites by ungulates followed expected patterns but were generally weak. Deer tended to be more abundant at sites close to preferred foraging areas (CRP and alfalfa fields) and near topography or vegetation that provided cover (stream channels, forests, and shrublands). White-tailed deer were more closely associated with flat, riparian areas than mule deer. Antelope were associated with flat, open terrain. Combinations of these factors in multivariate models did not improve site-specific predictability. The vegetation characteristics and livestock numbers at individual sites also showed little promise of producing tight predictive models. The associations we found were consistent with those outlined in earlier studies in the area (Egan 1957, Campbell 1970, Freeman 1971, Griffiths 1990, Olenicki 1993).

Our failure to discover a strong correlation between numbers of animals at specific sites and habitat factors was not due to selection of inappropriate independent variables or to poor sampling design. The habitat features measured in this study are widely recognized as important to deer and antelope in dry northern prairies (Severson 1981, Pyrah 1987, Kitchen and O'Gara 1982, Petersen 1984, Wood et al. 1989). Because we were able to sample large animals in open terrain and were able to sample individual sites frequently and systematically, we obtained much better

estimates of use patterns at individual sites than most landscape level studies. We did not have large sample sizes of sites, but we were able to use reasonably robust statistical models to search for landscape associations. The loose associations between animal numbers and habitat features we observed accurately reflect reality in southeastern Montana.

Deer and antelope are large, long lived animals who occupy large ranges and depend heavily on learning to form habitat use patterns within those ranges. They can and do change use patterns in response to favorable and unfavorable changes in resources and disturbance. Given these conditions, the past history of each site would have to be reduced to a mathematical term to produce a valid predictive model, and each site would likely have a unique value for this term. Even if terms were developed, the variability in use of sites may actually be small when compared to variability in attitudes towards wild ungulates among individual farmers and ranchers (Irby et al. unpublished data).

This is not encouraging for managers interested in working from a computer terminal. It does suggest a strategy for managing wild ungulates on private agricultural land in eastern Montana: managers should concentrate on working with individual landowners rather than searching for global solutions. Research projects should be used to identify conditions where problems might develop and to determine the efficacy of different approaches to resolving problems, but landowners and agency personnel should plan on discussing options for resolving problems on a site-by-site basis.

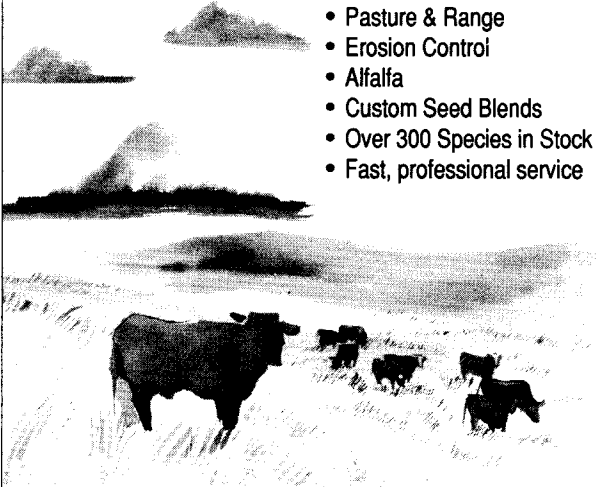
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Impact of prescribed burning on vegetation and bird abundance at Matagorda Island, Texas

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Abstract

We measured the impact of prescribed summer and winter burns on vegetation characteristics and spring abundance of birds in a *Spartina/Paspalum* grassland at Matagorda Island National Wildlife Refuge and State Natural Area, Texas, 1993-94. We burned 8 (4 summer burn, 4 winter burn), 122-ha plots. We estimated bird abundance by surveying once a week from March through May at 12-16 fixed-radius point count stations in each plot. We measured forb and grass foliar cover, litter depth, visual obstruction, and woody and residual stem density at each point count station 6-10 months after burning and 18-22 months after burning and found few differences in vegetation between summer and winter burns. Litter depth, visual obstruction, and woody stem density values were greater on control plots 6 to 10 months post-burn. By 18 to 22 months post-burn, only litter depth and visual obstruction remained higher on control plots than on either burn treatment. At 6 to 10 months after burning, wrens were more abundant on control plots and sparrows were more abundant on the burned plots. By 18 to 22 months post-burn, wren abundance had increased on the burned plots, but was still highest on control plots. Sparrow abundance remained highest on burned plots 18-22 months after burning. Precipitation was higher in 1993 than 1994; we believe blackbirds responded more to annual precipitation differences than to burning treatment. In this coastal island grassland, wren abundance was highest on unburned plots and sparrow abundance was highest on burned plots. We suggest that land managers could burn at > 2 year intervals in this grassland without negatively impacting most resident bird species.

Key Words: bird families, coastal barrier island, grassland, habitat, prescribed burning, Texas

The U.S. Fish and Wildlife Service's Breeding Bird Survey indicates that certain migratory bird species have declined (Robbins et al. 1989). These declines may be attributed to habitat loss on either wintering or breeding grounds (Gradwohl and

Resumen

Se midió el impacto de incendios intensionales en verano e invierno, sobre la vegetación y abundancia de aves durante la primavera en un pastizal de *Spartina/Paspalum* en el Area Natural Estatal y Refugio Nacional de Vida Silvestre Isla Matagorda, Texas, 1993-1994. Se quemaron 8 parcelas de 122 ha cada una (4 en verano y 4 en invierno). Estimamos la abundancia de aves mediante un muestreo semanal desde Marzo hasta Mayo utilizando 12 a 16 puntos de conteo de radio fijo por parcela. Se midió cobertura foliar de los pastos y matas, profundidad del mantillo, obstrucción visual y densidad de tallos leñosos y residuales, entre los 6 y 10 meses y los 18 y 22 meses después de las quemadas en cada parcela, encontrándose pocas diferencias en la vegetación entre las quemadas de verano e invierno. Los valores de profundidad del mantillo, obstrucción visual y densidad de tallos leñosos, fueron mayores en las parcelas controles luego de 6 a 10 meses de la quema. Luego de 18 a 22 meses, sólo la profundidad del mantillo y la obstrucción visual se mantuvieron altas en parcelas controles respecto de cualquier otro tratamiento. Durante los 6 a 10 meses después de las quemadas, individuos de la familia Troglodytidae, fueron mas abundantes en las parcelas controles mientras que Emberizinae fue mas abundante en las parcelas quemadas. La abundancia de Troglodytidae se incrementó en las parcelas quemadas luego de 18 a 22 meses, manteniéndose alta en las parcelas controles mientras que la abundancia de Emberizinae, se mantuvo alta en los sitios quemados. El régimen de precipitación fue más alto en 1993 que en 1994, nosotros creemos que individuos de la familia Icteridae respondieron más a las diferencias en la precipitación anual que a los tratamientos por quemadas. En este pastizal costero de isla, la abundancia de Troglodytidae fue más alta en parcelas no quemadas mientras que la abundancia de Emberizinae fue más alta en parcelas quemadas. Sugerimos que los dueños de tierras en la reserva, podrían realizar quemadas a intervalos mayores de 2 años en este pastizal sin generar un impacto negativo en la mayoría de las especies residentes.

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Greenburg 1989), Robbins et al. 1989, Askins et al. 1990, Finch 1991). One frequently overlooked consideration that may contribute to the decline is the availability of suitable stop-over habitat where birds rest during migration (Hutto 1985, Moore et al. 1990).

Large numbers of migrants use coastal habitats along the Gulf of Mexico during migration (Moore and Kerlinger 1987, Moore and Simons 1992). It is on these islands that species can replenish energy before continuing to their breeding grounds or build energy reserves for the long migration flight to the wintering grounds. The alteration or disturbance of in-transit habitat may detrimentally affect how these species meet the costs of migration (Ward 1987, Finch 1991, Moore and Simons 1992).

We assessed prescribed burning as a management tool on Matagorda Island National Wildlife Refuge and State Natural Area, Texas. Our objectives were to evaluate the impact of summer and winter burns on vegetative characteristics and bird abundance.

Materials and Methods

Study Area

Matagorda Island is a 22,943 ha coastal barrier island along the mid-coast of Texas in Calhoun county (Blankenship et al. 1990). It is 1 of 5 large barrier islands adjacent to the Texas coast and is located about 14.5 km southwest of Port O'Connor and 81 km southeast of Victoria. The island is 60.8 km long and varies in width between 1.2 to 7.2 km.

The climate is maritime and largely controlled by the Gulf of Mexico and associated warm, moist air masses (Mowery and Bower 1978, Blankenship et al. 1990). Peak rainfall periods are May, June, August, and September with an annual precipitation of 98 cm. Temperatures are fairly constant throughout the year with an average annual temperature of 21°C.

Major physiographic areas include the beach-dune complex, barrier flats, salt marsh, and wind-tidal flats (Blankenship et al. 1990). These areas are flat to gently rolling with the exception of the sand dunes. Barrier flats are dominated by grassland habitat typical of coastal barrier islands in Texas (Blankenship et al. 1990). Grass species include primarily gulf cordgrass (*Spartina spartinae* (Trin.) Merr. authority for soil type names), marshhay cordgrass (*Spartina patens* (Ait.) Muhl.), and gulf dune paspalum (*Paspalum monostachyum* Vasey). Baccharis (*Baccharis* sp. Vasey), a shrub indigenous to barrier islands, occurs in scattered clumps.

Sampling Design

We located 6 plots each year, approximately 122-ha each, on the mid-portion of Matagorda Island in the barrier flats and established a matrix of 12–16 survey point count stations, 300 m between each station, in each plot. In 2 irregularly shaped plots, we reduced the number of count survey stations to 12 and 15. We randomly assigned 2 burn treatments to 2 plots each year. We conducted our first summer burns on 27–28 August 1992 and our second summer on 24–25 August 1993. We burned our first winter burns on 6 and 14 January 1993 and the second burns on 4–5 January 1994. Four plots served as controls. All burns were conducted with half a headfire and half a backfire technique on each plot (C. M. Britton and S. D. Brown, Tex. Tech Univ., pers. commun.).

We used a fixed-radius point count method to estimate bird abundance (no./40 ha) from 1 March to 30 May 1993 and 1994 (Verner 1985, Verner and Ritter 1985) and recorded all birds heard or sighted over a 5-minute period and within 50 m at each point count station. We repeated all surveys 12 times on each plot

in both years with about 7 days between surveys on individual plots. In 1993, we estimated bird abundance on 2 summer burn plots, 2 winter burn plots, and 2 control plots. We defined this sampling period as 6–10 months post-burn. In 1994, we surveyed birds on 2 'new' (1993–1994) winter and summer burns and 2 additional control plots. The 'new' plots provided another sample from 6–10 months post-burn. In addition, in 1994, we resurveyed the 2 control and 4 treatment plots burned in 1992–93; these surveys provided samples 18 to 22 months post-burn.

At each point count station, we measured vegetation along a 50-m tape extended in the 4 cardinal directions. We estimated forb and grass foliar cover with an ocular sighting tube (Yahner 1986) and measured litter depth to the nearest centimeter at 5-m intervals along each 50-m line. We used a Robel pole (Robel et al. 1970) at a 1-m sighting height and distance to estimate visual obstruction (i.e., lowest height that vegetation obstructed 100% of the pole) at 10-m intervals along each line. To estimate density, we counted all woody and residual (i.e., dead woody and sunflower stalks) stems contained in a 50-m radius at point count stations. We obtained annual precipitation data from the U.S. Fish and Wildlife Service's headquarters on Matagorda Island.

Statistical Methods

We used 2 analyses to test for differences ($P < 0.10$) in bird abundance and characteristics of the vegetation among treatments. We used a randomized block two-way analysis of variance to test for the influence of year and burn treatment on vegetation variables and bird abundance 6–10 months after burning. To test for differences between vegetation variables and bird abundance on plots that we sampled at both the 6–10 months and 18–22 months interval, we used a randomized block repeated measures two-way analysis of variance (SAS. 1989). We used Tukey's HSD mean separation tests when we found significant main effects and interactions. We investigated trends in diversity (Shannon and Weaver 1949) at the species and family/subfamily taxonomic level using one-way analysis of variance. We estimated abundance for families/subfamilies of birds when we had at least 5 observation/plot/survey during the 12 survey periods.

Results

Six to 10 months post-burn

Vegetation

Burning changed vegetation characteristics by decreasing litter, visual obstruction, and woody stem densities (Table 1). Litter depth decreased from 1993 to 1994, but was greater on unburned plots in both years. Precipitation was higher in 1993 (110 cm) than 1994 (52 cm).

Birds

We recorded 6827 birds of 136 species and 36 families/subfamilies in 1993 and 6624 birds in of 135 species and 40 families in 1994. Because abundance of individual bird species was low and we found no difference in diversity at the species ($P > 0.95$) or the family ($P > 0.94$) level, we grouped birds into families or subfamilies (Samson 1979, Short 1983) for analyses of abundance. We present estimates of spring bird abundance for 10 resident families/subfamilies: Anatidae (waterfowl), Ardeidae (herons, egrets),

Table 1. Vegetation characteristics measured at point count stations ($n = 24-32$) on the barrier flats 6 to 10 months after burning, Matagorda Island National Wildlife Refuge and State Natural Area, Texas, July 1993 and 1994.

Vegetation Variables	1993			1994		
	Control	Summer	Winter	Control	Summer	Winter
Forb Cover (%)	18.9(6.1) ^a	23.9(4.9)	30.5(5.3)	27.3(2.8)	32.0(7.1)	36.1(8.8)
Grass Cover (%)	57.6(1.2)	58.6(8.4)	49.7(2.3)	40.3(7.2)	36.3(8.1)	28.8(13.4)
Litter Depth (cm)	9.9(0.6) ^b A	0.0(0.0) ^b B	0.0	6.6(0.4) ^a A	0.0(0.0) ^b B	0.0(0.0) ^b B
Visual Obstruction	17.3(2.2) ^c	11.0(0.2)	10.0(0.8)	11.0(0.9)	2.6(0.4)	3.1(0.3)
Residual Stems (no./ha)						
<1 m	0.0 ^d (0.0)	1.6(0.9)	0.3(0.2)	0.0(0.0)	6.2(3.7)	1.2(0.1)
1-2 m	5.9(3.1)	7.2(6.5)	7.0(6.9)	17.0(3.1)	18.5(14.3)	8.4(3.5)
Woody Stems (no./ha)						
<1 m	4.7(3.6) ^e B	1.4(1.4) ^a A	2.1(1.9) ^a A	4.0(0.9) ^a A	0.0(0.0) ^b B	0.3(0.3) ^c C
1-2 m	21.0(8.3) ^a A	4.8(4.3) ^b B	2.5(1.7) ^b B	38.3(20.9) ^a A	0.5(0.5) ^b B	0.1(0.1) ^b B

^aMean (standard error)

^bWithin years, variables followed by the same letter were not different ($P > 0.05$).

^cHeight of vegetation at 100% obstruction.

^dDead herbaceous and sunflower stalks.

^eAll woody stems, except sunflower stalks

Rallidae (rails), Scolopacidae (shorebirds), Caprimulgidae (nightjars), Hirundinidae (swallows), Troglodytidae (wrens), Icteridae (blackbirds), Fringillidae (roses), and Emberizinae (sparrows). We found few differences in bird abundance among treatments (Table 2). Wrens ($P = 0.03$) were most abundant on control plots and sparrows ($P = 0.08$) were most abundant on the burned plots. Blackbirds ($P = 0.04$) were more abundant in the year of higher precipitation (1993).

6-10 month vs. 18-22 month post-burn

Vegetation

By 18-22 months after burning, we found the treatment effect was not detectable for most vegetation characteristics we measured (Table 3). Within treatments, we found grass cover decreased on all but winter burns, visual obstruction decreased on all treatments, and residual stem density increased on all treatments.

Birds

Wren ($P = 0.01$) abundance remained highest on control plots than either of the burn treatments, but had increased over levels

found 6-10 months post-burn. Sparrow ($P = 0.01$) abundance remained highest on both burn treatments 18-22 months after burning (Table 4).

Discussion and Conclusions

There were few differences in vegetation variables between burned and unburned areas when we measured at 6-10 months post-burn and 18-22 months post-burn. Drawe and Kattner (1978) reported that burning in September on Padre Island, Texas, produced greater forb response, but burning in February depressed grass and forb production the first growing season after treatment. In contrast to the work on Padre Island, we found grass and forb foliar cover did not differ among our treatments in either the 6-10 or the 18-22 month sampling period. In our work, litter depth remained unchanged from the first to the second post-burn period. We suspect that litter may take longer than 2 seasons after a fire to accumulate. Our results agree with Wright and Bailey (1982) who reported litter accumulated after 2 to 3 years following a fire and generally returned to normal on grasslands within 5 years after burning depending on annual precipitation.

Table 2. Spring abundance (no./40 ha) of resident birds on 2 control (C), summer burn (S), and winter burn (W) plots surveyed 6 to 10 months post-burn, Matagorda Island National Wildlife Refuge and State Natural Area, Texas, 1 March to 31 May 1993 and 1994.

Families/ subfamilies	Bird Abundance								
	1993			1994			P ^b		
	Plot ^a			Plot					
	C	S	W	C	S	W	T	Y	I
	----- (no./40ha) -----								
Anatidae	18.6	6.0	9.9	4.4	4.5	0.3	0.67	0.09	0.85
Ardeidae	0.9	3.3	0.0	0.2	9.9	1.4	0.53	0.44	0.61
Rallidae	1.6	1.5	0.1	0.0	0.0	0.0	0.44	0.13	0.44
Scolopacidae	2.2	1.3	3.5	1.0	1.9	0.9	0.70	0.39	0.09
Caprimulgidae	0.2	0.0	0.2	0.0	0.4	0.2	0.50	0.50	0.50
Hirundinidae	0.5	0.0	1.8	1.6	2.1	3.4	0.61	0.42	0.97
Troglodytidae	28.2	3.1	0.9	20.7	1.8	0.7	0.03	0.44	0.60
Icteridae	23.3	52.9	34.4	22.8	42.9	28.3	0.15	0.04	0.74
Fringillidae	0.3	0.1	0.5	1.9	1.1	0.3	0.67	0.16	0.54
Emberizinae	2.9	18.9	11.0	8.4	30.1	15.7	0.08	0.11	0.50

^a $n = 12-16$ survey points per plot, 12 visits per plot.

^bT = treatment effect, Y = time after burn effect, I = interaction effect.

Table 3. Vegetation characteristics measured at point count stations ($n = 24\text{--}32$) at 6 to 10 and 18 to 22 months post-burn, Matagorda Island National Wildlife Refuge and State Natural Area, Texas, July 1993 and 1994.

Vegetation Variables	6–10 months post-burn			18–22 months post-burn		
	Control	Summer	Winter	Control	Summer	Winter
Forb Cover (%)	18.9(6.1) ^a A	23.9(4.9)A	30.5(5.3)	26.7(6.4)	25.6(3.1)A	26.4(3.3)A
Grass Cover (%)	57.6(1.2)A	58.6(8.4)A	49.7(2.3)	42.5(0.6)B	53.7(9.9)B	54.7(3.8)B
Litter Depth (cm)	9.9(0.6)A	0.(0.0)B	0.(0.0)B	5.5(0.3)B	1.0(0.4)A	0.3(0.3)A
Visual Obstruction	17.3(2.2) ^b A	11.0(0.2)A	10.0(0.8)	11.0(1.2)B	5.4(0.7)B	3.9(0.6)B
Residual Stems (#/ha)						
<1 m	0.0(0.0) ^c A	1.6(0.9)A	0.3(0.2)A	0.4(0.4)A	14.7(14.6)	
1–2 m	5.9(3.1)A	7.2(6.5)A	7.0(6.9)B	19.4(9.6)	17.3(14.6)	71.2(1.3)B
Woody Stems (#/ha)						
<1 m	4.7(3.6) ^d A	1.4(1.4)A	2.1(1.9)A	3.7(3.6)A	6.0(6.0)A	
1–2 m	21.0(8.3)A	4.8(4.3)A	2.5(1.7)A	40.0(3.4)B	3.3(2.9)A	1.9(1.9)A

^aMeans (standard error). Variables followed by the same letter were not different ($P > 0.05$) in a comparison within treatments between 6–10 and 18–22 months after burning.

^bHeight of vegetation at 100% obstruction.

^cDead herbaceous stems and sunflower stalks.

^dAll woody stems, except sunflower stalks.

We believe the trends in vegetation variables on individual treatments in the second post-burn season may be explained by annual weather patterns. Rainfall plays a major role in the structure of grasslands (Wright and Bailey 1982). Weather conditions differed between years in our study: 1993 was an average year, 1994 was a dry year. On control plots, we found that grass cover, litter depth, and visual obstruction were higher in 1993 than in 1994. These variables followed the same trends on burned areas by the second post-burn sampling.

Weather (e.g., rainfall) is also thought to influence breeding grassland bird density (Smith 1982, Cody 1985, George et al. 1992). Zimmerman (1992) noted that burning in drought years in tallgrass prairie may influence breeding birds more strongly than in average years. He suggested that this could be due to lower above ground biomass and structural simplicity on burned areas in drought years. Because weather conditions differed between years in our study, we expected lower bird abundance in the dry year, 1994. However, we detected differences in abundance between years in only 10% of the families. We speculate that precipitation levels in 1994 must have not been severe enough to impact bird abundance.

We could not generalize across bird families about response to prescribed burning. Generally, wrens were most abundant on unburned, control plots. Burning removes the accumulated dead plant material and creates a more open habitat; wrens may prefer dense vegetation. Although, wrens were seldom seen on burned plots 6–10 mo. after burning, they increased significantly in the second post-burn season. The difference may have been due to the low visual obstruction on burned plots in the first post-burn season. By the second post-burn season, wrens abundance increased on burned areas where vegetation resembled control plots. Herkert (1994) noted that Sedge Wrens (*Cistothorus platensis*) were never encountered on transects in recently burned grassland in the first year post-burn, but were sighted again after 2 or more post-burn seasons.

Sparrows tended to frequent burn areas when we surveyed 6–10 months as well as 18–22 months after the burns. Recently burned areas were more open and presented more bare ground than controls. Herkert (1994) also showed that sparrows (e.g., Grasshopper Sparrow [*Ammodramus savannarum*], Savannah Sparrow [*Passerculus sandwichensis*]) were more common on recently burned areas and then decreased in numbers following

Table 4. Spring abundance (no./40 ha) of resident birds on 2 control (C), summer burn (S), and winter burn (W) plots surveyed 6 to 10 months and 18–22 month after burning at Matagorda Island National Wildlife Refuge and State Natural Area, Texas, 1 March to 31 May 1993 and 1994.

Families/ subfamilies	Bird Abundance								
	6-10 months			18-22 months			P ^b		
	Plot ^a			Plot					
	C	S	W	C	S	W	T	Y	I
	----- (no./40ha) -----								
Anatidae	18.6	6.0	9.8	6.6	1.9	0.4	0.37	0.15	0.79
Ardeidae	0.9	3.3	0.0	1.4	0.4	0.0	0.41	0.46	0.43
Rallidae	1.6	1.5	0.1	0.4	0.2	0.1	0.24	0.11	0.40
Scolopacidae	2.2	1.3	3.5	2.5	0.3	0.6	0.25	0.14	0.22
Caprimulgidae	0.2	2.0	0.2	0.0	0.2	0.6	0.52	0.51	0.83
Hirundinidae	0.5	0.1	1.8	0.0	0.0	0.1	0.49	0.30	0.55
Troglodytidae	28.2	3.1	0.9	21.7	14.8	15.1	0.01	0.08	0.04
Icteridae	23.3	52.9	34.4	23.0	28.5	26.8	0.08	0.07	0.18
Fringillidae	0.3	0.1	0.5	1.3	2.9	3.8	0.76	0.20	0.80
Emberizinae	2.9	18.9	11.0	6.5	15.6	16.7	0.01	0.25	0.16

^a $n = 12\text{--}16$ survey points per plot, 12 visits per plot.

^bT = treatment effect, Y = time after burn effect, I = interaction effect.

the second post-burn season. These species generally prefer low to medium height vegetation on their breeding grounds and our burn treatments may have provided sparrows with the appropriate vegetative structure for their foraging activities (Wiens 1969).

Our bird survey results should be interpreted cautiously because statistical power in our research was variable, ranging from 0.10 to 0.90 depending on family (Lipsey 1990). We found that the highest effect sizes came from resident bird families on Matagorda Island and lower effect sizes from migratory bird families. Other researchers (Moore and Kerlinger 1987, Moore et al. 1990, Moore and Simons 1992) reported large variation in bird numbers for bird species in migration. Moore et al.'s (1990) description of marsh/meadow habitat on Horn Island, Mississippi, was similar to the barrier flats on Matagorda Island. They noted that migratory bird species used marsh/meadow habitat less than others on Horn Island. Although we did not look at other habitats, migrant bird families seemed infrequent on the barrier flats of Matagorda Island and this infrequency may account for the low effect sizes. In our experience, migrant bird use of Matagorda Island can vary on an hourly basis; this makes powerful sampling very difficult to achieve.

Vegetation on Matagorda Island seems highly resilient to prescribed fire. This resiliency may be the result of a long growing season. Since vegetation attributes return quickly to pre-burn conditions, the impact of burning on bird abundance was weak by the second post-burn season and may decline further after 2 or more growing seasons. Wren abundance was negatively impacted by burning and sparrows were more abundant on burned areas. For groups of birds other than wrens, we suggest that prescribed burning be applied about once every 2 or more years since vegetation and bird abundance on the barrier flats returned to near pre-burn conditions by 18–22 months post-burn.

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Grass hay as a supplement for grazing cattle

I. Animal performance

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Abstract

Regrowth grass hay produced on subirrigated meadows in the Nebraska Sandhills was evaluated as a supplement for gestating beef cows grazing winter range. Ninety-six crossbred spring calving, gestating beef cows were used in a winter supplementation study on upland Sandhills range from 5 November to 27 February in 1990 and again in 1991. Cows were divided into 4 treatments (24 cows/treatment): 1) control (range forage only, no supplement); 2) range forage and 2.2 kg cow⁻¹ day⁻¹ of meadow regrowth hay (15.5% crude protein); 3) range forage and 1.2 kg cow⁻¹ day⁻¹ of a 30% wheat grain and 70% soybean meal:30% wheat supplement (36.0% crude protein); and 4) range forage with supplements in treatments 2 and 3 fed on alternate days. Meadow hay and soybean meal:wheat supplements provided 0.32 kg of crude protein/cow daily. Supplemented cows gained 3 to 53 kg body weight/year and maintained body condition, while control cows lost an average of 24.5 kg body weight/year and lost body condition. Intake of range forage was less ($P < 0.05$) by cows fed meadow hay and soybean meal:wheat supplements on alternate days than by cows on other treatments. Digestibility of range forage was lower ($P < 0.05$) for supplemented cows than control cows, but differences were small (avg. = 2%). Calving date, birth and weaning weights, and pregnancy rate were similar ($P > 0.05$) for all treatments. We concluded that subirrigated meadow regrowth grass hay was an effective alternative to traditional soybean meal-based supplements for maintaining body weight and body condition of gestating beef cows grazing winter range.

Key Words: subirrigated meadow, intake, digestibility, body condition

Rasby (1990) reported that feed costs were the greatest and most variable costs in the production of a calf by Nebraska beef producers. Grazing rather than feeding hay during winter decreases feed costs and increases profitability of cow-calf operations (Adams et al. 1994). Cows should be in moderate body condition at calving if they are to breed early in a controlled breeding season (Richards et al. 1986). Body condition at spring calving of cows wintered on range is influenced by body condition of the

cow the previous fall (Adams et al. 1987) and protein supplementation during winter grazing (Cochran et al. 1986a).

Protein supplements have traditionally been based on grain and protein concentrates. Alfalfa has been used effectively as an alternative to soybean meal-sorghum grain (DelCurto et al. 1990) or cottonseed meal-barley supplements (Cochran et al. 1986a) for maintaining body condition of cows grazing dormant forage. Little information is available on other forages as supplements for dormant forages on range. Nichols et al. (1990) demonstrated that high protein grass hay can be produced from subirrigated meadows in the Nebraska sandhills, and such hay might have potential as an alternative to traditional protein supplements. Hence, our objective was to evaluate the efficacy of grass hay produced from regrowth following hay harvest on subirrigated meadows as a supplement for gestating beef cows grazing sandhills winter range.

Materials and Methods

The study area was located on typical sandhills range at the University of Nebraska-Lincoln Gudmundsen Sandhills Laboratory near Whitman, Neb. The primary range site was sands, which was dominated by blue grama [*Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths], little bluestem [*Andropogon scoparius* (Michx.) Nash], prairie sandreed [*Calamovilfa longifolia* (Hook.) Scribn.], sand bluestem (*Andropogon hallii* Hack.), switchgrass [*Panicum virgatum* L.), and sand lovegrass [*Eragrostis trichodes* (Nutt.) Wood]. Common forbs and shrubs included western ragweed (*Ambrosia psilostachya* Dc.) and leadplant [*Amorpha canescens* (Nutt.) Pursh]. Standing forage on a similar nearby range site was 1,399 kg/ha and 1,419 kg/ha in August of 1990 and 1991, respectively (Northup 1993).

Ninety-six, 4-year-old crossbred gestating beef cows were used in a winter supplementation study from 5 November 1990 to 28 February 1991 and again from 5 November 1991 to 28 February 1992. Cows were 1/4 Hereford, 1/4 Angus, 1/4 Simmental and 1/4 Gelbvieh. In each year, cows were assigned randomly to 1 of 4 treatments (24 cows/treatment). Cows within each treatment were divided into 2 groups and each group was assigned randomly to graze in 1 of 8 different 36.5 ha paddocks (2 paddocks/treatment) that were similar in dimension and vegetation. Treatments were: 1) control (range forage only); 2) range forage plus 2.2 kg cow⁻¹ day⁻¹ in 1990 to 1991 and 2.0 kg cow⁻¹ day⁻¹ in 1991 to 1992 of meadow regrowth hay supplement (DM basis); 3) range forage plus 0.90 kg

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cow⁻¹ day⁻¹ of a 70% soybean meal:30% wheat grain supplement (DM basis); and 4) range forage with supplements in treatments 2 and 3 fed on alternate days. Supplements provided 0.31 to 0.43 kg of crude protein/cow daily.

The hay was subirrigated meadow regrowth harvested during late August of both years following a hay harvest and fertilization in June. Fertilizer applied consisted of 14.7 kg/ha nitrogen, 7.4 kg/ha phosphate, and 3.7 kg/ha sulfur. The subirrigated meadow soils were classified as Gannett-Loup fine sandy loam (course-loamy mixed mesic Typic Haplaquoll). Dominant meadow vegetation was smooth brome grass (*Bromus inermis* Leyss.), redtop (*Agrostis stolonifera* L.), timothy (*Phleum pratense* L.), slender wheatgrass [*Agropyron trachycaulum* (Link) Malte], quackgrass [*Agropyron repens* (L.) Beauv.], Kentucky bluegrass (*Poa pratensis* L.), prairie cordgrass (*Spartina pectinata* Link), and several species of sedges (*Carex* spp.) and rushes (*Juncus* spp.). Less abundant grass species were big bluestem (*Andropogon gerardii* Vitman), indian grass [*Sorghastrum nutans* (L.) Nash], and switchgrass. Forbs and legumes were a minor component of the standing vegetation.

Fall pregnancy rate and calf weaning weight were determined. From calving to weaning, study cows were integrated into a larger herd. Cows were fed meadow hay (approximately 8.0% CP) ad libitum from 1 March to 15 May and grazed sandhills range until weaning on 5 October. The breeding season was 55 days in length beginning 1 June of each year.

Individual cow body weight was recorded after 16 hours without feed or water on 7 November, 5 December, 3 January, 31 January, and 28 February during winters of 1990 to 1991 and 1991 to 1992. Individual cows were scored for body condition on 7 November, 3 January, and 28 February. Body condition scores were based on a palpated determination of fleshing over the ribs and thoracic vertebrae. Body condition was scored from 1 (thinnest) to 9 (fattest) according to the system described by Richards et al. (1986). Calves were weighed at birth and at weaning on 7 October. Pregnancy was determined by rectal palpation at weaning.

Voluntary forage intake by cows was determined 10 through 15 December 1990 and 5 through 10 February 1991 and again 11 through 16 December 1991 and 28 through 31 January 1992. Forage intake and digestibility were determined for 6 cows/treatment, consisting of 3 cows from each of the 2 paddocks assigned/treatment. Six days before and during the 6-day intake trials, these cows were moved to a common paddock similar in dimension and vegetation to treatment paddocks and were individually fed their assigned supplements on a daily basis. Each cow on the intake trial was dosed orally with an intraruminal continuous chromium (Cr) releasing device¹ 5 days before the 6-day fecal collection period. Three to 500 g of feces were obtained daily at about 0800 hours from each cow.

Four steers (avg weight = 250 kg) were assigned to control, meadow hay supplement, and soybean meal:wheat supplement treatments during 1990 to 1991; and 5 steers were assigned to control and the meadow hay supplement treatment during 1991 to 1992. Steers were fitted with fecal collection bags for total collection and dosed with the same intraruminal continuous release Cr device as the cows to obtain a correction factor for fecal output

(Adams et al. 1991a, Hollingsworth et al. 1995). Feces contained in collection bags were weighed, mixed, subsampled (150 to 300 g), and emptied once daily at 0800 hours during the 6-day collection period.

Six esophageally-fistulated cows (avg. body weight = 400 kg) were used to obtain diet samples. Diets were collected on 2 days within each 6-day fecal collection period, 10 and 14 December 1990, 6 and 8 February 1991, 11 and 15 December 1991, and 28 and 30 January 1992. After an overnight fast, cows were fitted with screen bottom canvas collection bags. Forage samples were collected from the esophagus during a 30- to 45-min grazing period and composited for the 2-day collections for each cow within each 6-day fecal collection period. All fecal and extrusa samples were frozen and stored for subsequent chemical analyses.

In vivo dry matter digestibility of the meadow hay supplement was determined for hay harvested in August 1990 and August 1991 in a replicated 2 × 2 Latin square with 4 steers (avg body weight = 411 kg) by standard methods (Schneider and Platt 1975) in 1992. Steers were fitted with fecal collection bags and harnesses for a 7-day adaptation period followed by a 6-day measurement period. Fecal bags were weighed, mixed, subsampled, and emptied twice daily at 0800 and 2000 hours. Digestibility of soybean meal:wheat supplement was estimated by in vitro digestibility (Tilley and Terry 1963).

Extrusa and fecal samples were freeze dried and ground to pass a 1-mm screen in a Wiley mill. Dry matter and crude protein (CP) of extrusa and supplements were determined by standard methods (AOAC 1990), neutral detergent fiber (NDF) was determined according to Van Soest et al. (1991), and acid detergent fiber (ADF) was determined by the method of Van Soest (1963). Diet indigestible ADF was determined on meadow hay supplement, soybean meal:wheat supplement, esophageal extrusa, and fecal samples as described by Cochran et al. (1986b). Fecal samples were analyzed for Cr concentration by atomic absorption spectrophotometry using an air-plus-acetylene flame (Williams et al. 1962).

Fecal output, forage intake, and total intake (e.g., range forage + supplement) were calculated according to Kartchner (1980) using indigestible ADF as the internal marker and Cr as the external marker. For the December 1990 and February 1991 intake trials, fecal output of cows was corrected using a 0.77 adjustment factor, obtained from the Cr recovery estimates derived by total collection from steers. During December 1991 and January 1992 intake trials, fecal outputs estimated from the Cr-continuous release device and total fecal collections in the steers did not differ ($P > 0.05$); hence, no correction was made on cow fecal output estimates. Digestibility of supplements and amount of supplement fed were used to determine supplement contribution to fecal output. Fecal output attributed to supplements was subtracted from total fecal output so that intake and digestibility of the range forage could be estimated.

Chemical composition of diets was analyzed with a one-way analysis of variance (SAS 1990). In vivo dry matter digestibility of the meadow hay supplement for both years was analyzed as a 2 × 2 replicated Latin square with steer, period, and treatment in the model (Steel and Torrie 1980).

Range forage and total dry matter intake (range forage + supplement), and range forage and total dry matter digestibility were analyzed with the GLM procedure of SAS (1990). The model included treatment, year, collection period, treatment × year, treatment × year × collection period, and paddock (treatment ×

¹Captec Chrome manufactured by Captec Pty. Ltd., Australia, distributed internationally by Nufarm Limited, Manu Street, P.O. Box 22-407, Otahunu, Auckland 6, New Zealand.

Table 1. Chemical composition of range diets, protein supplements, meadow hay in vivo digestibility, and in vitro digestibility of the soybean meal:wheat supplement.

Item ¹	Native range				Meadow hay		Soybean meal:wheat supplement	
	Collection period							
	Dec. 1990	Feb. 1991	Dec. 1991	Jan. 1992	1990	1991	1990	1991
CP, %	4.3 ^b	6.4 ^a	5.0 ^b	4.8 ^b	15.1	15.5	36.0	36.0
NDF, %	76.3 ^c	74.1 ^c	78.9 ^a	81.2 ^a	73.5	69.1	----	----
ADF, %	53.8 ^a	54.3 ^a	51.1 ^b	51.4 ^b	37.4	35.9	----	----
Digestibility ² , %	----	----	----	----	61.8	59.8	84.6	83.0

¹Percent of dry matter, CP = crude protein, NDF = neutral detergent fiber, ADF = acid detergent fiber.

²Meadow hay in vivo DM digestibility and soybean meal:wheat supplement in vitro DM digestibility.

^{a,b,c}Means within a row with different superscripts are different ($P < 0.05$).

year). Cow was the experimental unit and cow (paddock treatment \times collection period \times year) was used as the error term. Body weight, body condition score, calving date, and birth and weaning weights were analyzed using a model including treatment, year, treatment \times year, paddock (treatment \times year). Paddock was the experimental unit and cow (paddock \times year \times treatment) was used as the error term. Treatment sums of squares were partitioned by orthogonal contrasts. Orthogonal contrasts were: 1) control vs all supplement treatments; 2) hay + soybean meal:wheat supplements vs hay and soybean meal:wheat supplements on alternating days; and 3) soybean meal:wheat supplement vs hay supplement (Steel and Torrie 1980). Pregnancy rates were transformed to a logit (Cox 1970) before analysis.

Results and Discussion

A year \times collection period interaction occurred ($P < 0.05$) for crude protein, ADF, and NDF; therefore, means are reported on a within-year basis. Chemical composition of esophageal extrusa varied between collection dates ($P < 0.05$) in crude protein, NDF,

and ADF (Table 1); but values were within the range reported by Powell et al. (1982) and Yates et al. (1982) for dormant range in Nebraska. In vivo digestibility of meadow hay supplement averaged 61.8% in 1990 to 1991 and 59.8% in 1991 to 1992 and in vitro digestibility of the soybean meal:wheat supplement averaged 84.6% for 1990 to 1991 and 83.0% for 1991 to 1992.

Body weight. Cows on all supplement treatments maintained or gained body weight, and control cows lost body weight during both winters (Table 2). A year effect ($P < 0.05$) was observed only for the beginning body weight (7 November). Body weight on 7 November and 5 December were similar ($P > 0.05$) for all treatments. A year \times treatment interaction was detected for the 3 January body weight ($P < 0.05$). Body weight on 3 January was lowest for the meadow hay treatment in 1990 to 1991 and greatest in 1991 to 1992 compared with the other supplement treatments. On 3 January and 31 January, supplemented cows were heavier ($P < 0.05$) than control cows. Final body weight on 28 February was greater for the 3 supplement treatments in both years. Cows fed the meadow hay supplement were heavier than cows fed soybean meal:wheat at the final body weight on 28 February 1991 to 1992. In both winters, body weight gains over

Table 2. Body weight (kg) and body weight gain of gestating beef cows grazing native range without supplement, supplemented with meadow hay, soybean meal:wheat supplement, or meadow hay and soybean meal:wheat supplement fed on alternate days during winters of 1990 to 1991 and 1991 to 1992.

Item	1990 to 1991				SE	Contrast ²	1991 to 1992				SE	Contrast ²
	C	H	S	SH			C	H	S	SH		
	kg						kg					
7 Nov., beginning weight	506	503	492	502	9.08	NS ³	520	531	521	525	9.08	NS
5 Dec., 28 day	524	529	525	535	9.03	NS	506	543	531	535	9.03	NS
3 Jan., 56 day ⁴	519	533	535	545	8.91	NS	480	559	539	554	8.91	1
31 Jan., 84 day	504	540	537	554	9.02	1	492	566	543	556	9.02	1
28 Feb., 112 day, final weight	495	544	542	555	8.93	1	482	564	524	554	8.93	1,3
Body weight gain over 112 days	-11	41	50	53		1,3	-38	33	3	29		1,2,3

¹C = control, H = meadow hay supplement, S = soybean meal:wheat supplement, and SH = soybean meal:wheat supplement + meadow hay supplement fed on alternate days.

²Orthogonal contrast ($P < 0.05$), Contrast 1 = C vs [(S + H + SH)/3]; 2 = [(H + S)/2] vs SH, 3 = H vs S.

³NS = not significant ($P > 0.05$).

⁴A treatment \times year interaction occurred ($P < 0.05$) for 3 Jan. body weight.

Table 3. Body condition score and change in body condition score of gestating beef cows grazing native range without supplement, supplemented with meadow hay, soybean meal:wheat supplement, or meadow hay and soybean meal:wheat supplement fed on alternate days during winters of 1990 to 1991 and 1991 to 1992.

Item	1990 to 1991				SE	Contrast ²	1991 to 1992				SE	Contrast ²
	C ¹	H	S	SH			C	H	S	SH		
7 Nov., beginning body condition score	5.9	5.7	5.9	5.6	.12	NS ³	5.4	5.5	5.4	5.4	.12	NS
3 Jan. 56 day ⁴	5.5	5.6	5.9	5.6	.12	NS	4.7	5.7	5.5	5.5	.12	1
28 Feb., Final body condition score ⁴	4.7	5.7	6.1	5.7	.13	1,3	4.2	5.7	5.3	5.5	.13	1
Change in - body condition score over 112-day trial	-1.2	.0	.2	.1	.09	1	-1.2	.2	-.1	-.1	.09	1

¹C = control, H = meadow hay supplement, S = soybean meal:wheat supplement, and SH = soybean meal:wheat supplement + meadow hay supplement fed on alternate days, SE = standard error.

²Significant orthogonal contrast $P < 0.05$, Contrast 1 = C vs [(S + H + SH)/3]; 2 = [(H + S)/2] vs SH; 3 = H vs S.

³NS = Nonsignificant ($P > 0.05$).

⁴Significant year \times treatment interaction, $P < 0.05$.

the 112-day grazing period were greater ($P < 0.05$) for supplemented cows vs control cows and for cows receiving meadow hay and soybean meal:wheat supplements on alternate days vs the average of cows receiving meadow hay or soybean meal:wheat supplements. In 1991 to 1992, gains over the 112-day period were greater ($P < 0.05$) for cows on the meadow hay treatment vs the soybean meal:wheat treatment.

Studies on the use of forages as supplements for cattle grazing dormant winter range forage have been mostly limited to alfalfa hay. Response of cow weight gain has been similar for alfalfa hay compared to cottonseed meal—or soybean meal—based supplements in other winter range grazing studies (Cochran et al. 1986a, DelCurto et al. 1990).

Body condition score. Cows on all supplement treatments maintained body condition; whereas, control cows lost body condition during both winters. Body condition scores at the beginning of the trial varied between 1990 and 1991 ($P < 0.05$) but were similar ($P > 0.05$) for cows in all treatments (Table 3). A year \times treatment interaction occurred for the 3 January (day 56) body condition score. The 3 January body condition score was not different ($P > 0.05$) for control vs supplement treatments in 1990 to 1991, but in 1991 to 1992 body condition of control cows was lower ($P < 0.05$) than the average of supplemented cows. The 3 January body condition score was similar ($P > 0.05$) for all supplement treatments in both winters.

A year \times treatment interaction occurred for 28 February final body condition score. During 1990 to 1991, cows receiving the meadow hay supplement were 0.37 body condition score lower ($P < 0.05$) than cows receiving the soybean meal:wheat supplement. In 1991 to 1992, no differences ($P > 0.05$) occurred between supplement treatments. Final body condition score on 28 February was 1.14 and 1.30 units less ($P < 0.05$) for control cows than the average of cows receiving the 3 supplement treatments in 1990 to 1991 and 1991 to 1992, respectively.

Body condition score is more closely related to reproduction than body weight in beef cattle (Dziuk and Bellows 1983). Cows in low body condition score (e.g., < 4) at calving may breed later or fewer will breed during a controlled breeding season than

cows in higher body condition (e.g., > 5), especially if the cow loses body condition score between calving and the beginning of the breeding season (Richards et al. 1986).

Protein supplement helped the cows maintain body condition during winter grazing, but it did not increase body condition scores above those recorded at the beginning of the trial. This is in agreement with studies by Adams et al. (1991b). Body condition scores of cows in the fall or at the beginning of winter grazing should be taken into consideration when determining if a protein supplement should be fed during winter grazing. With or without protein supplement, thin cows or cows with a low body condition score are likely to stay thin during winter grazing (Adams et al. 1991b, Adams et al. 1987).

Dry matter intake and digestibility. Intake (kg/100 kg of body weight) was affected ($P < 0.05$) by treatment, year, and collection period within year (Table 4) but all interactions were nonsignificant ($P > 0.05$). Intake of range forage and total intake (i.e., range forage + supplement) were similar ($P > 0.05$) for the control vs all

Table 4. Forage and total dry matter intake and digestibility by gestating beef cows grazing native range without supplement, supplemented with meadow hay, soybean meal:wheat supplement, or meadow hay and soybean meal:wheat supplement fed on alternate days.

	Treatment ¹					
Intake	C	H	S	SH	SE ²	Contrast ³
	----- Intake, kg/100 kg of body weight -----					
Range forage	2.07	1.82	2.09	1.64	.11	2
Total	2.07	2.19	2.29	1.91	.11	2
	----- Digestibility, % of dry matter -----					
Range forage	60.48	58.8	59.1	59.7	.39	1
Total	60.48	59.2	61.5	61.1	.37	3

¹C = control, H = meadow hay supplement, S = soybean meal:wheat supplement, and SH = soybean meal:wheat supplement + meadow hay supplement fed on alternate days. All year and year \times treatment effects were not significant ($P > 0.05$).

²SE = Standard error.

³Significant orthogonal contrasts ($P < 0.05$); 1 = C vs [(S + H + SH)/3]; 2 = [(H + S)/2] vs SH; 3 = H vs S.

Table 5. Reproductive performance of cows and birth and weaning weight of calves.

Item	Year (winter)								Contrast
	1990 to 1991				1991 to 1992				
	Treatment ¹								
	C	H	S	SH	C	H	S	SH	
Pregnancy rate, %	96	94	96	98	95	93	95	97	NS
Calving date, Julian	91	91	87	92	91	84	86	90	NS
Birth weight, kg	42	43	41	43	40	42	43	39	NS
Weaning weight, kg	250	252	242	260	251	260	261	248	NS

¹C = control, H = meadow hay, S = protein supplement, and SH = protein supplement + meadow hay fed on alternate days.

²NS = Nonsignificant $P > 0.05$.

supplement treatments and for meadow hay supplement vs soybean meal:wheat supplement. Intake of range forage and total intake were greater ($P < 0.05$) by the average of cows supplemented with meadow hay or soybean meal:wheat than by cows fed meadow hay and soybean meal:wheat supplements on alternate days.

Digestibility of range forage was greater ($P < 0.05$) for the control vs the average of all supplements. Total digestibility was greater ($P < 0.05$) for the soybean meal:wheat supplement vs meadow hay supplement, reflecting the difference in digestibility between the forage and concentrate supplement (Table 1). Digestibility of the range forage was relatively high compared to values reported for sandhills range forage (Rittenhouse et al. 1970), but was similar to other values reported for winter range (Powell et al. 1982, Ward et al. 1990).

Results of research evaluating effects of protein supplement on intake and digestibility of winter range forage have been inconsistent. Digestibility and/or intake has increased in response to some supplementation studies but not in others (Rittenhouse et al. 1970, Kartchner 1980, Caton et al. 1988, Ward et al. 1990). Inconsistency of associative effects of protein supplementation on intake and digestibility is related to crude protein content in the diet, forage availability (Hafley 1990), and harsh weather (Adams et al. 1986).

Control cows lost body weight and body condition score during both years despite similarity in total intake and digestibility compared with supplemented cows. This difference is best explained by the additional protein consumed in the supplements meeting protein requirements of the cow that were not met by the range forage (Judkins et al. 1987). Villalobos (1993) fed steers a basal diet of prairie hay at 1.5% of body weight and replaced the prairie hay with increasing amounts of meadow hay supplement (same meadow hay as used in this study) from 0 to 40% of the dry matter consumed. Dry matter intake was constant for all levels of prairie hay and meadow hay supplement, but nitrogen intake and nitrogen flowing to the duodenum increased linearly with additions of meadow hay supplement. Improved livestock performance in response to increased duodenal protein supply may occur as a result of correction of a protein/energy imbalance in absorbed nutrients (Egan 1977), correction of an amino acid deficiency, increased availability of glycogenic substrates (Egan 1965, Annisson and Armstrong 1970), and improved efficiency of metabolizable energy utilization (McCullum and Horn 1990).

Reproduction, birth, and weaning weight. Fall pregnancy rate following the winter supplement trials was 95.5% with all treatment, year, and interactions nonsignificant ($P > 0.05$; Table 5). Seemingly, loss of cow body condition score during winter graz-

ing was not great enough to affect pregnancy rate. During more severe winter weather, loss of body condition might be greater and thereby negatively impact pregnancy rate.

In our study, there were no differences ($P > 0.05$) in calving date (avg Julian day = 89), birth weight (avg = 41.6 kg), or weaning weight (avg = 253 kg), and all treatment, year, and interaction effects were nonsignificant ($P > 0.05$). Bolze and Corah (1988) and Sanson et al. (1990) reported similar responses.

Implications

Regrowth grass hay from a subirrigated meadow hay was an effective alternative to traditional soybean meal-based protein supplements for maintaining body weight and body condition score of gestating beef cows grazing native winter range. Supplements did not affect pregnancy rate or weaning weight. If cows begin winter grazing with a body condition score > 5.5 , protein supplementation may not affect economic traits such as weaning weight and pregnancy rate in years with mild winters. During harsh winters (snow and cold temperatures) or if cows begin winter in a body condition score < 5.5 , the effects of protein supplementation on economic traits may be different than in mild winters.

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Grass hay as a supplement for grazing cattle

II. Ruminant digesta kinetics

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Abstract

This study evaluated the effects of supplementing a diet of range hay (5.7% crude protein, 68% NDF) with grass hay from subirrigated meadows (16.5% crude protein, 53.5% NDF), or with a 70% soybean meal:30% wheat grain supplement (40% crude protein) on intake and ruminal digesta kinetics. Twelve ruminally fistulated steers were assigned to 3 treatments (4 steers/treatment) at 2 levels of intake. Treatments were: 1) control, range hay; 2) range hay supplemented with meadow hay (meadow hay was 20% of intake); and 3) range hay supplemented with soybean meal:wheat supplement (supplement was 8% of intake). Intake levels were: 1) ad libitum and 2) equal intake (1.5% of body weight). Range hay was Yb-labeled, and meadow hay and soybean meal:wheat supplements were Er-labeled to measure passage. Intake and digestibility of range hay was not affected by supplementation ($P > 0.05$). During ad libitum intake, total intake (range hay + supplement) was greater ($P < 0.05$) for supplement treatments than for the control. No supplement treatment \times level of intake interactions were detected ($P > 0.05$). Total digestibility (range hay + supplement) was greater ($P < 0.01$) for the soybean meal:wheat treatment than for the control or meadow hay treatments. Total digestibility was similar ($P > 0.05$) for control and meadow hay treatments. Ruminal passage rate (% hour⁻¹), total tract mean retention time, and intestinal transit time of range hay did not differ among treatments ($P > 0.05$), but ruminal passage rate, total tract mean retention time, and intestinal transit time were greater ($P < 0.01$) with ad libitum than equal intake. We conclude that a meadow hay supplement produced similar effects on ruminal kinetics and intake of range hay as a soybean meal:wheat supplement.

Key Words: subirrigated meadow, intake, digestibility, passage rate

Protein supplementation of cattle grazing dormant rangelands is a common practice that improves body weight gains by growing animals (Clanton 1982) and maintains body weight and body condition of cows on winter range (Villalobos et al. 1997).

Forage supplements have been fed as winter protein supplements for gestating beef cows grazing on range (Cochran et al. 1986, Villalobos et al. 1997), and 15% crude protein hay was an effective supplement for maintaining body condition of gestating beef cows grazing winter native range (Villalobos et al. 1997).

Gut fill may limit intake of forage diets (Campling 1970), and increased voluntary intake of low-quality forages with supplementation is believed to result from increased rate of digestion and/or passage (Ellis 1978). Forage intake and/or digestibility are sometimes increased as a result of protein supplementation, but results are not conclusive (Rittenhouse et al. 1970, Kartchner 1980, Ward et al. 1990). Greater intake and/or digestibility of range forage could improve animal performance. However, there is evidence that improved livestock performance with protein supplementation may result from meeting protein requirements without changes in forage intake or digestibility (Judkins et al. 1987, Freeman et al. 1992, Villalobos 1993).

Our objective was to evaluate the effects of supplementing a basal diet of native range hay with high-quality meadow hay or a soybean meal-based supplement on nutrient status. Measurements included forage intake, forage digestibility, and ruminal digesta kinetics.

Materials and Methods

Treatments and feeding. Twelve crossbred steers (avg. body weight = 431 kg) fitted with 10.2-cm ruminal cannulas were used. Steers were fistulated and housed under conditions described in animal use protocols approved by the Institutional Animal Care and Use Committee at the University of Nebraska-Lincoln. Steers were assigned to 3 treatments (4 steers/treatment). Treatments were: 1) control, native range hay only; 2) native range hay supplemented with meadow regrowth grass hay (supplement was 20% of dry matter intake); and 3) native range hay supplemented with a 70% soybean meal:30% wheat grain supplement (supplement was 8% of dry matter intake). There were 2 feeding periods: ad libitum and equal intake. During the ad libitum period, native range hay and supplement intake were adjusted daily to assure continual access to range hay and supplements; whereas, during the equal intake period, total dry matter (e.g.,

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range hay + supplement) intake was maintained at 1.5 kg/100 kg body weight. Range hay and supplements were fed in separate feed containers so that orts could account for hay and supplement. Periods were 15 days with 7 days for adaptation and 8 days for collection. Steers were housed in a 25° C temperature-controlled environment in 1.78 m × 2.13 m individual stalls. Periods were confounded with intake level, but effects were expected to be negligible because of the controlled environment. Forage was chopped and fed twice daily at 0800 and 2000 hours. Steers had free access to water and trace mineral salt blocks. Trace mineral blocks were 93% to 98% salt, 0.35% zinc, 0.28% manganese, 0.175% iron, 0.035% copper, 0.007% iodine, and 0.007% cobalt. Native range hay intake was measured during the first 7 days of collection, and hay refusals were collected daily.

Upland range hay was harvested at the Gudmundsen Sandhills Laboratory near Whitman, Nebraska during mid-October 1990. Major species were blue grama [*Bouteloua gracilis* (H.B.K.) Lag ex Griffiths], little bluestem [*Andropogon scoparius* (Michx.) Nash], prairie sandreed [*Calamovilfa longifolia* (Hook.) Scribn.], sand bluestem [*Andropogon hallii* Hack.], switchgrass [*Panicum virgatum* L.], sand lovegrass [*Eragrostis trichodes* (Nutt.) Wood], and ragweed [*Ambrosia psilostachya* Dc.).

Grass hay for supplement was subirrigated meadow regrowth harvested during late August 1990 following an initial harvest and fertilization in June. Harvest procedures and species composition of regrowth hay from subirrigated meadows are described in a companion study (Villalobos et al. 1997). Chemical composition of range hay, soybean meal:wheat supplement, and meadow hay supplement is given in Table 1.

Table 1. Chemical composition of native range hay, meadow hay supplement, and soybean meal:wheat supplement fed to steers.

Item	CP ^a	NDF	ADF	IVDMD
	----- (% of dry matter) -----			
Native range hay	5.7	79.0	52.5	53.9
Meadow hay supplement	16.5	73.0	40.2	61.8 ^b
Soybean meal:wheat supplement	40.0	---	---	85.7

^aCP = crude protein, NDF = neutral detergent fiber, ADF = acid detergent fiber, IVDMD = in vitro dry matter digestibility.

^bEstimated in vivo.

Particulate passage estimates. To account for physical factors and moistening effects of saliva (Krysl et al. 1987), 3 steers were selected randomly and their rumens were evacuated by hand. After evacuation, steers were allowed to consume native range hay until an adequate amount of forage to be labeled was obtained. Forage boluses were removed from the rumen and dried in a forced-air oven (50° C). The same evacuation and sampling procedure was followed for the subirrigated meadow hay using 3 different steers.

After drying, the masticated native range hay sample was labeled with Yb using modified procedures described by Teeter et al. (1984). Masticate samples were washed to remove salivary contaminants and soaked for 24 hours in a 12.4 mM aqueous solution of Yb acetate. After soaking, excess fluid was poured off and the remaining sample was soaked in 100 mM acetic acid solution for 5 to 6 hours with occasional stirring. The sample was then washed with slowly flowing tap water overnight in a plastic tub covered with several layers of cheese cloth and then squeezed

dry. It was then soaked again in 100 mM acetic acid solution for 5 to 6 hours with occasional stirring, squeezed dry, spread on trays, and dried in a forced-air oven at 50° C.

Subirrigated meadow hay supplement and soybean meal:wheat supplement were labeled with Er following the same procedure as described for Yb using 35 mM aqueous solutions of Er acetate. Labeled forages and supplements were divided into equal portions with 1 aliquot/treatment for Yb and Er dose determinations. On day 1 of the collection phase in both the ad libitum and equal intake periods, steers were pulse-dosed with labeled range forage and their assigned supplement administered intraruminally at 0800 before feeding. The dose was placed in the mid dorsal region of the rumen (Krysl et al. 1987). Marker doses were 150 g of range hay containing 0.23 g of Yb, 100 g of meadow hay containing 0.35 g Er, and 100 g of soybean meal:wheat supplement containing 0.42 g Er. Rectal grab samples were collected at 0, 8, 12, 16, 20, 24, 28, 32, 36, 42, 48, 54, 60, 72, 84, 96, 108, 120, 132, and 144 hours after dosing. Fecal samples were stored frozen (-40° C).

Laboratory analyses. Forage, orts, and fecal samples were dried in a forced-air oven (50° C) and ground in a Wiley mill to pass a 1-mm screen. These samples were analyzed for dry matter (AOAC 1984), NDF (Van Soest et al. 1991), and ADF (Van Soest 1963). Dry matter digestibility of the soybean meal:wheat supplement was estimated using the Tilley and Terry (1963) 2-stage technique (48 hour rumen fluid, 48 hour pepsin digestion on 0.5-g samples in duplicate). Dry matter digestibility of meadow hay supplement was estimated by in vivo digestion performed in a companion study (Villalobos et al. 1997). Apparent total dry matter digestibility (forage plus supplement) was calculated (Schneider and Flatt 1975) using the equation: [(dry matter consumption - dry matter fecal output)/(dry matter consumption)] × 100, where dry matter fecal output was estimated from Yb (Pond et al. 1987). Digestibility of range hay by steers fed meadow hay supplement and soybean meal:wheat supplement was calculated by subtracting the contribution of the supplement from the dry matter intake and feces and calculating digestibility from adjusted dry matter intake and fecal output. We assumed no associative effects of range hay on digestibility of supplements.

Labeled forages and supplement aliquots and fecal samples were prepared for analysis (Karimi et al. 1986) adding 15 ml of 0.01 M DTPA (Diethylenetriaminepentaacetic acid) to 0.2 g of sample in a 20 ml screw cap tube. Tubes were rotated 40 min., centrifuged at 500 × g for 15 min.. Supernatant fluid was filtered (Whatman #4 filter paper, Whatman, Maidstone, UK) into vials for analysis by atomic absorption spectroscopy with a nitrous oxide plus acetylene flame.

Calculations and statistical analyses. Fecal Yb and Er excretion curves were analyzed by nonlinear regression procedures (Marquardt method) of the Statistical Analysis System (SAS 1990) using a 1-compartment model (Pond et al. 1987).

Data were analyzed as a split plot with supplement treatment in the whole plot and intake level and supplement treatment × intake level in the subplot. Steer (supplement treatment) was the whole plot error term and steer (supplement treatment × intake level) was the error term for the subplot (Steel and Torrie 1980) using the GLM procedure (SAS 1990).

Results and Discussion

During ad libitum and equal intake feeding periods, dry matter intake of range hay was similar ($P > 0.05$) for all treatments. The supplement treatment by level of intake interaction effect was significant for total dry matter intake ($P < 0.05$). During ad libitum intake, dry matter intake of range hay was not different ($P > 0.05$) among treatments (Table 2). During ad libitum intake, total dry matter intake (range hay + supplement) was greater ($P < 0.05$) for meadow hay and soybean meal:wheat supplement treatments than for the control. Total dry matter intake was similar ($P > 0.05$) for meadow hay and soybean meal:wheat supplement treatments. The difference in total dry matter intake between the control and supplement treatments resulted from addition of supplement and not from an associative effect of supplements on intake of range hay. Similar results were noted by Judkins et al. (1987). During equal intake, total intake was similar ($P > 0.05$) for all treatments.

Table 2. Range hay and total dry matter intake (e.g., forage + supplement) and total dry matter digestibility in steers fed native range hay, range hay supplemented with meadow hay, and range hay supplemented with soybean meal:wheat supplement.

	Range hay	Range hay + meadow hay	Range hay + Soybean meal:wheat	SE ^a
Range hay intake, kg/100 kg of body weight	1.37	1.31	1.46	.06
Total intake, kg/100 kg of body weight ^b				
Ad libitum intake	1.37 ^c	1.69 ^d	1.59 ^d	0.04
Equal intake	1.44	1.51	1.45	0.04
Range hay digestibility, %	53.9 ^{cd}	52.6 ^d	56.1 ^c	1.3
Total digestibility, %	53.9 ^e	54.7 ^e	58.5 ^f	1.17

^aSE = Standard error.

^bSupplement treatment \times level of intake interaction was significant ($P < 0.05$).

^{c,d}Means in the same row with different superscripts differ ($P < 0.05$).

^{e,f}Means in the same row with different superscripts differ ($P < 0.01$).

Arthun et al. (1992) fed blue grama hay (7.6% crude protein) or barley straw (3.5% crude protein) ad libitum to steers with or without alfalfa hay at 23% or 42% of total diet, respectively. They found that when alfalfa hay was mixed with grass hay at 23% of diet, dry matter intake increased from 1.85 kg/100 kg of body weight for grass-only diets to 2.03 kg/100 kg of body weight for grass-plus-alfalfa diet. When alfalfa was mixed with barley straw at 42% of the diet, dry matter intake increased from 1.16 kg/100 kg of body weight for straw only to 1.71 kg/100 kg of body weight for straw plus alfalfa hay. Results of our study are intermediate to these numbers. Total dry matter intakes were lower in a companion study (Villalobos et al. 1997) in which the same supplements were fed to cows grazing winter range.

Results of protein supplementation on voluntary forage intake have been contradictory. Supplements have had only a small influence on intake and/or digestibility of grazed diets when crude protein content of extrusa samples was 6.3 to 8.5% (Rittenhouse et al. 1970, Kartchner 1980). Effects of supplemental protein on forage digestibility and intake appeared to be greater during periods of harsh winter weather (Kartchner 1980).

Total dry matter digestibility was not affected ($P > 0.05$) by intake level and no interactions were detected ($P > 0.05$). Total

dry matter digestibility was lower ($P < 0.01$) for range hay and range hay supplemented with meadow hay than for range hay with the soybean meal:wheat supplement (Table 2). Total dry matter digestibility was similar ($P > 0.05$) for range hay and range hay with meadow hay. Similar effects have been reported by Egan and Doyle (1985) in sheep fed a basal diet of chopped oaten hay (5.2% crude protein) at 90% of ad libitum intake and supplemented with either no supplement or urea infused into the rumen. Sanson et al. (1990) reported a difference in dry matter digestibility between control and protein-supplemented steers fed low-quality hay (4.3% crude protein).

Feeding a highly digestible supplement directly affects total dry matter digestibility. Digestibility of the range hay was greater when supplemented with the soybean meal:wheat supplement than when supplemented with meadow hay ($P < 0.05$; Table 2). Digestibility of the unsupplemented range hay was intermediate to the digestibility of range hay when supplemented with meadow hay and range hay supplemented with soybean meal:wheat.

Conrad et al. (1964) showed that at lower ration digestibility, voluntary intake was mostly related to animal ration digestibility and body weight. They proposed that over a range of lower ration digestibilities, voluntary intake was controlled by gut fill. Van Soest (1982) demonstrated a negative relationship between NDF intake or NDF diet content and forage intake. Native range hay and meadow hay supplement used in our study contained 79 and 73% NDF, respectively, values considered to limit intake (Arthun et al. 1992).

Ruminal particulate passage rate of range hay was faster ($P < 0.01$) for ad libitum than restricted intake. Total tract retention time and intestinal transit time were longer ($P < 0.01$) for restricted intake than ad libitum intake. All supplement treatment \times level of intake interaction effects for ruminal digesta passage rate, total tract retention time, and intestinal transit time were nonsignificant ($P > 0.05$). Ruminal particulate passage rate, total tract retention time, and intestinal transit time of native range hay were not

Table 3. Digesta kinetics of steers fed range hay, range hay with meadow hay supplement, and range hay with soybean meal:wheat supplement, ad libitum or restricted intake.

Item	Range hay ^a	SE ^b	Supplements ^c		SE
			Meadow hay	Soybean meal:wheat	
Digesta passage rate, %/hour				3.33 ^c 4.9 ^d	0
Ad libitum intake	3.52	0.12			
Restricted intake	2.94	0.12			
Total tract retention time, hour					
Ad libitum intake	52.4	1.32	53.7 ^c	43.6 ^d	1.36
Restricted intake	61.7	1.32	60.6 ^d	47.0 ^d	1.36
Intestinal transit time, hour					
Ad libitum intake	18.1	0.49	19.2	18.6	0.64
Restricted intake	20.4	0.49	22.7	21.8	0.64

^aFor range hay, intake effects (e.g., ad libitum vs. restricted intake) were significant ($P < 0.01$) for digesta passage rate, total tract retention time, and intestinal transit time; all supplement treatment and supplement treatment \times level of intake interactions were nonsignificant ($P > 0.05$); therefore, the avg range hay intake for the supplement treatments is reported.

^bSE = Standard error.

^cFor supplements, level of intake effects were significant ($P < 0.01$) for total tract retention time and intestinal transit time; level of intake effects were nonsignificant ($P > 0.05$) for digesta passage rate; all supplement treatment \times level of intake interactions were nonsignificant ($P > 0.05$).

^dMeans under supplement with different superscripts differ ($P < 0.01$); all other mean were nonsignificant ($P < 0.05$).

affected ($P > 0.05$) by supplementation (Table 3). Freeman et al. (1992) found no effects of protein supplementation on particulate passage rate and ruminal retention time of prairie hay fed at 1.5% of body weight. However, supplements lowered total tract retention time. Krysl et al. (1987) noted no effect of either soybean meal or steam-flaked milo on passage rate estimates in steers grazing mature blue grama compared to controls. Particulate passage rates obtained in this study concur with those of McCollum and Galyean (1985) and Krysl et al. (1987).

Ruminal particulate passage rate of meadow hay and soybean meal:wheat were not affected ($P > 0.05$) by level of intake (Table 3). Total tract retention time and intestinal transit time of meadow hay and soybean meal:wheat were shorter ($P < 0.01$) during ad libitum intake than restricted intake. Ruminal particulate passage rate and total tract retention time of the meadow hay supplement and soybean meal:wheat supplement (Table 3) were different ($P < 0.05$ and $P < 0.01$, respectively), and intake level effect and the treatment \times intake level interaction were nonsignificant ($P > 0.05$). Meadow hay supplement had a slower passage rate and longer total tract retention time than soybean meal:wheat supplement. Differences in passage rate and retention time are a result of differences in chemical composition and digestibility (Table 1) between forages and protein concentrate supplements (Van Soest 1982). Freeman et al. (1992) reported no differences in passage rate and ruminal retention time between a cottonseed meal and cottonseed meal-corn protein supplement in steers fed prairie hay.

Intestinal transit time was not different between meadow hay and soybean meal:wheat supplements ($P > 0.05$). Judkins et al. (1987) obtained similar results with steers grazing blue grama rangeland supplemented with either no supplement, ground pelleted alfalfa, or cottonseed cake.

Implications

Protein supplementation had minimal effects on forage intake and ruminal kinetics when the control forage had 5.7% CP. We conclude that steers fed either meadow hay or soybean meal:wheat supplement would have greater total dry matter intake and crude protein intake than steers fed only range hay. Grass regrowth may also appear to be an effective alternative to traditional soybean meal-based protein supplements for hay harvested from native range.

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Creating aversions to locoweed in naive and familiar cattle

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Abstract

The objective of this study was to determine if cattle that were familiar with white locoweed (*Oxytropis sericea* Nutt, ex T&G) could be aversively conditioned to avoid eating it. In the first preliminary trial, we tried to aversely condition native steers that were already eating locoweed. Six of 12 steers were penned, fed fresh-picked locoweed, then dosed via a stomach tube with lithium chloride (LiCl, 200mg/kg BW). When released into the locoweed-infested pasture, they gradually increased locoweed consumption over the next 5 days. The conditioning procedure was repeated with a lower dose (100 mg/kg BW), but locoweed consumption increased within 10 days until they were consuming as much as the non-averted controls. In the second trial, we compared the strength and longevity of aversion between steers that were familiar with locoweed ($n = 6$) and naive steers ($n = 6$). Both groups were averted to locoweed as described in Trial 1 and returned to locoweed-infested pasture. The Familiar group decreased locoweed consumption for the first 2 days, then gradually increased locoweed consumption and extinguished the aversion. The Naive group subsequently refused to graze locoweed. In the third trial, aversions were reinforced following grazing locoweed in the pasture. Three steers from the Familiar group were allowed to graze locoweed for 30 min. periods, then were returned to the pen and dosed with LiCl (100 mg/kg BW). These steers were kept in the pen and allowed to recover for 36 hours. This reinforcement process following grazing was repeated 4 times. Steers in the Reinforced group abstained from eating locoweed when released into the locoweed-infested pasture for the remainder of the trial. Reinforcement of aversions following field grazing of locoweed prevented cattle that were familiar with locoweed from grazing it.

Key Words: conditioned taste aversion, cattle grazing, poisonous plant, white locoweed, *Oxytropis sericea*

Livestock can be trained to avoid eating specific foods through conditioned taste aversion. Zahorik and Houpt (1977, 1990) first demonstrated that cattle, sheep, goats, and horses (Haupt and Zahorik 1990) form aversions to feeds paired with an emetic. Provenza (1995) developed principles of both aversive and positive conditioning in sheep. We have developed procedures to aversely condition cattle to avoid eating tall larkspur (*Delphinium*

barbeyi Nutt.) as a management tool to prevent poisoning (Olsen and Ralphs 1986, Lane et al. 1990, Ralphs and Olsen 1990, Ralphs and Cheney 1993).

Ranchers in locoweed areas (*Astragalus* and *Oxytropis* spp.) watch their cattle closely and remove those that start eating locoweed. If these cows could be aversively conditioned to avoid eating locoweed, they could be returned to the pastures without risk of further intoxication. However, it is difficult to create aversions to familiar foods.

Novelty of taste is important in creating food aversions because the first exposure presents the orienting response to the new taste (Nachman et al. 1977). If the novel taste is quickly followed with illness, a strong aversion is created to that food. If no harmful effects follow, the food is considered safe. If illness is subsequently paired with a safe food, conflicting messages are sent as to the value of the food. Memory retrieval is confused between a foods acceptance during non-reinforced exposure, and its pairing with illness during conditioning; thus the aversion is weakened. This phenomenon has been referred to as learned safety (Kalat and Rosin 1973), latent inhibition (Lublow 1973), learned familiarity (Best and Barker 1977), and learned non-correlation (Kalat 1977).

However, aversions can be formed to familiar foods, although it is more difficult. Kruz and Levitsky (1982) found that the aversion was strongest when a novel food was presented in a familiar environment, but a moderate aversion was created to a familiar food in a familiar environment. More pairings of the familiar taste with illness are required and the aversions extinguish faster (Fenwick et al. 1975).

The objective of this study was to determine if cattle that were familiar with white locoweed (*Oxytropis sericea* Nutt ex T&G) could be aversively conditioned to avoid eating it. Specific objectives were: 1) to verify the difficulty in creating an aversion to locoweed as a familiar food; 2) compare the strength and longevity of an aversion to locoweed in steers that were familiar with it compared to naive steers; and 3) determine if reinforcement under field grazing conditions can successfully maintain an aversion in steers that were familiar with locoweed.

Methods

The experiments were conducted in field grazing trials in Union County, N.M., 16 km south of Des Moines. The site was an old field that had reverted to short-grass prairie. Dominant

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species included bluegrama (*Bouteloua gracilis* (H.B.K.) Lag. ex Steudel), western wheatgrass (*Elymus smithii* (Rybd) Gould), squirreltail (*Elymus elymoides* (Raf.) Swezey), and white locoweed. Standing crop was clipped at the beginning of each trial to determine forage availability. Ten .25 × 1 m quadrats were systematically located at 20-step intervals along paced transects running through the middle of the pastures. Forage classes (warm-season grasses, cool-season grasses, broom snakeweed, locoweed, and other forbs) were clipped at ground level, dried at 60° C for 48 hours, and weighed.

Trial 1, Establishing Aversions in Steers Familiar with Locoweed

This was a preliminary trial in which we tried to aversively condition steers that were already eating locoweed. Twelve native steers (230 kg) had been grazing locoweed on the site for 20 days in a previous trial to determine the influence of over-wintering regimen on locoweed consumption (Ralphs et al. 1997). Locoweed averaged 30% of their diets; however, maximum locoweed consumption reached 75% of diets on some days. Steers were allocated to 2 treatment groups (Averted or Control) so that the same number of steers from the previous treatment groups were represented in each new group.

Steers in the Averted group (n=6) were penned and feed was withheld overnight. Fresh-picked locoweed was offered the next morning, and we observed that all steers readily consumed it. Steers were then restrained in a chute and dosed with lithium chloride (LiCl, 200 mg/kg BW) using a stomach tube. The regular morning feed was withheld so there was no interference between the induced illness and the taste of other feed. Sudangrass hay was fed in the evening, and for the next 3 days while the steers recovered. Fresh locoweed was offered in the morning and evening of the third and fourth day to test the aversion, but all steers refused it. They were then released into the locoweed-infested pasture. Two pastures (6.8 ha) were fenced with temporary electric fence and treatment groups were randomly allotted to separate pastures.

Diet composition was estimated by a bite count technique. Each steer was observed for 5-min. periods during the major grazing periods during the day (3–6 observations per day). The number of bites of each forage class was recorded (cool-season grass, warm-season grass, locoweed, and other forbs), and the percentage of each class was calculated on a daily basis. Percentage of bites of each forage class was analyzed by analysis of variance (ANOVA) in a split-plot design comparing groups over days of the trial. Differences between groups were tested by the animal (within group) factor, and the day and treatment × day interaction was tested by the residual error. Individual animals were the experimental units to which the aversion treatment was applied, and the individual response of each animal was measured in the pastures. The pastures were merely the area in which the response to aversions were expressed. The treatment groups were grazed in separate pastures to prevent the non-averted group from influencing the averted group to graze locoweed. We switched the groups between the pastures half way through the trial to minimize any pasture difference. Furthermore, we analyzed for differences in locoweed consumption between the pastures by ANOVA, using animals (within pastures) to test for differences between pastures.

Trial 2, Familiar vs Naive Steers

Twelve steers were obtained from the New Mexico State Univ. Clayton Livestock Research Center (large framed, mixed Continental and British crosses, 210 kg). These steers were new to the area and had never been exposed to locoweed. The steers were allotted randomly to 2 treatment groups (Familiar or Naive). The Familiar group was placed on locoweed-infested rangeland (6 ha) on 23 April, and allowed to graze locoweed for 16 days. Locoweed averaged 56% of the total bites. The Naive group grazed on locoweed-free range during this period at the Clayton Research Center (25 ha). Both groups were then averted to locoweed.

During aversion conditioning, both groups were penned at the study site, fasted overnight, and offered fresh-picked locoweed (15 kg) the next morning. The groups were mixed together so social facilitation helped induce the naive steers to eat locoweed. We observed all steers eating the locoweed. Steers were then restrained in a chute, dosed with LiCl (200 mg/kg BW), and allowed to recover for 3 days. They were fed sudangrass hay while in the pen. On the morning of the third day, the steers were offered locoweed to test the aversion. Four steers in the familiar group ate locoweed and were dosed with a lower dose of LiCl (100 mg/kg BW). The steers were offered locoweed the next day, which they refused, then were released into the locoweed-infested pasture.

Diets were quantified by bite count as described in Trial 1. The Naive and Familiar groups grazed in 2 adjacent pastures (3 ha each) for 6 days. Percentage of bites of each forage class was analyzed by ANOVA in a split-plot design comparing groups over the 6-day trial, as described in Trial 1. Individual steers were considered experimental units. However, the preconditioning treatments (Familiar or Naive to locoweed) were applied to the groups. The aversion treatment was applied to individual steers, and their individual response to the aversion was measured in the pastures as described above. The groups were switched to the other pasture half way through the trial to reduce potential differences in diet selection between pastures. Differences in diets between pastures were compared using a similar model.

Trial 3, Reinforcement of Aversion in the Pasture

The Familiar group gradually lost their aversion to locoweed in Trial 2. Steers in the Familiar group were systematically allocated into 2 subgroups. Three steers eating the most locoweed in Trial 2 were placed in the Reinforced group, whereas the 3 steers eating the least amount of locoweed remained in the Familiar group. The Familiar group returned to the pasture and served as a control to the Reinforced group. Steers in the Reinforced group were fasted overnight, then offered fresh locoweed, which they refused. They were then released into a small pasture (.5 ha) heavily infested with locoweed, and allowed to graze for 30 min. during which bite counts were recorded. All steers grazed large amounts of locoweed and were brought back to the pen and dosed with LiCl (100 mg/kg BW). They were allowed to recover for 36-hours, and the process was repeated for 4 cycles.

The Reinforced group was released into a larger 3 ha pasture and allowed to graze for the 8 day trial. Half way through the trial, steers from the Familiar and Reinforced groups were switched between pastures to reduce potential pasture differences. Five-minute bite counts were recorded and percentage of forage classes in diets were compared between groups by ANOVA in a split-plot design over days of the trial as described

in Trial 1. Differences in diets between pastures were also compared using a similar model.

Results

There was no difference in standing crop of forage classes between the pastures at the beginning of the trials (Table 1). Furthermore, there were no differences in locoweed consumption between pastures in any of the trials ($P > 0.05$).

Table 1. Standing crop of forage classes at the beginning of the trials.

Year Trial	Warm-season grass	Cool-season grass	Other forbs	Broom snake-weed	Locoweed	Total
(kg/ha \pm SE)						
1994 1	124 \pm 10	14 \pm 3	54 \pm 13	67 \pm 16	28 \pm 5	287 \pm 26
1995 2	534 \pm 62	83 \pm 17	99 \pm 23	—	130 \pm 34	846 \pm 64
1995 3	383 \pm 32	21 \pm 12	40 \pm 17	—	91 \pm 21	595 \pm 44

Trial 1, 1994

A visual comparison of locoweed consumption before aversion conditioning indicates there was little difference between treatment groups (Fig. 1). Following conditioning, the Averted group consumed less locoweed than the Control group ($P = 0.001$, Table 2), but there was a treatment \times day interaction ($P = 0.0001$). The averted group gradually increased locoweed consumption up to 10% of their bites (Fig. 1). They were brought back into the pens on 1 May, fasted overnight, then offered fresh picked locoweed,

Table 2. Percentage of bites (\pm standard error) of forage classes in steer diets in Trial 1, 1994.

Group	Cool-season grass	Warm-season grass	Other forbs	Locoweed
----- (%) -----				
Averted	16 ^a \pm .69	62 ^a \pm .60	13 ^a \pm .57	8 ^a \pm .51
Control	14 ^a \pm .38	53 ^b \pm .70	12 ^a \pm .56	21 ^b \pm .90

^{a,b} Means in the same column followed by the same letter are not significantly different ($P < 0.05$).

which they refused. They were fasted another day and offered locoweed again on 3 May. Two steers ate locoweed and were dosed a second time with a reduced level of LiCl (100 mg/kg BW). There was little locoweed consumption in the pasture for 2 days, then consumption began to increase. By 7 May, all averted animals were eating locoweed, and eventually consumed as much locoweed as the Control group (Fig. 1).

Locoweed consumption started to decrease on 19 May and essentially ceased by 2 June (Fig. 1). Nighttime temperatures increased and warm-season grasses began rapid growth. In previous studies, locoweed consumption ceased when warm-season grasses became abundant (Ralphs et al. 1993, 1994, 1997).

Trial 2, Familiar vs Naive Steers

Steers in the Familiar group consumed locoweed for an average of 56% of bites before aversion conditioning (Fig. 2). Following conditioning, the Familiar group consumed about the same amount of locoweed as before conditioning on the first round of bite counts, but greatly decreased locoweed consumption on the second round of counts about an hour later (Fig. 2). Little locoweed was consumed the second day. Steers increased

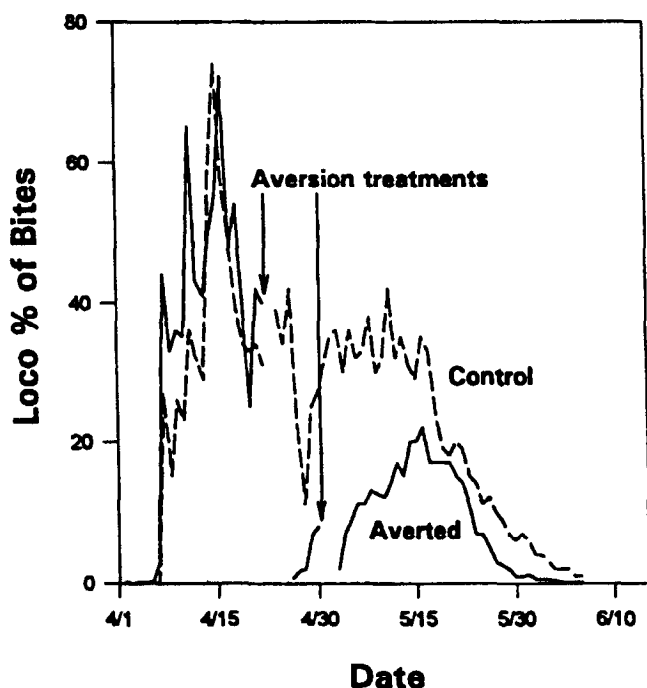


Fig. 1. Trial 1—Locoweed consumption of Control and Averted steers in 1994.

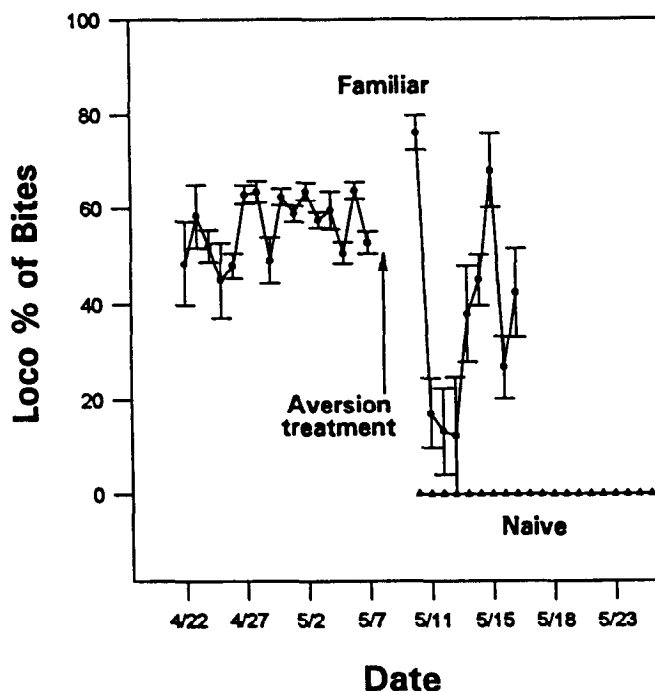


Fig. 2. Trial 2—Locoweed consumption (% of bites \pm SE) of steers familiar with locoweed, and of the Familiar and Naive group following aversion conditioning.

Table 3. Percentage of bites (\pm standard error) of forage classes in diets of Familiar and Naive groups in Trial 2, 1995.

Group	Cool-season grass	Warm-season grass	Other forbs	Locoweed
	----- (%) -----			
Familiar	35 ^a \pm 3.1	20 ^a \pm 2.4	8 ^a \pm 1.5	37 ^a \pm 3.6
Naive	23 ^a \pm 3.2	68 \pm 3.2	9 ^a \pm 1.3	0 ^b \pm 0

^{a,b}Means in the same column followed by the same letter are not significantly different ($P < 0.05$).

locoweed consumption up to an average of 37% of bites for the remainder of the trial (Table 3).

The Naive group did not consume any locoweed in the pasture (Fig. 2). However, they consumed more warm-season grasses than the Familiar group (Table 3). The locoweed-free pasture they grazed before aversion conditioning had mostly dormant warm-season grasses which they were apparently conditioned to eating.

Trial 3, Reinforcement of Aversion in the Pasture

The Reinforced group refused to eat fresh-picked locoweed when offered in the pen, but readily consumed locoweed in the small 0.5 ha pasture (86% of bites). Locoweed consumption decreased following each successive dose of LiCl paired with pasture grazing of locoweed (Fig. 3). When released into the larger locoweed-infested pasture, the Reinforced group abstained from eating locoweed for the remainder of the trial. The Familiar group continued eating locoweed for an average of 21% of bites (Table 4). Steers selected for the Familiar group had the lowest mean consumption of locoweed in Trial 2; thus they probably underestimated locoweed consumption of a non-averted control group.

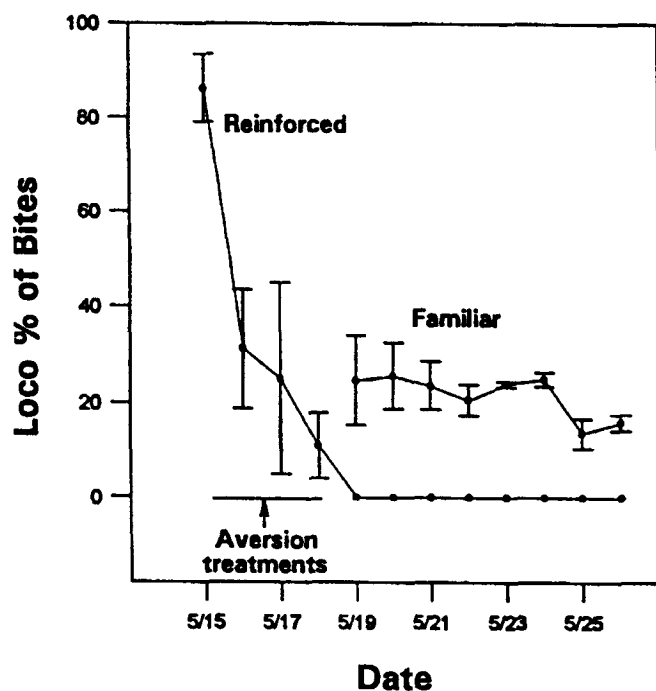


Fig. 3. Trial 3 - Locoweed consumption (% of bites \pm SE) of Familiar and Reinforced steers following reinforcement of aversion in the pasture.

Table 4. Percentage of bites (\pm standard error) of forage classes in diets of Familiar and Reinforced groups in Trial 3, 1995.

Group	Cool-season grass	Warm-season grass	Other forbs	Locoweed
	----- (%) -----			
Familiar	25 ^a \pm 1.4	39 ^a \pm 1.7	15 ^a \pm 1.2	21 ^a \pm 1.5
Reinforced	29 ^a \pm 2.3	48 ^b \pm 2.0	24 ^b \pm 1.9	0 ^b \pm 0

^{a,b}Means in the same column followed by the same letter are not significantly different ($P < 0.05$).

Discussion

Trial 1 illustrates the difficulty in creating aversions to familiar plants. Steers consumed locoweed for an average of 30% of their diets before aversion conditioning. They were dosed with a relatively high dose of LiCl and they refused to consume any locoweed when subsequently offered it in the pen. When released into the pasture, they gradually started eating locoweed, and after 6 days, were returned to the pen for a reinforcement dose. After an overnight fast, all steers refused locoweed in the pen. After a second day of fasting, only 2 of 6 steers consumed locoweed. The majority of steers could not be starved to eat locoweed in the pen, even though they readily consumed it in the pasture. Context clues associated with the environment where the aversions are formed play a role in retrieval of the taste-illness association (Bonardi et al. 1990, Archer et al. 1985). Steers avoided locoweed in the pen where it was paired with illness, but accepted it in the pasture because there was no negative reinforcement from grazing it. We had similar experiences in aversively conditioning cattle to avoid eating tall larkspur. We created the aversion in a pen by offering yearling heifers fresh larkspur, then dosed them with LiCl. They were transported to tall larkspur-infested mountain rangeland where the aversion extinguished while the heifers grazed with non-averted cohorts. However, the aversion renewed when the heifers were brought back to the pen and the environment where the aversion was created (Ralphs and Olsen 1990). These 2 studies emphasize the difficulty of reinforcing an aversion in the pen; animals must consume the plant prior to dosing with the emetic.

Results from trial 2 supports the conclusion from trial 1: aversions are difficult to create to familiar foods. Naive steers required only one dose of LiCl to be completely averted to locoweed for the remainder of the trial. Four of 6 steers in the Familiar group were dosed twice and still the aversion rapidly extinguished. Burritt and Provenza (1995) reported that sheep preexposed to wheat or rice for 7 days or longer, rapidly extinguished aversions to the respective grains, compared to sheep that were averted to these grains when they were novel. This verifies the fact that novelty of a food is important in creating a strong and persistent aversion (Nachman et al. 1977).

An unusual phenomenon occurred in Trial 2 when the Familiar group were released from the pen into the pasture following aversion conditioning. On the first round of bite counts, they selectively grazed locoweed at about the same level as before conditioning. However on the second round of bite counts about an hour later, all but 1 steer greatly decreased intake of locoweed. The next day, all but the 1 steer abstained from eating locoweed. On the third day, all steers started eating locoweed again.

Theoretically, the feeding response is a complex integration of the physiological state of the animal (degree of hunger), the flavor of the food, its nutrient value or potential toxic effect, the context in which the food is consumed, and the social interaction between grazing animals (C.D. Cheney, personal communication). When the steers were released from the pen, they resumed eating locoweed in the pasture as they had prior to aversion conditioning. Their prior acceptance of locoweed as a preferred food, and the social facilitation of all steers in the group eating it, apparently overwhelmed the more recent association of the taste-illness pairing. However, within an hour, 5 of 6 steers made the association between the taste of locoweed in the pasture and the prior LiCl-induced illness and stopped eating locoweed. An hedonic shift occurred in the palatability and subsequent acceptance of locoweed. Garcia et al. (1977) suggested that "following aversion conditioning, the food may look, and even smell attractive, but the animal may be surprised that it tastes bad." The longer period of time it took our steers to make the association between locoweed in the pasture and the previously induced illness, may have been due to locoweed's familiarity and previous preference when grazed in the pasture. Adverse feedback from the locoweed toxin swainsonine would not be expected in this short period. Locoism is a chronic poisoning, requiring several weeks of locoweed consumption. Furthermore, the mechanism of action is at the cellular level and would not cause gastrointestinal malaise, which is required to be associated with taste to form an aversion. Over the next few days, all steers gradually increased consumption of locoweed and the aversion eventually extinguished. Post conditioning exposure to a food without reinforcement from the illness can extinguish an aversion (Kraemer and Spear 1992). A second hedonic shift occurred when illness did not follow consumption of locoweed in the pasture. The positive feedback from nutrients in locoweed, in the absence of the induced illness, apparently elevated its palatability (Provenza 1995).

In Trial 3, the subgroup of Familiar steers eating the most locoweed in Trial 2 were selected for the reinforcement treatment. They refused to eat fresh-picked locoweed in the pen, but readily grazed locoweed in the pasture. The conditioning protocol was changed to dose these steers after grazing locoweed in the pasture. These steers were slow to form an aversion to locoweed that they grazed in the pasture; one steer required 4 doses of LiCl, another required 3 doses, and the third required 2. However, this method successfully averted these steers that were familiar with locoweed. They abstained from eating locoweed for the remainder of the trial.

Conclusions

It is difficult to create an aversion to a plant to which cattle are familiar. They learned that eating locoweed in the pen was associated with illness, but sampling it in the field without adverse consequences gradually extinguished the aversion.

The protracted method of reinforcing the aversion following short grazing periods in the pasture was successful. This was an extremely difficult test for the Reinforced steers. They had gone through an aversion and extinction period in Trial 2, and had the greatest preference for locoweed of all the steers in the study. This method of repeatedly allowing cattle to graze a particular

plant, then dosing them with an emetic was successful in creating a complete aversion to a familiar plant.

The other significant finding of this study was the relative ease of creating an aversion to an unfamiliar plant in the Naive group. In other studies, naive cattle have been conditioned to avoid eating larkspur, and the aversion lasted over 2 (Lane et al. 1990) or 3 years (Ralphs 1997) without any reinforcement while the averted cattle grazed separately. It appears that aversions are retained in long-term memory.

Conditioned food aversion may be a relatively simple procedure to train naive animals to avoid grazing particular poisonous plants. Animals that are familiar with the plant will require reinforcement with repeated doses of an emetic following field grazing sessions. Ranchers in locoweed areas watch their cattle and remove those that start eating locoweed. Creating and reinforcing aversions to locoweed in these cattle may prevent progression of intoxication, and prevent them from influencing others to graze locoweed.

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Persistence of aversions to larkspur in naive and native cattle

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Abstract

The objective of this study was to create and maintain a long lasting aversion to tall larkspur (*Delphinium barbeyi* Huth) under field grazing conditions. Two grazing trials were conducted: the first used cattle naive to larkspur, and the second used cattle that were familiar with larkspur. In the first trial, 12 mature cows that were not familiar with larkspur were randomly allocated to Averted and Control groups ($n = 6$). They were fed larkspur (a novel food) and the Averted group was dosed with lithium chloride (200 mg/kg body weight) to create the aversion. Both groups were then taken to larkspur-infested mountain rangeland where they grazed in 2 separate pastures during the late summer of 1993, 1994, and 1995. The aversion was not reinforced in 1994 or 1995. Diets were quantified by bite count. The Averted group abstained from eating larkspur for 3 years. The Control group grazed larkspur for an average of 14% of bites. Three Control cows died from larkspur poisoning in 1993, and another cow was poisoned, but survived in 1994. During the last 2 weeks of the 1995 trial, the Averted and Control groups were placed together, and the social influence of the Control cows eating larkspur caused the Averted cows to sample larkspur and gradually extinguished the aversion. In the second trial (1994 and 1995), 5 native cows that had grazed on the allotment and were familiar with larkspur were averted to larkspur by the procedure described above. They abstained from eating larkspur while grazing separately, but extinguished the aversion when placed with non-averted Control cows at the end of the study in 1995. Aversions are retained in long term memory and may last indefinitely if averted cattle graze separately.

enable managers to shape grazing behavior of animals to meet management goals. Our goal has been to condition animals to avoid eating poisonous plants and thus avoid poisoning.

A series of experiments were conducted to aversely condition cattle to avoid eating tall larkspur (*Delphinium barbeyi* L. Huth), an important poisonous plant on mountain rangelands. Lane et al. (1990) fed heifers fresh larkspur in a pen, then dosed them with lithium chloride (LiCl). They associated the induced illness with the taste of larkspur and avoided eating larkspur when released in larkspur-infested pastures. This aversion lasted into the next year's grazing season. However, when the averted heifers were placed with non-averted cohorts that were readily grazing larkspur, they started sampling larkspur and the aversion extinguished. Averted cattle must be grazed separately to maintain the aversion (Ralphs and Olsen 1990). We also found that mature cows retained aversions better than younger animals (Ralphs and Cheney 1993), and that novelty of taste is important in forming strong aversions (Ralphs et al. 1996, Burritt and Provenza 1996).

The objective of the first study was to implement the knowledge gained from previous research to create and maintain a long lasting aversion in cattle that were naive to tall larkspur. A second study was conducted to determine if native cows with previous exposure to larkspur could be averted. Aversions to familiar foods are more difficult to create because these foods are considered safe (Nachman et al. 1977).

Methods

The grazing studies were conducted 16 km west of Yampa, Colo. on the Routt National Forest. The habitat type was aspen (*Populus tremuloides* Michx.)/tall forb. Tall larkspur was the dominant forb, with cow parsnip (*Heracleum lanatum* Michx.), sweetcicely (*Osmorhiza occidentalis* [Nutt] Torr.), meadowrue (*Thalictrum fendleri* Engelm. ex Gray) and American vetch (*Vicia americana* Muhl. ex Wild.) comprising the majority of palatable forbs. Mountain brome (*Bromus carinatus* Hooker & Arn.) was the dominant grass, and Kentucky bluegrass (*Poa pratensis* L.) occurred in the understory. Standing crop of tall larkspur, other forbs, and grasses was estimated at the beginning of each trial by clipping ten, 1×0.25 m quadrats systematically located at 20 step intervals along paced transects through the middle of each pasture. Samples were dried in a forced air oven at 60° C for 48 hours then weighed. Total standing crop averaged 2,856 kg/ha over the 3 years. Tall larkspur comprised 41% of the standing crop, other forbs comprised 46%, and grasses 13%.

Key Words: conditioned food aversion, social facilitation, cattle grazing, poisonous plant, tall larkspur, *Delphinium barbeyi*

The study of conditioned food aversions is a prominent field of research in the behavioral sciences (Braveman and Bronstein 1985). Zahorik and Houpt (1977, 1990) first demonstrated that livestock could be averted to specific foods. Laycock (1978) introduced this concept to the Range Management profession, and suggested it may have potential to prevent livestock from eating poisonous plants. Provenza and Ralph (1988) proposed that diet training (which encompass aversion conditioning) may

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Naive Cows 1993 to 1995

Twelve cows (Hereford and Angus) were purchased from ranches in southeastern Idaho. The cows were mature (3–4 yr old, 435 kg \pm 15 SE) and had not been on mountain rangeland nor were they familiar with larkspur. The cows were allotted randomly to Averted and Control treatment groups.

The cows were transported to a ranch in Yampa, Colo. near the study site and allowed 2 days to acclimate to the new surroundings. The evening before aversion conditioning, regular feed was withheld, and the cows were offered 9 kg fresh larkspur. Some of the cows were reluctant to eat it on the first exposure. They were offered 15 kg of larkspur the next morning and all of them readily ate it. Cows in the Averted group were restrained in a chute and gavaged with lithium chloride (LiCl 200 mg/kg body weight) via stomach tube. Their regular ration of hay was withheld until evening so there was no interference between the induced illness and the taste of the novel larkspur. The Averted cows were allowed to recover for 3 days and fed alfalfa hay morning and evening. The Control group was fed 5 kg of larkspur morning and evening before their regular ration of hay.

The aversion was tested and reinforced in paired and group feeding tests. Averted and Control cows were randomly paired together and each pair was offered fresh larkspur for 10 min. each morning and evening for 3 days. The groups were then placed together in a group feeding situation and offered 9 kg of fresh larkspur. The social facilitation of the Control cows eating larkspur induced 2 of the Averted cows to sample larkspur, and they were dosed a second time with a lower dose of LiCl (100 mg/kg BW).

The 2 groups were transported to the grazing site and each group was randomly assigned to 1 of 2 adjacent larkspur-infested pastures. Diets were estimated by bite counts. Each cow was observed for 5 min. periods and the number of bites of forage classes were counted (tall larkspur, other forbs, grass, shrubs). Cows were observed during the morning and evening grazing periods for an average of 3 to 5 observations on each cow each day.

The cows were retained for 3 years and the grazing trial was repeated in 1994 and 1995 at the same site to determine the longevity of the aversions. The aversions were not reinforced in 1994 or 1995. In 1993, the study ran from 2 to 25 August and the pasture sizes were 1.7 ha. The pasture size was increased to 3.3 ha in 1994 to accommodate the longer trials (21 July to 22 August). In 1995, the persistence trial ran from 2 to 15 August, and the social facilitation trial ran from 16 to 31 August. Individual cows were the experimental units to which the aversion treatment was applied. Hence, pastures were merely the area where the aversion was expressed. However, groups were rotated to the other pasture halfway through each trial to reduce any pasture difference in diet selection.

Percentage of bites of each forage class in diets during the 3 years the cattle grazed separately were transformed by arcsin and analyzed by a general linear model (SAS 1988) using a split-plot design. Difference between groups was tested by the animal (within group) factor, and the year and group \times year interaction was tested by the year \times animal (within group) factor. There was a group \times year interaction for forbs and grasses in the diets, so the model was reduced and data were analyzed for each year separately comparing groups over days in a split-plot model. The difference between groups was tested by the animal (within group) factor, and day and the group \times day interaction was tested by the residual error. The percentage of bites of each forage class was averaged over observation periods each day for each cow before the analysis. Non-transformed means are presented in the tables and figures.

Social Facilitation Trial, 1995

The Averted and Control group were placed together at the end of the 1995 trial to determine if the aversion would remain under the pressure of social facilitation. The gates were opened and the cows were allowed to graze freely between the 2 pastures from August 15 to 31. Bite counts were recorded as described previously. Diet data during the part of the trial when groups grazed together were transformed by arcsin and analyzed in a split plot design comparing groups over days of the trial.

Native Cows, 1994 and 1995

The objective of this trial was to determine if native cows that were familiar with larkspur, could be averted and abstain from eating it. Five native cows were obtained from a local rancher. They had grazed on the allotment for 2 to 5 years and had been exposed to larkspur. They were averted to larkspur as described in the first trial. Regular feed was withheld overnight, and they were offered fresh-picked larkspur the evening before and morning of conditioning. The Native cows readily ate larkspur and were gavaged with LiCl (200 mg/kg BW). They were allowed 3 days to recover, and offered larkspur morning and evening for 2 more days, but they refused. They were transported to the grazing area on the mountain and allowed to graze a larkspur-infested pasture (1.6 ha) from August 20 to September 6, 1994. The Control cows from the previous study were placed in an adjacent pasture for a comparison of larkspur intake. Bite counts were taken as described previously.

Three of the Native cows were available in 1995 (one had a calf), and were returned to the grazing site. They grazed a 2 ha pasture from August 16 to 23. The control cows were placed with the native cows from August 23 to 31 to assess the influence of social facilitation on the larkspur aversion. Diet data were transformed by arcsin and analyzed separately for each year while the cattle grazed separately (persistence trial), and when they grazed together in 1995 (social facilitation trial), using the split-plot model described above.

Results and Discussion

Naive Cows 1993–1995

Following conditioning with LiCl in 1993, the Averted cows abstained from grazing larkspur for 3 years while they grazed separately (Table 1). The optimal conditions for maintaining aversions (mature animals, averted to novel food, using a high dose of LiCl to induce intense gastrointestinal illness, and groups grazed separately to avoid social facilitation) combined to promote a long-lasting aversion to tall larkspur.

The Control cows consumed larkspur from 11 to 20 % of their bites (Table 1). In 1993, 3 of the control cows died from larkspur poisoning. Symptoms of poisoning (muscular tremors and collapse) were observed in 2 other cows, but they survived. In 1994, one cow showed symptoms of poisoning; she collapsed and was not able to stand for 10–15 minutes, but she recovered. Even though these cattle were severely poisoned, they continued to eat larkspur after they recovered. Natural aversions to larkspur did not occur. Zahorik and Houpt (1977) suggested that free-ranging animals may have difficulty associating illness with a particular plant consumed during the course of a day.

Table 1. Percentage of bites (\pm standard error) of forage classes in Averted and non-averted Control cows.

Year	Group	Larkspur	Forb	Grass	Shrub
<hr/>					
		----- (%) -----			
1993	Averted	0 *	34 \pm 0.7 *	64 \pm 0.8 *	2 \pm 0.3 *
	Control	20 \pm 0.7	28 \pm 0.7	45 \pm 1	6 \pm 0.6
1994	Averted	0 *	34 \pm 0.6 *	63 \pm 0.5	3 \pm 0.2
	Control	12 \pm 0.4	23 \pm 0.4	63 \pm 0.4	3 \pm 0.2
1995 Separate	Averted	0 *	67 \pm 2 *	33 \pm 2	0
	Control	11 \pm 1	58 \pm 1	31 \pm 1	0
1995 Together	Averted	6 \pm 1 *	73 \pm 2 *	19 \pm 1	2 \pm 0.4
	Control	10 \pm 1	66 \pm 2	23 \pm 2	2 \pm 0.4

*Means in the same column within year and trial are different ($P < 0.05$).

Although grasses comprised only a small part of the standing crop, they dominated cattle diets in 1993 and 1994 (Table 2), but forbs dominated diets in both trials in 1995. Cow parsnip, sweet-cicely, and vetch were preferred forbs. Small amounts of snow-berry (*Symphoricarpos oreophilus* Gray) were consumed toward the end of the trials each year.

Table 2. Percentage of bites (\pm standard error) of forage classes in Native cows that were averted to larkspur and non-averted Control cows.

Year	Group	Larkspur	Forb	Grass	Shrub
<hr/>					
		----- (%) -----			
1994	Native	1 \pm 0.2 *	29 \pm 0.6	62 \pm 0.7	8 \pm 0.5 *
	Control	5 \pm 0.3	28 \pm 0.6	62 \pm 0.6	5 \pm 0.3
1995 Separate	Native	0 *	80 \pm 3	18 \pm 3	1 \pm 0.6
	Control	10 \pm 0.8	61 \pm 1	29 \pm 1	1 \pm 0.1
1995 Together	Native	6 \pm 2 *	74 \pm 3 *	16 \pm 3 *	5 \pm 1
	Control	13 \pm 2	61 \pm 2	23 \pm 2	2 \pm 1

* Means in the same column within year and trail are different ($P < 0.05$).

Native Cows 1994–1995

The averted Native cows generally abstained from eating larkspur while grazing separately in both 1994 and 1995 (Table 2). One cow started eating larkspur in 1994 and consumed it for 4% of bites, but the other 4 cows abstained. The native cow that ate larkspur in 1994 was not available for the 1995 study.

These cows grazed on this allotment for 2 to 5 years, and had been exposed to larkspur, although it is not known whether they consumed it. The herd from which these cows were taken had experienced large losses to larkspur over the years. Even though it is difficult to form aversions to familiar foods (Nachman et al 1977, Burritt and Provenza 1996), these native cows formed aversions to larkspur. Ralphs et al. (1997) also averted steers that were familiar with white locoweed (*Oxytropis sericea* Nutt, T&G) by dosing them with LiCl following their consumption of locoweed in the pasture.

Social Facilitation Trials from Both Studies

In the first study, Averted and Control groups were placed together on 16 August, and the Averted group gradually extinguished the aversion (Fig. 1). The mean larkspur consumption for the Averted group was lower than the Controls ($P = 0.007$, Table 1), but there was a group \times day interaction ($P = 0.02$), indicating the Averted group increased larkspur consumption during the trial. They were consuming as much larkspur as the non-averted Control group at the end of the trial (Fig. 1). The Averted group did not consume larkspur for 7 days after the groups were placed together. In other larkspur aversion grazing trials, the averted groups started to eat larkspur within 3–4 days after being placed together (Lane et al. 1990, Ralphs and Olsen 1990, 1992). The optimal conditions described above apparently created a stronger aversion that lasted a few days longer than in previous trials, but the aversion extinguished in the end.

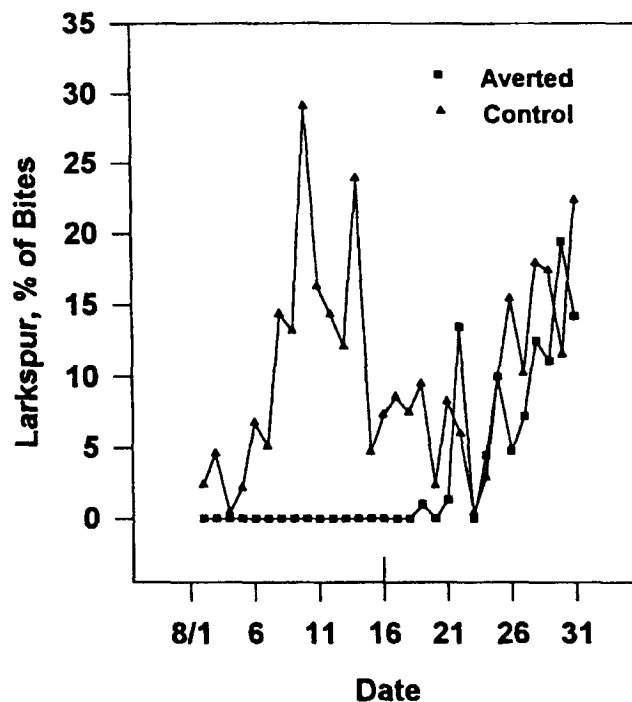


Fig. 1. Larkspur consumption (% of bites) from Averted and non-averted Control groups during the 1995 grazing trial. Cattle grazed in separate pastures from August 1 to 15, and were placed together in the same pasture in the social facilitation trial 16 to 31 August.

In the second study, the Native cows extinguished the aversion when placed in with the non-averted Controls in 1995 (Table 2). They started eating larkspur after 2 days, however mean consumption was less than half that of the controls ($P = 0.01$, Table 2). There was no group \times day interaction in this part of the study ($P = 0.57$).

Our prior experiments have not been successful in reinforcing aversions to larkspur to withstand social facilitation. In our initial experiment (Lane et al. 1990), the averted heifers extinguished the aversion to larkspur when placed with non-averted cohorts that were readily grazing larkspur. We conducted several experiments to try to overcome the influence of social facilitation: rein-

forcement of the aversion (Ralphs and Olsen 1990); use of native cattle that were familiar with the plant community (Ralphs unpublished data); and the use of larkspur alkaloid extract as the emetic to create an internal feedback when cattle start to sample larkspur (Ralphs and Olsen 1992). None of these practices were completely successful in overcoming social facilitation and maintaining total abstinence to larkspur when averted animals grazed with non-averted cohorts in the field. Social facilitation also caused cattle to extinguish aversions to alfalfa pellets (Olsen and Ralphs 1996); and ewes and lambs to extinguish aversions to mountain mahogany (Burritt and Provenza 1989) and calf manna (Thorhallsdottir et al. 1990). Raccoons, effectively averted against killing chickens, extinguished the aversion when they observed their kits killing and eating the chickens (Gustavson and Gustavson 1985). Finally, rats extinguished aversions to flavored liquids when exposed to cohorts that were consuming, or had recently consumed the liquid (Galef 1986). In rats, livestock, and humans, social influence is an important determinant of diet selection (Rozin and Zellner 1985). We conclude that aversions are not likely to be maintained in mixed group feeding or grazing situations.

Conclusions

Conditioned food aversion is a powerful experimental tool to modify animal diets (Galef 1985). We have shown that it is a potential management tool to prevent livestock from grazing poisonous plants. In the first experiment, naive cows retained aversions to larkspur for 3 years while grazing separately. In the second experiment, native cows retained aversions to larkspur for 2 years. Lane et al. (1990) also reported that heifers retained aversions to larkspur during his 2 year study. It appears that aversions, and subsequent hedonic shifts which make larkspur unpalatable, are retained in long-term memory (Garcia et al. 1985).

Aversion conditioning is an intensive management tool. It requires confining animals, forcing them to consume the target plant, dosing with an emetic, then testing the aversion. Large scale field and demonstration trials are needed to determine its practicality. However ranches which persistently lose animals to poisonous plants can afford to invest in practices that prevent losses.

Theoretically, novelty of taste is important in creating a strong and lasting aversion (Nachmann et al. 1977). However, native cattle that were familiar with larkspur, formed strong aversions to it. If native cattle can be successfully averted to larkspur, ranchers would not need to purchase naive replacement heifers that had not been exposed to larkspur.

Social facilitation is the most important factor preventing wide spread application of aversion conditioning. Averted animals, seeing others eating the target food, will sample it. If there is no adverse reaction, they will continue sampling and eventually extinguish the aversion. However, if averted animals can be grazed separately, aversion conditioning may provide an effective management tool to prevent animals from eating selected plants.

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Damage from the larkspur mirid deters cattle grazing of larkspur

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Abstract

The larkspur mirid (*Hopplomachus affiguratus*) is host specific to tall larkspur (*Delphinium barbeyi* Huth). These insects suck cell solubles from leaves and reproductive racemes, causing flowers to abort and leaves to desiccate. Cattle generally prefer larkspur flowering heads, pods, and leaves, and are frequently poisoned. The objective of this experiment was to determine if cattle would avoid eating mirid-damaged larkspur. A 2-choice cafeteria feeding trial was conducted to determine preference for mirid-damaged and undamaged larkspur. Four cows were offered a choice of the 2 types of larkspur in 10 min. feeding trials in the morning and evening for 5 days. Cows preferred the undamaged larkspur plants ($0.8 \text{ kg} \pm 0.08$, SE) over mirid-damaged plants ($0.1 \text{ kg} \pm 0.03$, SE). The cows were then turned out into a larkspur-infested pasture and consumption of mirid-damaged and undamaged larkspur was quantified by bite count. The cows did not select any mirid-damaged larkspur. Consumption of undamaged larkspur peaked at 17% of bites on the second day of the grazing trial, then declined as mirid damage on the plants increased. If the density of mirids on larkspur is sufficiently high to damage most of the leaves and flowering racemes, grazing by cattle may be deterred, and subsequent poisoning avoided.

These are the larkspur plant parts normally preferred by cattle (Pfister et al. 1988).

Peterson and Clementson (1989) observed dense mirid populations that apparently reduced the vigor of a tall larkspur population in western Colorado, and proposed the use of the larkspur mirid as a biological control for larkspur. However, classical biological control theory suggests there is limited potential for a native insect to control a native plant because they have evolved together and both have developed adaptive mechanisms for survival. The objective of this research was not necessarily to kill or control larkspur, but rather investigate the potential of the larkspur mirid to damage tall larkspur and render it distasteful to cattle. Our hypothesis was that cattle would not consume mirid-damaged larkspur.

Methods

Site Description

An existing larkspur mirid population was identified in a 3 ha larkspur patch near Ferron Reservoir on the Wasatch Plateau in central Utah. The site was in the subalpine zone (3,000 m elevation) with scattered subalpine fir pockets interspersed in the tall forb plant community dominated by tall larkspur, western cone flower (*Rudbeckia occidentalis* Nutt.), sweetcicely (*Osmorhiza occidentalis* [Nutt.] Torr.), and mountain brome (*Bromus carinatus* Hooker & Arn.). All of the larkspur plants in the patch were infested with mirids and had visibly damaged reproductive racemes and leaves. We estimated the average mirid density by counting the number of mirids on 3 leaves of 5 plants, and extrapolated from these plants to the general population of the patch.

Pen Feeding Trial

Four cows (3 Hereford and 1 Angus, 400 kg) that had been grazing tall larkspur in a previous experiment in Salina Canyon (Pfister et al. 1997) were used in this study. Undamaged larkspur was in full flower. Mirid-damaged and undamaged larkspur plants were harvested daily and fed to the cows in a 2-choice cafeteria trial. Only 25% of each infested plant was harvested to preserve the mirid population. The harvested stems were gently shaken to remove the mirids onto the remaining portions of the plant. Heavily infested leaves typically are covered with black dots of fecal material, but summer thunder storms occurred

Key Words: biological control, *Hopplomachus affiguratus*, cattle poisoning, *Delphinium barbeyi*

Larkspurs (*Delphinium* spp.) kill more cattle on mountain rangelands than any other poisonous plant, disease or predator (Kingsbury 1964, Nielsen and Ralphs 1988). The larkspur mirid [*Hopplomachus affiguratus* (Heteroptera: Miridae)] is a native insect that is host specific to tall larkspur (*Delphinium barbeyi* Huth) (Uhler 1895, Fitz 1972), and may provide a biological tool to reduce the risk of larkspur poisoning in cattle. The larkspur mirid is a sucking insect that extracts cell solubles from immature, rapidly growing plant parts. The insects concentrate on the flowering racemes, causing the buds to abort; and also damage the leaves which first appear mottled, then desiccate and senesce.

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before the study and washed all insect fecal material off the leaves. Therefore, neither the mirids nor their fecal material directly influenced the taste of the damaged plants.

Two feeding pens (3 m by 4 m) were partitioned within a larger corral to allow 2 cows to be fed separately at the same time. Two, 80 liter tubs were placed in each pen to hold the 1-m tall larkspur stalks upright. The location of the damaged and undamaged larkspur was alternated at each feeding to eliminate location bias. Two to 3 kg of damaged and undamaged larkspur were weighed and placed in each tub and the cows were allowed to eat for 10 min. The uneaten portion was weighed and consumption was calculated for each cow. The feeding trials were conducted each morning and evening for 5 consecutive days. Following each larkspur feeding, the cows were fed half their daily ration of certified weed-seed-free alfalfa hay (9 kg). A sample of the larkspur stalks at the end of the trial was weighed, then dried in a forced air oven (60° C for 48 hours) to determine dry matter content. The leaves were then plucked from the stems and analyzed for crude protein by the Kjeldahl total nitrogen method (AOAC 1965), and cell walls by neutral detergent fiber analysis (NDF, Goering and Van Soest 1970).

Consumption of damaged and undamaged larkspur was averaged over the 5 days for each of the 4 cows, then the average consumption was compared by a paired t-test. Also, a preference ratio (PR) for the undamaged larkspur was calculated: $PR = \text{undamaged} / (\text{undamaged} + \text{damaged})$. A 1-tailed t-test was used to determine if the preference ratio for undamaged larkspur differed significantly from the neutral preference of 0.5.

Grazing Trial

Following the pen trial, the cows were turned out into a 1.1 ha larkspur-infested pasture and allowed to graze freely for 15 days. Diets were quantified by bite count. Each cow was observed for 5 min intervals during the major daily grazing periods, and the number of bites of each forage class was counted (mirid-damaged larkspur, undamaged larkspur, other forbs, and grass). Four to 8 observations were made of each cow daily through the major grazing periods. Standing crop of forage classes was clipped from ten 1 × .25 m quadrats systematically placed at 20 step intervals along a paced transect through the middle of the pasture. These were dried in a forced air oven at 60° for 48 hours and weighed.

All larkspur plants in the pasture were infested with mirids. However, infestation and damage began on the south-east quarter of the plants (the preferred spatial orientation for mirids) then spread throughout the plant as the season progressed. A visual assessment was made of the percentage of flowering heads aborted and the percentage of leaf biomass damaged by mirids. At the beginning of the trial, approximately half of each plant was damaged. Thus, the comparison was made between cattle bites of damaged vs. undamaged plant parts.

The percentage of bites of damaged and undamaged larkspur was transformed by arcsin and analyzed in a general linear model (SAS 1988) in a split plot design over days. The type of larkspur was the main plot and was tested by the type × cow interaction. Day was the split plot and day and the day × type interaction were tested by the residual error. The untransformed mean daily bites of damaged and undamaged larkspur (\pm SE) were plotted.

Larkspur consumption by the cows while they were on the previous larkspur grazing study was also presented as a comparison of intake of undamaged larkspur.

Results and Discussion

Pen Feeding Trial

Cattle preferred the undamaged tall larkspur ($P = 0.007$), consuming an average of 0.8 kg ($\pm .08$ SE) during the 10 min. feeding periods, compared to 0.1 kg ($\pm .03$ SE) of the mirid-damaged larkspur. The preference ratio for undamaged plants was 0.90, which differed from neutral preference of 0.5 ($P < 0.01$). Most consumption of the mirid-damaged plants occurred at the beginning of the feeding periods when cows went first to the tubs containing damaged larkspur. After switching to the undamaged larkspur, they seldom went back to the damaged larkspur. Their behavior portrayed a clear preference for the undamaged larkspur.

Dry matter content of the mirid-damaged plants was slightly higher than the undamaged plants (20 vs. 17%), indicating that the aborted flowering heads and damaged leaves of the mirid-damaged plants were not as succulent as the undamaged plants. Crude protein content of the mirid-damaged leaves was lower than the undamaged leaves (16.9 vs 22.3%), but NDF was similar (31.8 vs 32.5%). Perhaps normal cell wall development was arrested in mirid-damaged plants, thus limiting fiber deposition. In a companion study, we found that damage from the larkspur mirid did not alter toxic or total alkaloid levels in tall larkspur plants (Ralphs et al. 1997), thus the mirids are likely to not affect toxicity or palatability associated with alkaloid levels. Further research is necessary to identify the nutrient and palatability factors responsible for the reduced acceptability of mirid-damaged larkspur.

Field Grazing Trial

Larkspur comprised 27% of the standing crop in the experimental pasture (Table 1). The cows did not consume mirid-damaged portions of larkspur plants in the pasture, but consumed undamaged larkspur for an average of 3% of bites (Table 1, $P = 0.12$).

Table 1. Standing crop of forage classes in the experimental pasture and percentage of bites of forage consumed by cattle (\pm SE).

Forage class	Standing crop --- (kg/ha) ---	Percentage of bites --- (%) ---
Larkspur	401 \pm 246	
mirid-damaged		0
undamaged		3 \pm 0.6
Other forbs	878 \pm 163	57 \pm 1
Grass	190 \pm 40	40 \pm 1

However, there was a larkspur type × day interaction ($P < 0.01$). Cattle consumed uninfested larkspur for 17% of bites on the second day of the trial, after which larkspur consumption steadily declined (Fig 1). The decline in larkspur consumption was apparently due to the progressive damage from the mirids. At the beginning of the trial, about half of each plant was damaged. Leaves on the northwest quarter of the plants were generally undamaged and were grazed by cattle. As the trial progressed, mirids moved into the non-infested parts and continued inflicting damage, thus rendering the remaining parts of the larkspur plants unpalatable. By the end of the trial, all of the larkspur reproductive heads had aborted or were grazed.

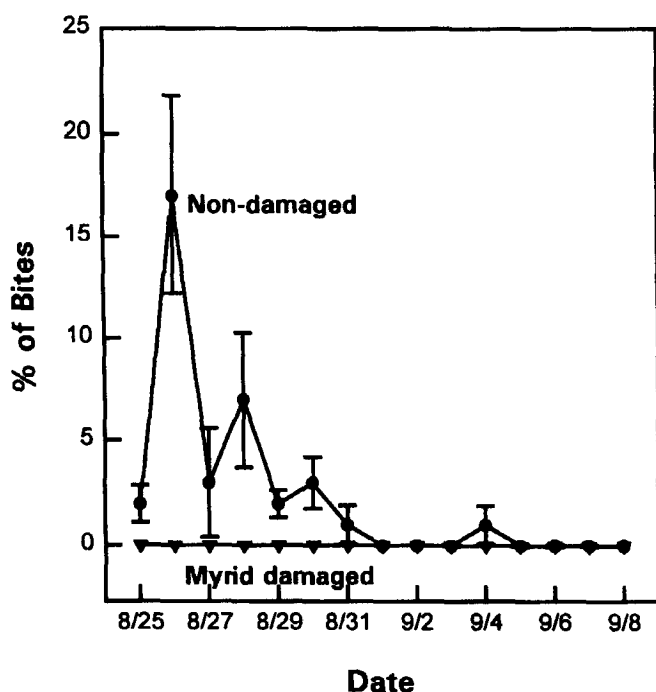


Fig. 1. Mean daily consumption (% of bites \pm SE) by cattle of mirid-damaged and undamaged tall larkspur in the field grazing trial.

These same cows consumed larkspur for 4 % of bites in the previous larkspur grazing trial at Salina Canyon (Pfister et al. 1997). In a series of 7 larkspur grazing studies between 1986 and 1990 in the same vicinity, larkspur consumption averaged 7% of bites (Ralphs and Pfister 1992), but reached as high as 80% of bites in some grazing periods. Cattle generally increase larkspur consumption as it matures from the flower into the pod stage (Pfister et al. 1988).

We estimated the mirid density on the study site at about 10,000 mirids per plant. There was an average of 90 mirids/leaf on the younger leaves on the upper half of the stem (6 leaves/stem), on about half the stems of each plant (20 stems/plant) at a given time. This density of mirids caused 100% of flowering heads to abort, and damaged 83% of leaf biomass on plants adjacent to the study pasture (unpublished data).

Another dense population of the larkspur mirid exists in the Bull Park area 18 km southwest of Yampa, Colo. This mirid population has been monitored since 1986, and has experienced dramatic cycles in mirid density. Over that period, the larkspur population declined in vigor and density, and the rancher observed a decline in cattle deaths in that area (Nancy Peterson, personal communication). This suggests that even though the mirids are native insects, they may be able to suppress larkspur over time if their populations remain high. We will continue to monitor the mirid populations at Yampa and Ferron Reservoir and measure their impact on larkspur vigor and density over time.

Conclusions

Cattle preferred undamaged larkspur plants in the pen feeding trial, and did not eat mirid-damaged portions of larkspur plants in the field grazing trial. Cattle initially consumed the undamaged

portions of larkspur plants at the beginning of the grazing trial, but larkspur consumption declined and ceased as mirid-damage increased. These results confirm our previous observations that cattle will not graze mirid-damaged portions of larkspur plants.

The larkspur mirid occurs in most tall larkspur populations we have observed; however, their density is generally low. Infestation and propagation techniques must be developed to enhance these natural populations if the larkspur mirid is to be used as a biological tool to reduce cattle poisoning. We infested new areas by transporting both young nymphs, and eggs in senescent stems, which subsequently damaged the newly infested plants (Jones and Ralphs 1997a). We also described the overwintering requirements for eggs in stems, and measured hatch rates (7 nymphs per inch of stem, Jones and Ralphs 1997b). Further research is necessary on the biology of the larkspur mirid to determine the environmental conditions that limit or constrain its populations, and determine if populations can spread throughout a larkspur patch and increase to a level that will significantly damage the larkspur plants. If the density of mirids described in this paper can be achieved in larkspur patches that persistently cause cattle deaths, then cattle may be deterred from grazing larkspur and the risk of poisoning will be substantially reduced.

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Habitat selection patterns of feral horses in southcentral Wyoming

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Abstract

Feral horse habitat selection patterns and forage attributes on available habitats were studied on public rangelands of southcentral Wyoming. Environmental assessments preceding roundup of excess horses requires resource data to justify the number of horses removed. Randomly selected bands of horses were followed for 24-hour observation periods during the spring and summer to determine if they utilized habitats in proportion to their abundance. We also determined if forage abundance, succulence (an index to forage palatability), percent utilization, and dietary composition were related to habitats selected. Stream-sides, bog/meadows, and mountain sagebrush habitats were preferentially selected ($p \leq 0.05$). Lowland sagebrush habitats were avoided and no apparent selection behavior was shown for grassland and coniferous forest habitats. Forage abundance, palatability, and percent utilization were higher ($p \leq 0.05$) in streamside and bog/meadow habitat classes. Diet composition indicated that sedges (*Carex* sp.), common in stream-sides and bog/meadows, were an important forage of feral horses. Palatability and abundance of graminoid vegetation and proximity to preferred habitats seemed to be the primary influences on habitat selection by feral horses.

Resumen

Se estudiaron la selección del hábitat y los atributos asociados del forrajear en cada hábitat disponible a los caballos silvestres en las dehesas públicas de la zona sur central del estado de Wyoming. Las evaluaciones del medio ambiente que preceden el rodeo de los caballos determinados de ser en exceso requieren la acumulación de datos de los recursos para justificar el número de caballos que se van a reubicar. Se observaron unas bandas de caballos elegidas al azar por períodos de veinticuatro horas durante la primavera y el verano para determinar si utilizaban cada hábitat en proporción con su abundancia. También se investigó si la abundancia del forraje, la succulencia (un índice del aspecto de deseo del forraje), el porcentaje de la utilización, y la composición dietética se relacionaron con cada hábitat elegido. Las orillas de los arroyos, las ciénagas/los prados, y el hábitat donde crece la artemisa de la montaña se destacaron por ser preferibles ($p \leq .05$). La abundancia del forraje, el deseo del forraje, y el porcentaje de utilización eran los variables más altos ($p \leq .05$) en las dos clases de hábitat de las orillas de los arroyos y las ciénagas/los prados. La investigación de la composición de la dieta indicó que las juncias (*Carex* sp.), una planta común en las orillas, las ciénagas y los prados, eran un forraje importante de los caballos silvestres. El deseo del forraje, la abundancia de la vegetación herbácea, y la cercanía de cada hábitat preferido parecían ser las influencias más importantes en la elección de hábitat por parte de los caballos silvestres.

Key Words: forage abundance, succulence, utilization

Management of rangeland is contingent upon understanding the influences of each species of herbivore on the system. The impact of feral horses (*Equus caballus*) on plant communities and physiographic areas must be determined to provide a basis for the planned herd size, to quantify numbers to remove, and potential impacts on other species.

A recently completed census estimated that over 46,000 feral horses inhabit federally owned rangelands in the western United States (USDI-BLM and USDA-FS 1993). The potential for rapid population growth (Eberhardt et al. 1982, Boyd 1980, Cook 1975) coupled with the management constraints of the Wild Free-Roaming Horse and Burro Act of 1971, has lead to excessive

feral horse densities in important habitats on many public rangelands (Krysl et al. 1984, Cook 1975).

Krysl et al. (1984), Denniston et al. (1982), Rittenhouse et al. (1982), Salter and Hudson (1979) suggest similarities in habitat selection and diet composition, thus a potential for interspecific competition between feral horses and other domestic and wild herbivores. Most feral horse habitat selection studies in the western U. S. were conducted in sagebrush steppe or desert areas (Ganskopp and Vavra 1986, Denniston et al. 1982, Miller 1983) ecosystems with a relatively low diversity of habitats, where water is often the determining factor in habitat selection. The area of the study described here has diverse habitats and abundant water sources. In such an area, Salter and Hudson (1979) found that forage attributes including standing crop and quality were the most important factors influencing habitat selection by horses and other large herbivores (Smith et al. 1992, Pinchak et al. 1991, and Senft et al. 1985).

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Our research was initiated to address the lack of information regarding feral horse habitat selection and activity patterns in an area of southcentral Wyoming. We hypothesized that greater standing crop and quality of forage would be positively related to habitat selection by feral horses, and that this would result in their preference for riparian plant communities over uplands. Explicitly tested hypotheses were that proportions of horses using each of the various habitat classes in the study area would not be the same as the proportion of the study area occupied by each habitat class, and that vegetation abundance, palatability (quality), and utilization, would not be equal for all habitat classes. We also nonstatistically evaluated the diet composition of feral horses to ascertain if feral horse diet composition was consistent with observed habitat selection patterns.

Materials and Methods

Study Area

The study area is located in the Sweetwater River valley of southcentral Wyoming, and includes the Willow, Cooper, and Spring Creek drainages on the north slope of Green Mountain (Fig. 1). To meet the assumptions of our statistical analysis, the

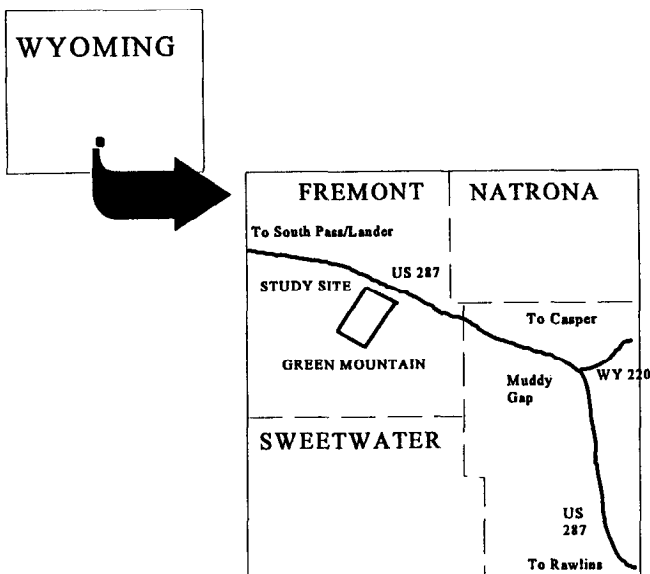


Fig. 1. Study area location in southcentral Wyoming.

study area was defined by the smallest convex polygon enclosing all horse relocation points (Johnson 1980). The study area is within the 28,633-ha Whiskey Peak grazing allotment administered by the Bureau of Land Management. Elevations on the allotment range from 1,976 to 2,812 meters. Thirty-year average annual precipitation (1951–1980) was 25.4 cm at the Muddy Gap Junction of highways US287 and WY220, one-half occurring as snowfall. Average annual high and low temperatures at the same station were 13.4 and 0.33°C, respectively (Martner 1986). The frost free period varies elevationally from 114 to <60 days (BLM 1990).

Topographic features of the study area include outwash plains, gently rolling hills, forested and open ridges, canyons, and rock

outcrops. Soils are generally well developed and of loamy texture, with the occurrence of some coarse sandy and skeletal, very gravelly, or very cobbly soils (BLM 1990).

Plant communities and associated physiographic habitats occurring on the Whiskey Peak allotment were designated for our purposes as streamside, bog/meadow, mountain sagebrush, lowland sagebrush, grassland, and coniferous forest. The delineation of these habitat classes was based on dominant vegetation, topographic position, and geographic location. Streamside habitats were areas within 5 m of a water course with a willow (*Salix* spp.)/graminoid plant community. Bog/meadow habitats were low-lying areas associated with surface and/or subsurface water (other than streamside) which supported a more mesic graminoid plant community than surrounding areas. Lowland sagebrush habitats were generally alluvial plains dominated by Wyoming big sagebrush (*Artemisia tridentata* Nutt. var. *wyomingensis* (Beetle and Young) Welsh) and graminoids situated geographically north from and not interspersed with other habitats. Coniferous forest habitats had a 50–90% canopy coverage of limber pine (*Pinus flexilis* James), lodge pine pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm. ex Wats.) and other conifers and usually supported understory graminoid/forb communities different from adjacent non-forested habitats. The mountain sagebrush habitat class was largely non-forested slopes and ridges of Green Mountain and Owl Hills dominated by mountain big sagebrush (*Artemisia tridentata* Nutt. var. *vaseyana* Rydb.) and graminoids, and intermingled with coniferous forest habitat. Grasslands were dominated by graminoids and usually occurred on high elevation, wind-swept slopes. Area estimates from digitized orthophoto maps (1:24,000 scale) indicate approximately 0.05, 0.06, 28, 59, 0.07, and 12% of the study area were streamside, bog/meadow, mountain sagebrush, lowland sagebrush, grassland, and coniferous forest, respectively.

The Whiskey Peak allotment supported approximately 75% of the 500 feral horses within the Green Mountain Wild Horse Herd Management Area prior to 1993. A roundup during the summer and fall of 1993 reduced the population to planned management levels of between 170 and 300 horses (BLM 1993). In addition to horses, the area also supports populations of pronghorn antelope (*Antilocarpa americana americana* Ord), elk (*Cervus elaphus nelsoni* Bailey), and mule deer (*Odocoileus hemionus hemionus* Rafinesque). Seasonal cattle (*Bos taurus*) use (7,723 animal unit months) occurs annually but did not occur in 1993 until after the conclusion of this study.

Habitat Selection

Habitat selection patterns of feral horses were observed in 1992 and 1993. During the June–August 1992 field season, habitat selection was estimated from 320 repeated observations of 20 individually identified horses of different sex and age classes. Daily surveys during daylight hours were conducted to relocate these individuals and determine their activity and habitat selection from independent, instantaneous observations. After the season, we suspected a visibility sampling bias in the 1992 observations resulting from potentially lower probabilities of horse relocation in wooded streamside and coniferous forest habitats (Oedekoven and Lindzey 1987, Neu et al. 1974).

To reduce potential bias in 1993, 23 randomly selected bands of undisturbed horses were followed and visually observed during daylight hours. Scan sampling (Altmann 1974) at 30-minute

intervals was used to determine the proportion of horses in the band in each habitat class, activity class (feeding, idling, or traveling), and time of day class (1=0500-0900 hours, 2=0901-1300 hours, 3=1301-1700 hours, 4=1701-2200 hours). Feeding included harvesting forage, drinking, and travel <5 steps while feeding. Idling included resting and minor movements. Traveling was directed movement of more than 5 steps. Geographic locations were recorded to allow determining distance to water and minimum convex polygon enclosing the study area.

Observation periods began during daylight hours, terminated at dark, resumed at daylight, and continued until the same time as the initial observation the previous day. Band relocations at daylight were usually close to where they were last seen at dark the previous evening. Horses were observed from a distance (≈ 200 m) that would not disrupt "normal" habitat selection and activity patterns with the aid of a 10 to 20 power spotting scope and binoculars. Horse bands were followed on horseback.

Habitat selection data from 1992 were summarized by determining the proportion of total observations occurring in each habitat. All 1993 observations were summarized by calculating the proportion of animals in each activity by habitat and time of day class.

Vegetation Utilization, Palatability, and Abundance

Percent utilization and percent moisture (succulence) were determined for the most abundant graminoid plant species on each habitat. Feral horses select primarily graminoid species (Krysl et al. 1984, Salter and Hudson 1979, Hansen 1976). Utilization will be indicative of the potential detriment of grazing on plant health. Utilization of plant species was determined through sequential biweekly late May through August 1993 estimates ($n=7$) of dry weight standing crop of 30 individually marked bunch grass plants or 0.01 m² quadrats containing one rhizomatous species along 3 transects (30m) in each habitat class (Smith et al. 1992). The difference between the average ending weight of grazed and ungrazed plants and ungrazed plants was used to calculate total percentage of herbage removal (utilization) for each habitat class. Bi-weekly utilization was not calculated because we observed relatively low levels of total utilization, and found no seasonal variation in feral horse habitat selection patterns with which to correlate seasonal utilization.

Forage succulence appears to be correlated with quality and palatability as herbivores usually graze plants with higher succulence, quality, and palatability (Smith et al. 1992, Pinchak et al. 1991, Senft 1985). Vegetation succulence was used as an index to forage palatability and quality. Randomly selected whole plant samples were collected from each habitat class (50 to 100 plants including major species with about 200-g total of plant material/habitat) at bi-weekly May–August intervals coinciding with utilization sampling. Green weights of these samples minus oven-dried (50°C, 36 hours) weights were divided by oven-dried weights to determine percent moisture (succulence).

Forage abundance as indicated by standing crop biomass of all herbage, above a minimum weight, was determined using visual obstruction measurements (following Robel et al. 1970). Bi-weekly May–August measurements were taken at 50 random points in each habitat class. The relationship between Robel readings and actual above-ground oven dry biomass was determined by taking the visual obstruction measurement in and harvesting 30 quadrats (0.25 m²), followed by determining coefficients by simple linear regression in each habitat class.

Diet Composition

Fecal samples from feral horses were collected during the spring, summer, and winter of 1991 and 1992. A minimum of 5 samples were collected by searching the vicinity of 4–6 sites (depending on seasonal access) on the allotment. Only fecal material determined by freshness and color to have been deposited during the seasonal period was collected. Fecal piles were subsampled, material was mixed and 5 subsamples taken. Subsamples were sent to a commercial lab (AFAB Laboratories in Ft. Collins, Colo.) for identification of plant species in feces. The relative frequency of fragments of each plant species in each sample were quantified by microhistological procedures outlined by Sparks and Malechek (1968). Plant epidermal characteristics determined from reference slides are used to identify species in microscope slides of fecal materials. Twenty fields per slide and 5 slides per sample were examined. Data were summarized by sites within seasons.

Statistical Analyses

Chi-square analyses (Neu et al. 1974) of 1992 and 1993 data separately were employed to determine whether feral horses utilized all habitat classes in proportion to their availability. Calculated χ^2 statistics may be biased if expected values are very low (eg. streamside, bog/meadow, and grassland habitat classes), thus creating an artificially large χ^2 and making the probability of a type I error greater than apriori p (Zar 1984). However, we did not combine these habitat classes because the mean (over all classes) expected value exceeded the minimum suggested by Roscoe and Byars (1971).

If χ^2 analyses indicated a significant difference existed between habitat selection and availability, relative preference for individual habitat classes was determined using the Bonferroni Z simultaneous confidence interval (CI) approach described by Neu et al. (1974) and revised by Byers et al. (1984). If the availability of a habitat class was less or greater than the CI, the habitat was considered to be preferred or not preferred respectively.

A General Linear Model analysis of variance (AOV) (Hicks 1973) was used to test for significant differences in vegetation attributes between habitat classes. If a significant difference was observed, a Scheffe mean separation test was employed. A factorial AOV design was used to evaluate the influence of time of day class, month, habitat class, and horse activity on proportions of horses in habitats. The 1993 data summary experimental unit for analysis was a monthly mean ($n=3$) proportion of horses for each time of day ($n=4$), habitat ($n=6$) and activity ($n=3$) class. The data assumptions of independence, normality of residuals, and equal variances necessary for AOV were evaluated prior to hypothesis testing.

Analyses were performed using the Statistical Analysis System (SAS Institute 1988) and Statistix (Statistix 1988) statistical software packages. All statistical tests were evaluated at the $p \leq 0.05$ level of significance.

Results and Discussion

Habitat Selection

Overall expected usage and observed usage (Table 1) were significantly different ($p \leq 0.05$) in 1993. Comparison of simultaneous confidence intervals to proportion of the area in each habitat (Table 1) indicated that the proportional use of streamside,

Table 1. Total area, relative area, expected use, and observed use by feral horses for 6 habitat classes on a study area within the Whiskey Peak Allotment, southcentral Wyoming, 1993.

Habitat Class	Total Area	Relative Area (P_{io})	Relative Usage (U_{io})	Expected Use ($E_i = n'p_{io}$)	Observed Use (O_i) ²	Bonferroni Intervals for U_{io}	Apparent ³ Selection Behavior
	(ha)						
Streamside	31	0.005	0.09	0.43	7.7	$0.008 \leq P_1 \leq 0.17^*$	+
Bog/Meadow	39	0.006	0.12	0.53	11.7	$0.029 \leq P_2 \leq 0.22^*$	+
Mtn. Sagebrush	1699	0.28	0.51	24.92	45.4	$0.37 \leq P_3 \leq 0.65^*$	+
Low. Sagebrush	3620	0.59	0.17	52.51	15.1	$0.03 \leq P_4 \leq 0.30^*$	-
Grassland	44	0.007	0.05	0.62	4.5	$0 \leq P_5 \leq 0.12$	=
Coniferous Forest	750	0.12	0.07	10.68	6.2	$0 \leq P_6 \leq 0.14$	=

¹n=86 for streamside and 89 for other habitat classes

² $\chi^2_5 = 44.1$, $p=0.00$; χ^2_5 (5, $\alpha=0.05$) = 11.07

³+ use greater than expected, $p \leq 0.05$

= use not different from expected, $p \leq 0.05$

- use less than expected, $p \leq 0.05$

bog/meadow, and mountain sagebrush habitats was significantly greater ($p \leq 0.05$) than the proportion of the study area occupied by these habitat classes. In contrast, lowland sagebrush habitats (Table 1) were used significantly less ($p \leq 0.05$) than the extent of these habitats within the study area. Feral horses used the coniferous forest and grassland habitat classes in similar ($p \leq 0.05$) proportion to their relative abundance on the study area.

Our suspicion of a visibility bias in the method of observing horses during 1992 appeared to be confirmed by the reduced proportion of horses observed in the streamside (1992=0.02, 1993=0.09) (Tables 1 and 2). Otherwise the 1992 results generally support the results of 1993 since (Byers et al. 1984) the observed proportions of habitat use in 1992 (Table 2) occur within the confidence intervals of proportional use in 1993 (Table 1). Many streamside habitats support dense stands of willow, cottonwood, and aspen which obscure horses. This problem was mitigated with the 1993 sampling method, likely increasing the proportion of streamside observations.

A feral horse monitoring program, independent of our study, was conducted in 1992 in the general vicinity of our study area, by the Lander Resource Area of the Bureau of Land Management

(unpublished). These results lend support to our overall conclusions that feral horses show a preference for riparian habitats.

The degree of selection for riparian habitats by unmanaged feral horses on this study area seems noteworthy considering the widespread concern for the condition of riparian vegetation; the streamside and bog/meadow habitats combined account for slightly over 1% of the study area, but received 21% of the use by feral horses. The preference of large herbivores for riparian habitats is well documented (Smith et al. 1992, Pinchak et al. 1991, Roath and Krueger 1982), yet this selection behavior in feral horses has not been widely reported in the literature. Ganskopp and Vavra (1986) reported that feral horses in the northern sagebrush steppe exhibited no preference for a particular plant community, and instead made the greatest use of the most prevalent habitat. In contrast, the results of Salter and Hudson (1979) and Hubbard and Hansen (1976) indicate that *Carices* were the major dietary constituent of feral horses, suggesting that horses select more mesic communities in their foraging behavior if they are available. Our findings are consistent with Salter's (1979) observations that feral horses utilized certain meadow types more heavily on a year-long basis. Berger (1986) also reported that

Table 2. Total area, relative area, expected use, and observed use by feral horses for 6 habitat classes on a study area within the Whiskey Peak Allotment, southcentral Wyoming, 1992.

Habitat Class	Total Area	Relative Area (P_{io})	Relative Usage (U_{io})	Expected Use ($E_i = n'p_{io}$)	Observed Use (O_i) ²	Bonferroni Intervals for U_{io}	Apparent ³ Selection Behavior
	(ha)						
Streamside	31	0.005	0.02	1.6	6.4	$0 \leq P_1 \leq 0.041$	=
Bog/Meadow	39	0.006	0.12	1.92	38.4	$0.072 \leq P_2 \leq 0.17^*$	+
Mtn. Sagebrush	1699	0.28	0.59	89.6	188.8	$0.52 \leq P_3 \leq 0.66^*$	+
Low. Sagebrush	3620	0.59	0.17	189.0	54.4	$0.12 \leq P_4 \leq 0.23^*$	-
Grassland	44	0.007	0.04	2.24	12.8	$0.01 \leq P_5 \leq 0.07^*$	+
Coniferous Forest	750	0.12	0.06	38.0	19.2	$0.25 \leq P_6 \leq 0.10^*$	-

¹n=320

² $\chi^2_5 = 320.4$, $p=0.00$

³+ use greater than expected, $p \leq 0.05$

= use not different from expected, $p \leq 0.05$

- use less than expected, $p \leq 0.05$

Table 3. Herbaceous vegetation standing crop (g/0.25m² ± SE¹) of 4 habitat classes on Whiskey Peak Allotment in southcentral Wyoming, 1993.

Habitat Class	Herbaceous Standing Crop Sampling Period					Average
	6/30	7/7	7/20	8/4	8/17	
	(g/0.25m ² ± SE ¹)					
Streamside	24 ± 1.84	22 ± 1.27	33 ± 1.97	43 ± 2.40	21 ± 1.27	29 ± 4.02a ³
Bog/Meadow	30 ± 1.84	33 ± 1.97	41 ± 1.84	66 ± 5.94	52 ± 3.68	44 ± 5.81b
Grassland	8 ± 1.27	48 ± 13.29	15 ± 1.84	13 ± 1.56	21 ± 2.12	20 ± 6.26c
Coniferous Forest	<4 ²	5 ± .424	4 ± .424	5 ± .57	6 ± .57	5 ± 0.22d

¹SE = Standard error N=5 dates, 50 observations within dates

²Standing crop below the minimum detectable amount

³Means followed by the same letter were not significantly different, p≤0.05

meadows received the greatest use in proportion to their availability, when compared to all other habitats.

Forages in the streamside and bog/meadow habitat classes had the greatest ($p < 0.05$) vegetation standing crop (Table 3) and were high ($p \leq 0.05$) in succulence (Table 4) compared to other habitats. Habitat selection by large herbivores is reported to be positively associated with forage biomass and succulence (Smith et al. 1992, Pinchak et al. 1991, Senft et al. 1985). Salter and Hudson (1979) found that seasonal variability in diet composition of feral horses was related to forage palatability and abundance. Utilization levels (Table 5) on these habitats, while not high

ence for these habitats may also be related to the close proximity of many mountain sagebrush habitats to streamside and bog/meadow habitats. Following feeding or watering in riparian habitat classes, horses moved into the adjacent mountain sagebrush habitats. However, the preference for the more abundant mountain sagebrush habitats was not reflected in significantly higher ($p \leq 0.05$) utilization (Table 5) because of the large area relative to animal numbers.

The lower use than availability of lowland sagebrush habitats may be related to low ($p \leq 0.05$) forage productivity (Table 3) and succulence (Table 4) compared to higher elevation habitats.

Table 4. Forage succulence (% moisture, dry weight basis⁴) of 6 habitat classes on Whiskey peak Allotment in southcentral Wyoming, 1993.

Habitat Class	Sampling Period ²						Mean ± SE ¹
	5/27 SD ¹	6/10	6/24	7/7	7/20	8/4	
	(% moisture)						
Streamside	70	72	70	65	68	64	67 ± 1.47a ³
Bog/Meadow	75	71	65	65	64	63	65 ± 2.49ab
Mtn. Sagebrush	74	64	62	58	54	49	58 ± 3.93bc
Low. Sagebrush	65	62	56	54	48	41	51 ± 4.27c
Grassland	72	69	65	59	42	47	56 ± 5.32c
Coniferous Forest	84	75	66	70	67	58	67 ± 4.08a

¹SE = Standard deviation

²Bi-weekly sampling from 5/27 to 8/18

³Means followed by the same letter were not significantly different, $p \leq 0.05$

⁴((wet weight-dry weight)/dry weight × 100=% moisture on a dry weight basis)

% moisture of fresh samples = ((%moisture dry basis/(% moisture dry basis + 100)) × 100

because of the herd reduction, was significantly higher ($p \leq 0.05$) than on all other habitats. Higher horse numbers would undoubtedly result in these habitats having the greatest potential to receive overuse of the vegetation resource.

The later growth initiation by forage species at higher elevations may partially explain the preference of horses for the mountain sagebrush habitat class over the lowland sagebrush habitats during the months of this study. Forage abundance (Table 3) was low for both habitats, being below the minimum measurable with the Robel et al. (1970) technique (≈ 4 g/0.25m²) but succulence (Table 4) was higher ($p \leq 0.05$) in mountain sagebrush areas. Topographic diversity and proximity to other preferred habitat offer a better explanation of why feral horses may prefer mountain sagebrush habitats. Feral horses may select the open ridges and slopes of this habitat class for refuge from insects (Keiper and Berger 1982), or to enhance their visual assessment of threats (Ganskopp and Vavra 1986). Miller (1983) also found that the proximity to ridges was a significant factor in the habitat selection of feral horses in the Red Desert of Wyoming. The prefer-

The avoidance of lowland sagebrush habitats by feral horses in this study illustrates seasonal movements from lower to higher elevations in summer. Area ranchers and agency personnel have observed that feral horses on the Whiskey Peak Allotment winter on lowland sagebrush sites where access to feed is less hampered by snow accumulation. We did observe a larger proportion of horses using the lowland sagebrush habitats during the early spring prior to initiation of observations. This selection behavior may also be a result of earlier growth initiation by forage species on these lower elevation sites. Miller (1983) and Salter and Hudson (1979) also concluded that areas which remained snow-free or had reduced snow depth throughout the winter were exploited as feeding habitat by feral horses. Salter (1979) also suggested that habitat selection during early spring was related to stage of forage growth and that areas which "green-up" first were most heavily used for grazing. Although water is abundant on the study area as a whole, during the summer distance to water from the northern reaches of the lowland sagebrush area may exceed 1.5 km. This distance to water may be sufficient to discourage feral horse use of these sites.

Table 5. Utilization (% \pm SE¹) of annual forage growth in 6 habitat classes on Whiskey Peak Allotment in southcentral Wyoming, as of 18 Aug. 1993.

Habitat Class	Utilization
	--- (% \pm SE ¹) ---
Streamside	7.5 \pm 1.5 a ²
Bog/Meadow	11.0 \pm 2.9 a
Mtn. Sagebrush	2.3 \pm .83 b
Lowland Sagebrush	2.0 \pm 1.09 b
Grassland	2.2 \pm 1.02 b
Coniferous Forest	2.9 \pm 1.02 b

¹SE = Standard Error N=5

²Means followed by the same letter were not significantly different, $p \leq 0.05$

No apparent selection behavior was observed for grassland habitats even though the abundance of forage (Table 3) on these sites was relatively high. Forage succulence (Table 4) was lower ($p \leq 0.05$) than on preferred habitats. The steep topographic position of grassland habitats and the distance to preferred riparian habitats may also have made these sites less attractive for foraging.

Coniferous forest habitats, used in proportion to their availability, had higher ($p \leq 0.05$) forage succulence (Table 4) but lower ($p \leq 0.05$) biomass (Table 3) than other habitats. This indicates that the influence of forage succulence on habitat selection is initiated above some minimum level of forage productivity. This habitat, as with all other abundant but less preferred habitats had lower ($p \leq 0.05$) utilization (Table 5) than the less abundant preferred habitats.

Horse Activities

The proportion of horses feeding, idling, or traveling did not differ significantly ($p \leq 0.05$) between habitat class or monthly categories. This lack of seasonal variation in habitat selection was also observed by Ganskopp and Vavra (1986) and Denniston et al. (1982).

Feral horses spent 61, 32, and 7% of their diurnal hours feeding, idling, and traveling, respectively. We observed a significant difference in feeding and loafing activities between different time classes (Fig. 2). Generally, horses spent morning and evening hours feeding and loafed during mid-day. Traveling was not significantly different between time classes. These results are consistent with observations reported by Salter and Hudson (1979). We found no significant interaction between diurnal activity pat-

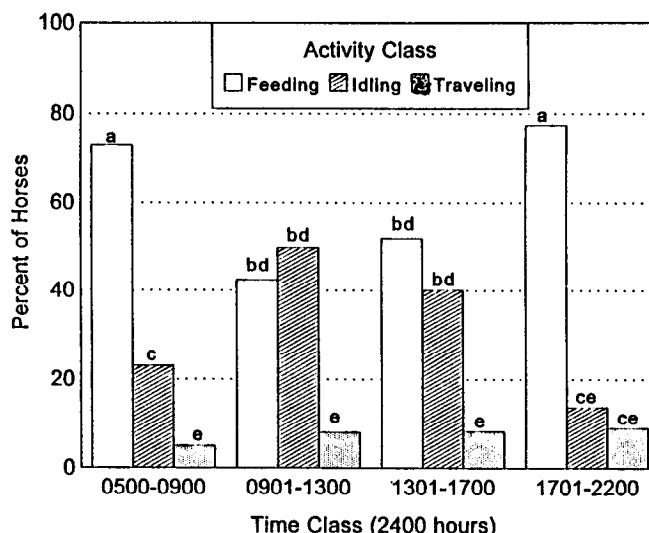


Fig. 2. Activity % in each time of day class in 1993.

terns and habitat selection which suggests that feral horse activity patterns are independent of habitats used.

Diet Composition

The annual diet of feral horses on this study area was comprised mostly of graminoid species with a relatively small and highly variable forb and shrub component (Table 6), similar to findings of Salter and Hudson (1979) and Hubbard and Hansen (1976). Forage species of the *Agropyron*, *Stipa*, and *Carex* genera were major dietary constituents during all seasons. The proportional intake of each forage species was relatively constant between seasons, except for *Carex* which increased in the spring and *Festuca* which increased in the summer consistent with the seasonal availability and use of habitats where these species occur. Microhistological analyses cannot distinguish between upland and mesic/aquatic *Carices*, however the increase in *Carices* consumption early in the growing season may reflect horses selection of upland species of this genus (threadleaf and needleleaf sedge, *C. filifolia* Nutt. and *C. stenophylla* Wahl., respectively) because of their early growth and high palatability in the spring. *Festuca* occurs on higher elevation sites of the study area that are only used in summer.

In general, *Carices* are the most important forage genus to feral

Table 6. Major dietary components (mean % \pm SE¹) of feral horses on the Whiskey Peak Allotment in southcentral Wyoming.

Plant Name	Winter 1991 (n=5)	Spring 1991 (n=5)	Summer 1991 (n=4)	Winter 1992 (n=6)	Spring 1992 (n=6)	Summer 1992 (n=4)
Graminoids	----- (% Relative Density \pm SD ¹) -----					
<i>Agropyron</i>	13 \pm 2.68	12 \pm 2.23	14 \pm 2	10 \pm 1.22	8 \pm 1.63	8 \pm 2
<i>Carex</i>	24 \pm 5.8	62 \pm 7.15	31 \pm 2.5	26 \pm 4.49	41 \pm 5.71	23 \pm 5
<i>Festuca</i>	4 \pm 1.34	< 1	18 \pm 1.5	6 \pm 2.44	8 \pm 1.63	24 \pm 12
<i>Juncus</i>	2 \pm .89	1 \pm .89	2 \pm 1	1 \pm .408	3 \pm .816	< 1
<i>Poa</i>	< 1	1 \pm .357	< 1	4 \pm .816	9 \pm 1.63	3 \pm .5
<i>Stipa comata</i>	22 \pm 7.15	18 \pm 2.68	19 \pm 1.5	28 \pm 4.89	27 \pm 4.49	32 \pm 9
<i>Oryzopsis</i>	1 \pm .89	2 \pm .447	7 \pm 3.5	1 \pm .244	3 \pm 1.22	1 \pm .3
Forbs and Shrubs						
Total	23 \pm 14.31	< 1	< 1	19 \pm 6.53	< 1	< 1

¹SE=Standard error of n sites. Data were averages of pooled samples within sites.

horses in this study area. Although a portion of the total *Carex* intake is from upland species, selective preference of horses for streamside and bog/meadow habitats indicate that mesic and aquatic species of this genus represent a significant proportion of feral horse diets compared to other forage species. Dietary composition generally follows patterns of habitats selected by horses.

Conclusions

Selectivity, diets, and utilization observed in this study indicate any detrimental impacts from excessive numbers of feral horses would first be apparent in the streamside, bog/meadow, and secondarily in mountain sagebrush habitats of this study area. These habitats were preferentially selected by feral horses during the growing season on the study area, the most probable season of negative grazing impact. The streamside and bog/meadow habitats represent a small portion of the study area and the allotment as a whole, yet these are also the habitats preferred by wildlife (Dealy et al. 1981, Leckenby et al. 1982, Collins 1980, Hubbard 1977) and livestock (Smith et al. 1992, Pinchak et al. 1991, Hart et al. 1991, Roath and Krueger 1982). Further evidence of potential for spatial overlap between feral horses and elk occurs with their common preference for the open ridges of the mountain sagebrush habitats (Hart et al. 1991, Oedekoven and Lindzey 1987, Thomas and Toweill 1982, Julander and Jeffery 1964).

Feral horse numbers must be kept at appropriate levels to mitigate the potential for detrimental impacts to habitats. Feral horses should also be managed with the knowledge that there appears to be a potential for interspecific competition between horses and other large herbivores.

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Degradability of Andean range forages in llamas and sheep

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Abstract

In sacco dry matter degradability (DMD) of the most commonly consumed range forages by llamas and sheep in the arid highlands of Bolivia was measured during the wet and dry seasons to determine if llamas exhibit a higher digestive ability than sheep. Results showed that degradability of low quality forages (DMD below 60% in sheep) was 20 to 30% higher for llamas than sheep, while no significant differences were found for highly digestible forages. There was a high correlation between DMD in llamas and sheep with a coefficient of determination of 0.96. Parameters of degradation curves indicated that llamas did not have higher microbial activity than sheep, since there was no consistent difference in degradation rates of the studied forages. Nonetheless, significantly higher potential degradability and effective degradability found in this study suggested that the longer retention time in the forestomach of llamas may be responsible for higher digestibility of poor quality forages.

Key Words: *in sacco* disappearance, kinetics of degradation, arid highlands, Bolivia

Andean livestock herding systems frequently include both camelids and sheep, which are grazed together (Browman 1990, Tichit 1995). In the arid highlands of Bolivia, the association of llamas and sheep, and sometimes alpacas, has been characterized by Tichit and Genin 1997. Climatic conditions (annual rainfall of 300 mm and almost 300 days of frost per year) hinder agriculture and other livestock species like cattle and horses, which are present in more favourable Andean environments such as the sub-humid Peruvian altiplano. The relative proportion of camelids within herds depends largely upon the nature of available forage resources and the overall size of the farms. Other factors such as particular historical transformations of communities, economic opportunities and socio-cultural patterns also influence herd structure. From an ecophysiological point of view, mixed herds of llamas and sheep allow for better utilization of the overall

Resumen

Se midió la degradabilidad *in sacco* (DMD) en llamas y ovinos de la materia seca de los principales forrajes nativos del altiplano árido de Bolivia, con el fin de comparar las capacidades digestivas de estas dos especies animales. Los resultados muestran que la DMD de los forrajes de baja calidad (DMD inferior a 60% en ovinos) es mayor en un 20 a 30% en llamas respecto a ovinos, mientras que no se observaron diferencias significativas en el caso de forrajes altamente digeribles. Se encontró una alta correlación en las DMD entre llamas y ovinos ($r^2=0.96$). Los parámetros de las curvas de degradación sugieren que las llamas no presentaron una actividad microbiana superior a la de los ovinos porque no hubo diferencias significativas en las tasas de degradación de los forrajes estudiados entre estas dos especies animales. Sin embargo, los valores significativamente superiores en la degradabilidad potencial y la degradabilidad efectiva encontrados en llamas indican que la superioridad de estos camélidos para digerir los forrajes de baja calidad se debe en primer lugar a un mayor tiempo de retención del alimento en el rumen.

available forage due to different grazing behavior (Pfister et al. 1989, San Martin 1987). In the arid highlands of Bolivia, Genin et al. (1994) showed that llamas consume significantly higher proportions of the dominant coarse bunchgrasses such as *Festuca orthophylla* Pilger and *Stipa ichu* (R & P.) Kunth than sheep. Sheep seek more of the fine herbaceous plants growing under the shrub canopies. Though shrub foliage is abundant in these rangelands (Alzerreca and Lara 1988), shrubs represent less than 20% of the dietary components of both llama and sheep.

Studies concerning the ability of these animal species to digest forage have been reviewed by San Martin and Bryant (1989) and Dulphy et al. (1994). They reported high discrepancies in digestion coefficients. These authors attribute these discrepancies to animal selectivity not taken into account in some experiments and to the quality of feed used. San Martin (1987) observed significantly greater digestion coefficients for llamas than sheep on low and medium quality reconstituted diets (less than 10% CP and less than 2.8 Mcal DE/kg DM) but did not find differences in high quality diets (15% CP and 3.2 Mcal DE/kg DM). In the Andean pastoral zone, animals graze exclusively on native range plants. Very few studies have emphasized the digestibility of range forages actually consumed by llamas and sheep in this

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region. Concerning the dominant coarse bunchgrasses of the Andean rangelands, Maiza and Cardozo (1992) reported a digestion coefficient for dry matter of *S. ichu* almost 20% greater in llamas than in sheep. Genin et al. (1994) found digestion coefficients of *F. orthophylla* significantly higher in llamas (54.2 and 41.3% during wet and dry seasons, respectively) than in sheep (41.4 and 39.4% during wet and dry seasons, respectively). No data are available concerning other classes of forages consumed by llamas and sheep in this area.

The purpose of this study was to compare *in sacco* dry matter degradability during wet and dry seasons and the kinetics of rumen degradation of range forages in llamas and sheep in the arid puna of Bolivia in order to determine if llamas can utilize more efficiently the dominant rangelands of this region.

Material and Methods

In Sacco Dry Matter Degradation

Three coarse bunchgrass species (*F. orthophylla*, *F. dolichophylla* Presl., *S. ichu*), 3 fine grass species (*Calamagrostis heterophylla* (Wedd.) Pilger, *Poa candamoana* Pilger, *Distichlis humilis* Phil.), 4 shrubs (*Adesmia spinosissima* Meyen & Vogel, *Tetraglochin cristatum* (Britton) Rothn, *Parastrephia lepidophylla* (Wedd.) Cabrera, *Baccharis incarum* Wedd.) and 1 forb (*Tarasa tenella* (Cav.) Krapovickas), representing the most commonly consumed forages in the arid highlands of Bolivia (Genin et al 1994, Villca and Genin 1995), were collected during the wet (February) and dry (August) seasons. Parts of the plants normally selected by livestock were dried, and ground to pass a 2-mm Wiley mill screen. Samples of approximately 2 g were placed in 10 × 15 cm nylon bags (50 µm mesh) for determining *in sacco* dry matter degradability (DMD), as described by Orskov et al. (1980). Six bags of each forage from each season were suspended in the rumen of 2 animals of each species for 48 hours, according to Michalet-Doreau et al. (1987). The experimental animals were four-year-old male llamas weighing 95 kg and two-year-old castrated sheep weighing 28 kg with rumen fistulas. They received ad libitum barley hay which fulfilled their nutritional requirements. Following removal from the rumen, bags were rinsed with water until effluent was clear, and frozen for storage. After drying the bags at 65°C for 48 hours, DMD was calculated as weight loss of material. Analyses of variance (6 repetitions × 2 animals/species) was performed to compare, by forage and by season, the differences in degradability between llama and sheep. Simple linear regression was used to describe the relationship between degradability of forages in sheep and llamas.

Degradation Kinetics

Six forage species representing the 3 types of forages consumed by animals (coarse bunchgrasses *F. orthophylla* and *F. dolichophylla*; fine grass *C. heterophylla*; forb *T. tenella*; and shrubs *A. spinosissima* and *P. lepidophylla*) were collected in February (wet season). Six samples of each of these forages were incubated for 4, 8, 12, 24, 48, and 72 hours in rumens of llamas and sheep, using the procedures described above. Soluble dry matter losses (DMD at time 0) other than those due to microbial and enzymatic degradation were measured by placing a sample bag in water bath for 24 hours (Silva and Orskov 1988). The model by Orskov and McDonald (1979) was used in kinetics

measurements to determine the plateau value of the different substrates and their rates of degradation:

$$p = a + b(1 - \exp(-ct))$$

where: *p* is the actual degradation after time *t*; *a* is the soluble fraction assumed to disappear instantly (intercept of the degradation at time zero); *b* is the insoluble but potential degradable component of the feed; and *c* is the rate constant at which *b* is degraded.

Effective degradability (ED) was calculated assuming particulate passage rates of poor quality forages of 3.1 and 4.1%/hour for llamas and sheep, respectively (San Martin 1987), and the formula by Orskov and McDonald (1979):

$$ED = a + (b(c/(c+k)))$$

where: *a*, *b*, and *c* were the constants from Eq. 1 and *k* was the particulate passage rate. The calculation for the DM degradation parameters was executed using the SAS program Proc NLIN (SAS, 1988).

Results and Discussion

In Sacco DMD

The *in sacco* dry matter digestibility (DMD) after 48 hours of incubation was higher in llama than in sheep for most forages, with differences varying from 1.1 to 13.7 degradability units (Table 1). Degradability values in llamas were approximately 1.25, 1.1, and 1.05 times those found in sheep for coarse bunchgrasses, forbs and fine grasses, and shrubs, respectively. The less degradable the forage, the greater was the difference between the 2 animal species. Significant differences were generally found for forages with DMD of roughly less than 60% in sheep. In the case of the Compositae shrubs *P. lepidophylla* and *B. incarum*, DMD values were very high and should be considered with caution because they may reflect high pulverization during milling with subsequent losses during washing.

There was a high correlation between DMD in llamas and sheep with a coefficient of determination *r*² of 0.96 (*p* < 0.01) (Fig. 1). Kayouli et al. (1991) compared degradability of mediterranean roughages in dromedary camels and sheep and found similar trends.

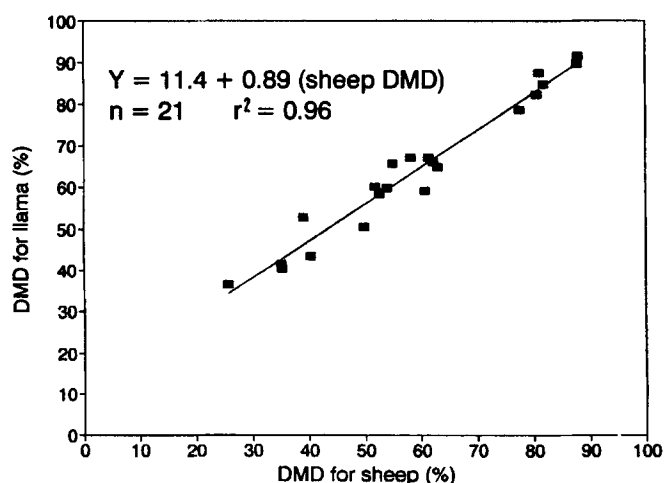


Fig. 1. Relationship between *in sacco* dry matter degradability in sheep and llamas.

Table 1. Percentage *in sacco* dry matter degradability after 48 hours in llamas and sheep (Mean \pm S.E.) of dominant Andean range forages collected during wet and dry seasons.

Classes and Forage species	growing period		dry period	
	llama	sheep	llama	sheep
	----- (%) -----			
Coarse grasses				
<i>Festuca orthophylla</i>	52.8 \pm 5.2 ^a	39.1 \pm 3.2 ^b	40.5 \pm 1.5 ^a	35.3 \pm 1.9 ^b
<i>Stipa ichu</i>	43.4 \pm 4.4 ^a	40.3 \pm 4.3 ^a	36.6 \pm 1.9 ^a	25.7 \pm 3.9 ^b
<i>F. dolichophylla</i>	65.7 \pm .8 ^a	55.0 \pm 0.6 ^b	50.5 \pm 7.0 ^a	49.9 \pm 4.3 ^a
Fine grasses and forb				
<i>Calamagrostis heterophylla</i>	66.2 \pm 2.0 ^a	62.2 \pm 4.7 ^a	41.6 \pm 4.5 ^a	35.2 \pm 1.1 ^b
<i>Poa candamoana</i>	67.1 \pm 4.2 ^a	58.2 \pm 2.3 ^b	58.3 \pm 4.2 ^a	52.6 \pm 4.4 ^b
<i>Distichlis humilis</i>	87.5 \pm 7.5 ^a	81.1 \pm 2.5 ^a	64.8 \pm 2.1 ^a	63.0 \pm 1.9 ^a
<i>Tarasa tenella</i>	89.7 \pm 1.3 ^a	88.0 \pm 0.4 ^a	---	---
Shrubs				
<i>Adesmia spinosissima</i>	59.8 \pm 4.7 ^a	53.9 \pm 3.4 ^b	59.2 \pm 4.0 ^a	60.7 \pm 1.5 ^a
<i>Tetraglochin cristatum</i>	67.2 \pm 1.8 ^a	61.4 \pm 2.7 ^b	60.2 \pm 3.8 ^a	51.9 \pm 3.3 ^b
<i>Parastrephia lepidophylla</i>	78.8 \pm 8.2 ^a	77.7 \pm 3.6 ^a	82.3 \pm 9.6 ^a	80.6 \pm 1.7 ^a
<i>Baccharis incarum</i>	84.8 \pm 8.7 ^a	81.9 \pm 5.5 ^a	91.5 \pm 1.6 ^a	88.1 \pm 2.0 ^b

^{a,b} Within period, means with different letters are different between animal species (P<0.01).

These authors reported differences in *in sacco* DMD between camels and sheep of more than 10 units for forage with a degradability of less than 50% in sheep, while there was little difference in degradability for high quality forages such as green ryegrass or ensiled sugar beet pulp. Cordesse et al. (1992) did not find any differences in digestibility between llamas and sheep utilizing lucerne hay and ammoniated wheat straw.

Degradation Kinetics

The degradation equation proposed by Oskov and McDonald (1979) provided a good fit of the data with coefficients of determination higher than 0.98 (Fig. 2, Table 2). This suggests that degradation patterns of forages proposed by these authors for ruminants are also relevant for pseudo-ruminants such as llamas.

The potential degradability (the factor a + b of the model) was significantly higher in llamas than in sheep for *C. heterophylla* and *F. orthophylla* (P < 0.01) and *A. spinosissima* (P < 0.05). No differences were found for highly degradable forages (Table 2).

In contrast, degradation rates (factor c) varied between llamas and sheep with no clearly defined pattern (Table 2). Values of c varied from less than 0.03% hour⁻¹ for coarse bunchgrasses to more than 0.15% hour⁻¹ for the highly digestible *T. tenella* in both

llamas and sheep. Degradation rates of coarse bunchgrasses were comparable to those of wheat straw found in sheep and goats, while degradation rates of *T. tenella* were superior to those of ryegrass (Flachowsky and Tiroke 1993). Degradation rates of shrubs were intermediate (0.05 to 0.08% hour⁻¹).

These results suggest the importance of the transit time of the feed. Blaxter (1963) stated that maximal digestion occurs only if the passage of food is delayed so that the food is exposed to those sites where microbial action takes place. San Martin (1987), studying passage rates in llamas and sheep, found digesta retention time of low and medium quality rations in the first 2 compartments of the stomach of llamas of 29 hours (see San Martin and Bryant (1989) for a full description of the digestive system in South American camelids), whereas the retention time in the reticulo-rumen of sheep was 22 hours. On the basis of San Martin's estimates of particulate passage rate in the rumen (3.1 and 4.1% hour⁻¹ for low quality diets in llama and sheep, respectively), effective degradability of the studied forages was almost 30% higher in llamas than in sheep for forages of low degradability and less than 10% for highly degradable forages. In this study, the estimated effective degradability of *F. orthophylla* in the rumen conformed to 62 and 67% of the apparent digestibility found *in vivo* in llamas and sheep, respectively (Genin et al.

Table 2. Parameters of degradation curves (DMD=a + b(1-(exp(-ct))), Orskov and McDonald 1979) of forages collected during growing season.

Forage species	Potential degradability ¹		Degradation rate ²		Effective degradability ³	
	Sheep	Llamas	Sheep	Llamas	Sheep	Llamas
	----- (%) -----		----- (% hour ⁻¹) -----		----- (%) -----	
Coarse grasses						
<i>Festuca orthophylla</i>	47.4 ^{b4}	71.4 ^a	0.025 ^a	0.013 ^b	27.6 ^b	33.5 ^a
<i>F. dolichophylla</i>	81.3 ^a	83.9 ^a	0.015 ^b	0.024 ^a	38.8 ^b	49.3 ^a
Fine grass and forb						
<i>Calamagrostis heterophylla</i>	58.2 ^b	63.3 ^a	0.024 ^b	0.075 ^a	32.5 ^b	49.3 ^a
<i>Tarasa tenella</i>	88.6 ^a	90.9 ^a	0.107 ^a	0.144 ^a	70.6 ^b	77.3 ^a
Shrubs						
<i>Adesmia spinosissima</i>	61.1 ^b	65.8 ^a	0.067 ^a	0.048 ^b	38.7 ^b	48.5 ^a
<i>Parastrephia lepidophylla</i>	79.5 ^a	84.6 ^a	0.079 ^a	0.054 ^b	60.7 ^a	62.3 ^a

¹ Potential degradability = a + b; a = soluble fraction b = insoluble but potential degradable

² Degradation rate = c

³ Effective degradability = a + (b(c/(c+k))) where k is passage rate (3.1 and 4.1% hour⁻¹ for llamas and sheep, respectively).

^{a,b} For each parameter, means followed by the same letter are not different between animal species (P<0.05).

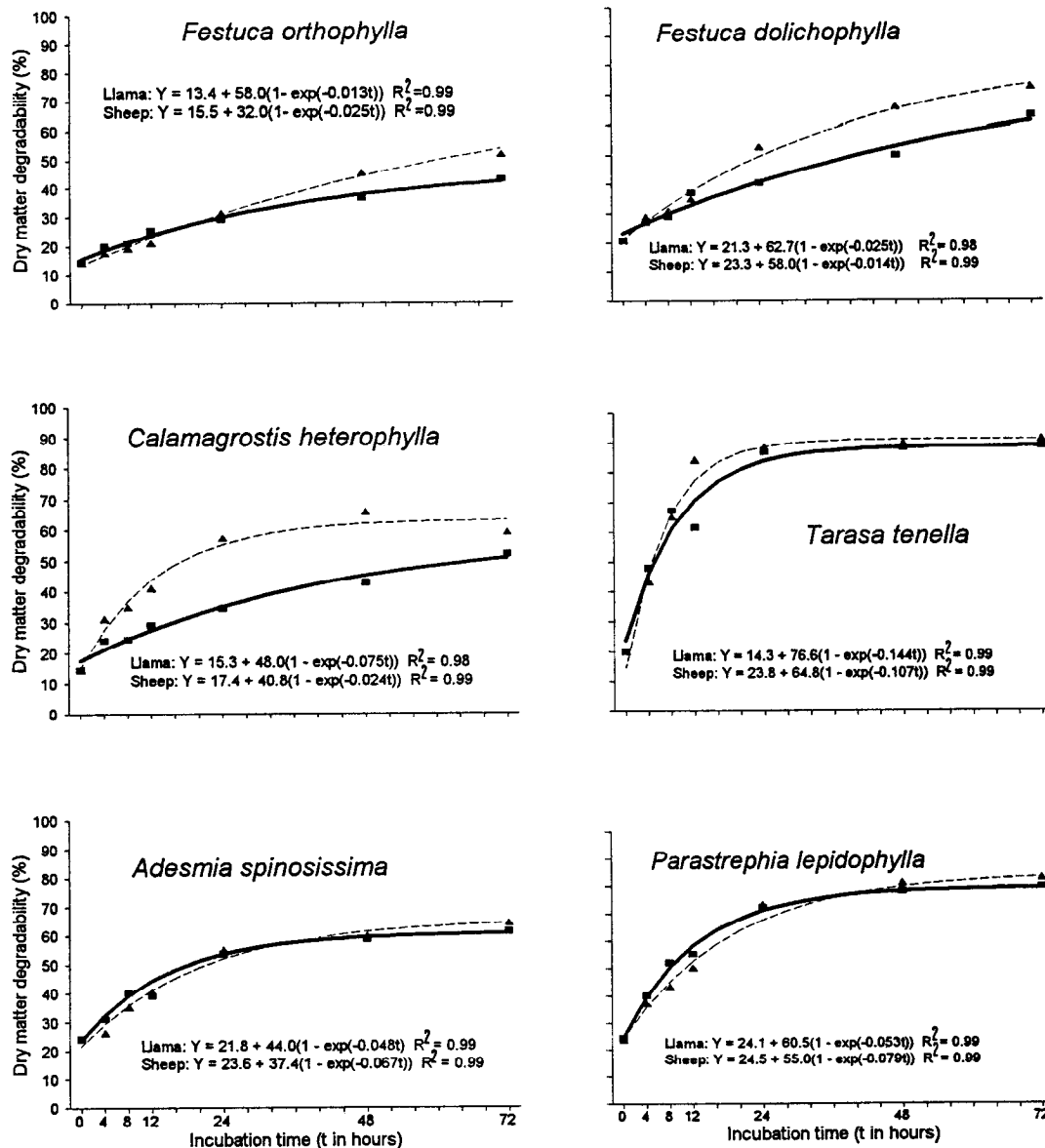


Fig. 2. Degradation curves of predominant Andean forages in llamas (dotted lines and triangles) and sheep (solid lines and squares). Values fitted to the equation $Y = a + b(1 - \exp(-ct))$ proposed by Orskov and McDonald (1979). Each symbol is the mean of 6 replicates.

1994). These proportions agree with those noted by Jarrige (1980) for forages of low digestibility (55 to 70% of the overall digestible OM effectively digested in the rumen). San Martin and Bryant (1989) suggested that longer retention time in rumen, associated with the peculiar morphology, histology and a higher motility of the forestomach confers a greater digestive efficiency of South American camelids, especially for low quality roughages. The enhanced ability to degrade low nitrogen feeds in llamas is also related to their capacity to maintain higher NH_4^+ concentrations in their forestomach compared to sheep (Hinderer and Engelhardt 1975., Engelhardt and Schneider 1977). Further, Kayouli et al. (1993) showed a greater cellulolytic activity of the ruminal microbes in llamas than in sheep. However, further studies are required in which these mechanisms can be investigated simultaneously.

Conclusions

Due to their feeding behavior (Genin et al. 1994) and higher digestive capabilities resulting from slower transit time for particulate matter, llamas exhibited a greater adaptation than sheep to utilize the poor quality rangelands found in the arid Andean highlands, especially those dominated by coarse bunchgrasses which cover extensive areas of the region. Degradability coefficients for low quality Andean range forages found in this study were 20 to 30% high in llamas than in sheep. Although llamas may be more efficient grazers, sheep present some advantages such as a higher reproductive rate and a more ready market for their meat (Tichit 1995). These aspects could strongly influence the choice of herd composition in unpredictable environments (Mace and Houston 1989). At the farm level, llamas and sheep play complementary roles in the use of the available resources, in the products they supply, and in their capability to respond to household's needs.

Raising these 2 species of livestock, combined in some cases with alpacas, is viewed as a sound strategy to spread different kinds of risks (i.e. drought, disease outbreaks, animal off-take in relation to reproductive capacities, and market price fluctuations).

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Effects of sheep grazing on a spotted knapweed-infested Idaho fescue community

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Abstract

Spotted knapweed (*Centaurea maculosa* Lam.), a Eurasian perennial forb, is replacing many native perennial grasses, such as Idaho fescue (*Festuca idahoensis* Elmer.), in foothills of the Northern Rocky Mountain region. Our objective was to determine if 3 summers of repeated sheep grazing would reduce spotted knapweed without impacting the dominant, associated native perennial grass. Each summer, small pastures were grazed for 1–7 days in mid-June, mid-July, and early September. Areas repeatedly grazed by sheep had lower densities of seedlings, rosettes, and mature spotted knapweed plants than ungrazed areas. In addition, the proportion of young plants in the population was less in grazed than ungrazed areas. Basal areas of spotted knapweed plants were greater in grazed (8.2 cm²) than ungrazed areas (4.0 cm²). There were fewer spotted knapweed seeds in soil samples from grazed areas (12 seeds m⁻²) than from ungrazed (49 seeds m⁻²). Idaho fescue plant density increased 40% in grazed areas from 1991 to 1994, but leaves and flower stems on these plants were 38% and 17% shorter, respectively, than in ungrazed areas. By 1994, frequency of Kentucky bluegrass (*Poa pratensis* L.) was 35% greater in grazed than ungrazed areas. Grazing did not alter the amount of litter; however the amount of bare soil increased from 2.2 to 5.6% in grazed areas, while it decreased from 4 to 1% in ungrazed areas. Three summers of repeated sheep grazing negatively impacted spotted knapweed, but minimally affected the native grass community. A long term commitment to repeated sheep grazing may slow the rate of increase of spotted knapweed in native plant communities.

Key Words: weeds, sheep, *Centaurea maculosa*, *Festuca idahoensis*, age class distribution, seed bank

Spotted knapweed (*Centaurea maculosa* Lam.), an aggressive, introduced perennial forb, has replaced native perennial grasses, including Idaho fescue (*Festuca idahoensis* Elmer.), in many foothill rangelands in the Northern Rocky Mountain region (Tyser and Key 1988, Lacey et al. 1992). Herbicides, insects, pathogens, and fire have not effectively contained the spread of this noxious weed. Large herbivores rarely graze spotted knap-

weed, possibly because it contains cnicin, a bitter tasting compound (Watson and Renny 1974, Kelsey and Locken 1987).

Livestock producers have observed sheep using spotted knapweed (Cox 1989), however its tolerance to grazing is unknown. In a greenhouse study, a single defoliation did not affect spotted knapweed, whereas defoliations repeated at monthly intervals reduced root and crown weights, and carbohydrate concentrations in roots, crowns, and stems (Kennett et al. 1992, Lacey et al. 1994). Our intent was to graze the pastures repeatedly with sheep during summer dormancy when the impact on cool-season perennial grasses would be minimal. The purpose of this study was to assess the effects of repeated grazing by sheep on spotted knapweed and associated plants to determine if sheep grazing could be used to reduce the importance of this weed in a native plant community.

Methods and Materials

The study site was 14 km south of Bozeman, Mont. (111° 4' 45" 36') at an elevation of 1,570 m. Soils were shallow to moderately deep, silty clay loam over sand and gravel Typic Argiboroll class, Beaverton series on an alluvial fan (USDA 1995). The 30-year precipitation average for the nearest weather station (Bozeman, Mont.) was 487 mm. Precipitation for 1991–1993 was 99, 115, and 123% of the 30-year average, respectively. The summer (June–August) of 1991 was drier and warmer than the 30-year average, whereas the summers of 1992 and especially 1993 were cooler and wetter than the long term average (Table 1). Standing crop of the vegetation in mid-June 1991 averaged 1,580 kg ha⁻¹, dominated by spotted knapweed (25%) and Idaho fescue (41%). Other common species at the site were arrowleaf balsamroot (*Balsamorhiza sagittata* (Pursh) Nutt.), Kentucky bluegrass (*Poa pratensis* L.), lupine (*Lupinus sericeus* Pursh), bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) Love), and sticky geranium (*Geranium viscosissimum* F. & M.).

Electronet[®] fencing enclosed three 0.1-ha pastures located randomly within a 3-ha pasture. This pasture was grazed heavily by horses before the study; there was no grazing in or near our small pastures during the study. Four 10-m permanent transects were established inside and outside each pasture. Along each transect, 0.5-m² permanent plots were established at 1-m intervals. Before grazing in 1991, densities of spotted knapweed (seedlings and mature plants), Idaho fescue, and arrowleaf balsamroot plants were determined, and frequency of Kentucky bluegrass was noted. Cover of bare ground and litter was estimated in these

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

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

plots. In the summers of 1991–1993, each pasture was grazed by 5 Targhee yearling ewes, which had never been exposed to spotted knapweed. Each pasture was grazed for 5 to 7 days in mid-June, 2 to 6 days in July, and 1 to 2 days in early September depending on available forage each year. Utilization of permanently marked plants of spotted knapweed and Idaho fescue was usually high, ranging from 75 to 95% based on grazed plant frequency (Olson et al., unpublished data). Utilization based on volume removed was less than based on frequency (Olson et al. unpublished data; Pechanac 1936). Flowering stems of spotted knapweed were counted along grazed and ungrazed transects each September following grazing.

Density and frequency measures were repeated before grazing in June 1992 and 1993, and in June 1994, 9 months after grazing ceased in September 1993. In 1991 and 1992, spotted knapweed rosettes were included in the mature plant category; in 1993 and 1994 they were counted as rosettes. Basal areas, numbers of flower stems, numbers of stems (tillers), leaf heights, and flower-stem heights of spotted knapweed and Idaho fescue plants were also measured in 1994. Leaf heights and flower-stem heights were the same for spotted knapweed because of its pattern of bolting.

Samples of soil seed banks were collected in the summers of 1991 and 1994 by removing 191 cm³ of soil with a tulip bulb corer (5.7 cm dia.) placed 7.5 cm deep in the soil. In 1991, 10 samples were extracted from adjacent grazed and ungrazed areas in each pasture ($n = 30$ per treatment). From this baseline seed bank sample, we estimated a density of 26 viable seeds m⁻². In 1994, 20 samples were extracted from adjacent grazed and ungrazed areas in each pasture ($n = 60$ per treatment). Seed bank samples were air-dried, weighed, washed through sieves to remove fine materials, and then floated to separate large sand grains. The remaining material was dried at 37°C for 48 hours and examined for spotted knapweed seed. Recovered seeds were tested for germination by maintaining them on moist blotter paper in petri dishes placed in a covered box in a greenhouse with 21°C daytime–13°C nighttime temperatures. Germinated seeds were counted and removed every 2 days for 14 days. Seeds not germinating within 14 days were tested for viability with tetrazolium (AOSA 1970).

Age-class distributions of spotted knapweed populations in previously grazed and ungrazed areas were determined in the summer of 1994. Inside each pasture, 3 parallel 17-m transects were placed 5 m apart. The nearest spotted knapweed plant at 0.5-m intervals along each transect was excavated, dried, and then aged by counting growth rings at 3 breaks in the upper 5 cm of the root (W. Good, pers. comm.). Rings were counted at 3 breaks to account for false or incomplete rings at a certain point along a

root. Spotted knapweed plants, located systematically outside each pasture, were sampled similarly as those inside ($n = 100$ –106 plants in each grazed and ungrazed area). Twenty three percent of the older plants (≥ 3 -years-old) had rotten centers, thus their ages represent conservative estimates.

Data for variables measured all 4 years were analyzed with repeated measures analysis of variance as a randomized-complete-block design ($n = 3$; GLM, SAS 1988). Year, and the year by treatment (grazed, ungrazed) interaction for repeated measures were assessed as within subject effects. For parameters measured in 1994 only (vigor, seed banks, etc.), analysis of variance as a randomized-complete-block design was used with treatment (grazed, ungrazed) as the main effect. Each plant species was analyzed separately. Residuals from analyses of variance were normally distributed. Age class distributions of spotted knapweed from grazed and ungrazed areas were compared with a Kruskal-Wallis nonparametric test (NPAR1WAY, SAS 1988). Age class distributions of spotted knapweed by pasture were analyzed initially to determine if there was a pasture by treatment interaction. Age class distributions of grazed and ungrazed areas were similar among the 3 pastures, so data were combined for analysis. Because of inherent variability in field studies such as this one, P -values less than 0.15 are presented (Gill 1981).

Results

Community Response

In grazed and ungrazed areas, density of spotted knapweed seedlings was much lower in 1992 than in 1991 (Fig. 1). Seedling density in grazed areas remained low through 1994. In ungrazed areas, density was greater in 1994 than in 1992 and 1993 (year by treatment interaction, $P < 0.07$). Density of spotted knapweed rosettes was less in grazed than ungrazed areas when rosette density was first determined in 1993. Rosette density was unchanged in grazed areas; in ungrazed areas, it was greater in 1994 than 1993 (year by treatment interaction, $P < 0.07$). Similarly, mature spotted knapweed plant densities in grazed areas were unchanged. In ungrazed areas, mature plant density in 1991 was less than in subsequent years of the study (year by treatment interaction, $P < 0.002$).

In grazed areas, density of Idaho fescue increased from 1991 to 1992 and then remained constant (Fig. 2). Idaho fescue density in ungrazed areas was unchanged from 1991 to 1994 (year by treatment interaction, $P < 0.002$). In grazed areas, Kentucky bluegrass presence was greater in 1994 than in 1991; in ungrazed areas its presence was unchanged from 1991 to 1994 (Fig. 2, year by treatment interaction, $P < 0.09$). Density of arrowleaf balsamroot was

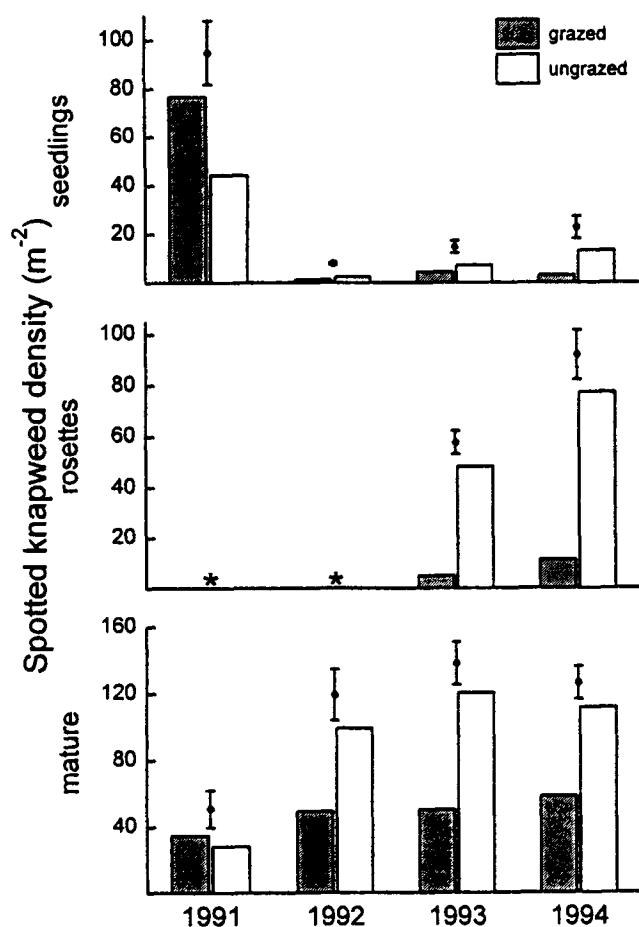


Fig. 1. Densities of spotted knapweed seedlings, rosettes, and mature plants from 1991–1994 in grazed and ungrazed areas. Densities in 1991 were determined before the sheep first grazed the pastures. Densities in 1994 were those determined after 3 years of sheep grazing. Rosettes were counted with mature plants in 1991 and 1992, and are indicated by the asterisks. Error bars represent ± 1 S.E.

not affected by grazing (year by treatment interaction, $P = 0.22$), varying from 7 to 8% frequency in grazed areas and 12 to 15% in ungrazed areas from 1991 to 1994.

The proportion of bare soil increased with grazing; it decreased without grazing (Fig. 3, year by treatment interaction, $P < 0.03$). Grazing reduced litter cover slightly (Fig. 3, grazing effect, $P < 0.08$). Litter cover varied depending on the year (year effect, $P < 0.05$).

Population Response

More viable spotted knapweed seeds were recovered from seed bank cores taken from ungrazed areas than grazed areas ($49 \text{ m}^{-2} \pm 16.5 \text{ S.E.}$ versus $12 \text{ m}^{-2} \pm 10.5 \text{ S.E.}$, $P < 0.04$). Mean age of spotted knapweed plants was greater in grazed than ungrazed areas (3.8 versus 2.9 years, $P < 0.0001$). In ungrazed areas, over 75% of the plants were younger than 4 years of age. In grazed areas, only 43% were younger than 4 years of age (Fig. 4). The modal age in grazed areas was 4, whereas the modal age in ungrazed areas was 2.

After grazing in September 1991, there were fewer spotted knapweed flower stems in grazed than in ungrazed areas (Fig. 5, $P < 0.03$).

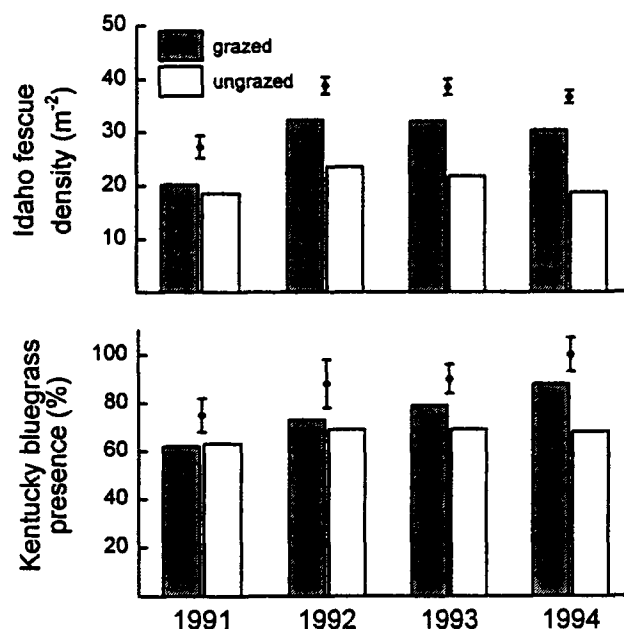


Fig. 2. Density of Idaho fescue plants and frequency of Kentucky bluegrass from 1991–1994 in grazed and ungrazed areas. Error bars represent ± 1 S.E.

In September 1992 and 1993, the number of flower stems were similar in grazed and ungrazed areas ($P = 0.33$, $P = 0.42$, respectively). In 1994, almost 1 year after grazing ceased, grazed areas had nearly twice as many spotted knapweed flower stems as ungrazed areas ($P < 0.05$).

Individual Response

Leaf and flower stem heights of spotted knapweed were similar in grazed and ungrazed areas (Table 2). Grazed plants had more

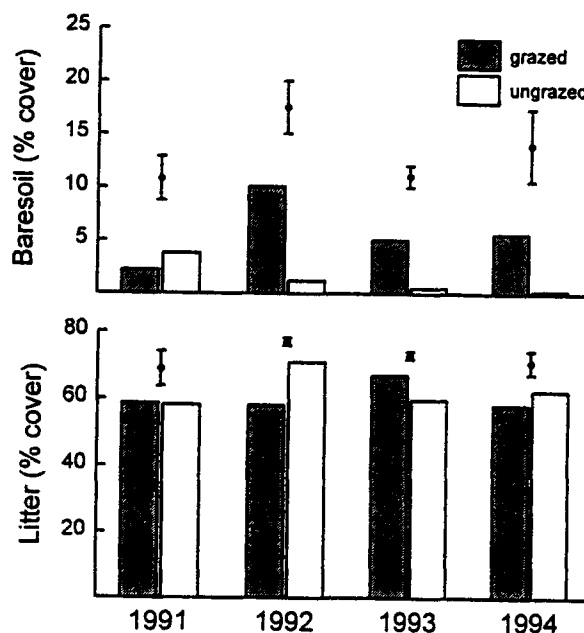


Fig. 3. Percent cover of bare soil and litter from 1991–1994 in grazed and ungrazed areas. Error bars represent ± 1 S.E.

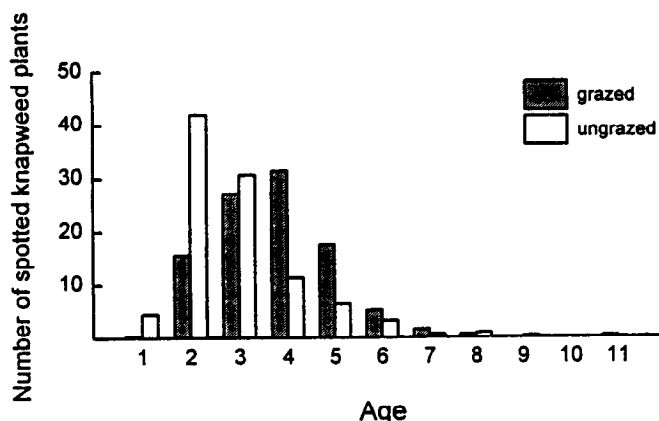


Fig. 4. Age class distribution of spotted knapweed plants excavated from grazed and ungrazed areas in 1994 after 3 years of sheep grazing.

stems (vegetative and flowering) and flowering stems than ungrazed plants, although the magnitude of these differences varied among the 3 pastures (pasture by treatment interaction; stems, $P < 0.001$; flowering stems, $P < 0.003$). Grazed plants had lower stem (vegetative and flowering) and flowering stem densities than ungrazed plants. Basal areas of grazed spotted knapweed plants were twice as large as ungrazed plants.

While aging spotted knapweed plants, we observed that some of the taproots occasionally had necrotic tissue. Plants from grazed areas had a higher frequency of necrotic tissue than plants from ungrazed areas (15.6% versus 7.6% S.E. 1.4%, $P < 0.06$).

Leaves and flower stems were shorter on grazed than ungrazed Idaho fescue plants (Table 2). Grazed plants tended to have more flowering stems, and greater flowering stem densities than ungrazed plants. Grazed and ungrazed Idaho fescue plants had similar basal areas.

Discussion

Response of a spotted knapweed infested Idaho fescue community was examined at 3 different ecological scales. At the community level, sheep grazing reduced spotted knapweed plant density, increased Kentucky bluegrass frequency, and minimally affected native species, Idaho fescue and arrowleaf balsamroot.

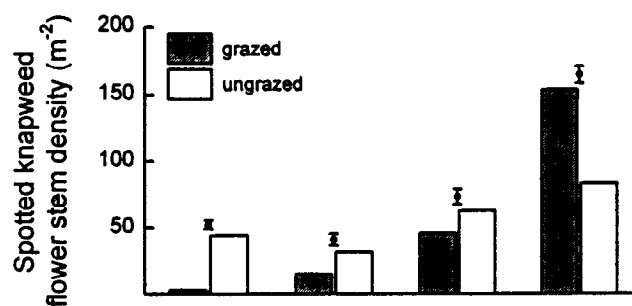


Fig. 5. Densities of spotted knapweed flower stems in 1991-1994. Densities in 1991-1993 were determined in early September after the last grazing period each summer. Densities in 1994 were determined in late July, 10.5 months after the last grazing period in early September 1993. Error bars represent ± 1 S.E.

The rhizomatous Kentucky bluegrass often increases with live-stock grazing. This could be a concern if it continued to increase with intensive sheep grazing of weed infested pastures.

At the population level, the reduced density of spotted knapweed seedlings with and without grazing could be attributed to a reduction of viable seed in the seed bank. Presence of only a few seedlings after 1991 in both treatments may have reflected the success of the seedhead fly (*Urophora* spp.) which was first observed on spotted knapweed flower heads at the site in 1992.

Grazing altered age class distribution of spotted knapweed plants. Apparently, sheep prefer younger, smaller, presumably more palatable spotted knapweed plants. Spotted knapweed stems on older plants are fibrous and tough (Kelsey and Mihalovich 1987). In addition, seasonal increases in cnicin, a bitter tasting sesquiterpene lactone contained in stems and especially leaves of spotted knapweed (Locken and Kelsey 1987), and the high fiber content of stems may have deterred herbivory. Thus, by preferring younger age classes of spotted knapweed and by reducing viable seed production from older plants, the sheep were reducing recruitment into the population. This reduction may have been more pronounced had the study continued several more years.

The increase in necrosis of crowns of grazed spotted knapweed plants may affect water and nutrient uptake, and allocation of carbohydrates, potentially reducing a plant's ability to compete and shortening its life span. Crown and root rot complexes in alfalfa, which has a similar tap-root as spotted knapweed, affect cortical and vascular tissue, thereby reducing plant vigor, and increasing wilting and mortality (Leath 1990). Equipment associated with

Table 2. Response of spotted knapweed and Idaho fescue in June 1994 after 3 years of repeated sheep grazing. Each year, pastures were grazed for 5 to 7 days in mid-June, 2 to 6 days in July, and 1 to 2 days in early September depending on available forage.

	Spotted knapweed			P-value	Idaho fescue			P-value
	grazed	ungrazed	SE		grazed	ungrazed	SE	
leaf height (cm)	57.6	59.9	2.2	0.47	17.5	28.4	1.8	0.0001
flower stem height (cm)	57.6 ¹	59.9	2.2	0.47	51.6	61.9	1.6	0.0002
stems plant ¹	5.0 ²	3.1	0.3	0.0002	30.6	31.6	3.3	0.84
flower stems plant ¹	5.0	3.0	0.3	0.0001	1.0	0.5	0.3	0.14
stem density (cm ⁻²)	1.1	1.3	0.03	0.0001	2.0	1.9	0.1	0.27
flower stem density (cm ⁻²)	1.0	1.2	0.03	0.002	0.04	0.02	0.01	0.12
basal area (cm ²)	8.2	4.0	0.50	0.0001	21.7	22.3	2.0	0.83

¹ Spotted knapweed bolts in late June-early July. When it bolts, stem and flower stem heights are the same.

² Stems include vegetative and flowering stems.

harvesting alfalfa has been implicated in wounding the crown of alfalfa plants, and thereby increasing the incidence of disease. Intensive grazing of spotted knapweed by sheep may also wound the crown of this plant.

The significant reduction in flowering stems at the end of the 1991 grazing season was not as pronounced following the 1992 and 1993 grazing seasons, indicating that sheep reduced their use of flower stems, or that there was compensatory increase in number of flowering stems by spotted knapweed in grazed areas (Paige and Whitham 1987), or both. The compensatory increase in flower stem production in 1994 indicates that using sheep as a sole means to control this plant would require a long-term commitment. Sheep will not eliminate the plant from the community given its long-term seed viability (Davis et al. 1993) and compensatory increase in flower stem numbers, however, sheep have the potential to reduce its dominance. The compensatory increase in flower stem numbers by Idaho fescue plants in 1994 indicated either a response to stress, i.e. plants increase reproductive effort as a last chance to continue their population, or an increase in belowground resources because of the reduced competitiveness of other species (Mueggler 1970), presumably spotted knapweed.

At the individual plant level, previously grazed Idaho fescue plants had shorter leaves than ungrazed plants which could indicate reduced vigor and competitiveness. Mueggler (1970) initially suggested that the number of flower stems was a good indicator of the vigor of Idaho fescue, but later suggested that maximum leaf length was the most appropriate indicator (Mueggler 1975). Several plant species become more prostrate with long-term grazing (e.g. Detling and Painter 1983) which may be an evolutionary response to reduce herbivory (Jaendl et al. 1995). Although leaf heights of Idaho fescue plants in grazed and ungrazed areas differed, basal areas were similar. In a related study at this site, above- and belowground biomass were less for grazed Idaho fescue plants than ungrazed plants (Olson and Wallander 1997). Given that size and biomass are positively correlated, shorter leaves on previously grazed Idaho fescue plants in this study agrees with reduced biomass in previously grazed plants from the other study.

Conclusion

Sheep will graze spotted knapweed. Repeated sheep grazing initially reduces current flower stem production, although flower stem production may increase in subsequent years if grazing is not continued. By controlling the time of grazing and by repeatedly grazing spotted knapweed while associated grasses were going dormant, the age class distribution of spotted knapweed was altered (i.e. there were fewer, albeit older and larger plants), and its reproduction was reduced with minimal impact on the associated grasses. Sheep grazing may slow the rate of increase of spotted knapweed in native plant communities.

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Early season grazing by cattle of tall larkspur- (*Delphinium* spp.) infested rangeland

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Abstract

A series of summer grazing studies were conducted to evaluate cattle consumption of preflowering tall larkspur (*Delphinium barbeyi* [Huth] or *D. occidentale* [Wats.] Wats.) on mountain rangeland in Utah, Colorado, and Idaho during 1987 to 1995. Cattle ate little or no larkspur before flowering racemes were elongated. Consumption of tall larkspur by cattle was also generally low during the early flower stage, with some notable exceptions at the Salina and Manti, Utah sites. These grazing studies indicate that risk of losing cattle to tall larkspur is low if plants have not flowered. Even though concentration of toxic alkaloids is typically much higher in immature compared to mature tall larkspur, toxicosis is unlikely to occur because consumption by cattle is low. Many livestock operations can gain 4 to 5 weeks of low-risk grazing on tall larkspur-infested rangeland early in the grazing season, and this should be considered in developing grazing management plans.

Key Words: grazing management, poisonous plants, alkaloids, methyllycaconitine, cattle diets

Tall larkspur (*Delphinium barbeyi* [Huth] or *D. occidentale* [Wats.] Wats.) toxicity is a severe problem for cattle grazing western mountain ranges. Cattle death losses from tall larkspur average 5% and may exceed 15% annually in areas where the plant is abundant (J.A. Pfister, personal observations); losses to tall larkspur cost cattle producers millions of dollars annually (Nielsen and Ralphs 1988). Tall larkspur infestations often dictate summer grazing management of cattle on mountain rangelands. Significant amounts of forage are ungrazed each year on these highly productive ranges because many producers defer grazing of tall larkspur-infested pastures until late summer or early fall when tall larkspur declines in toxicity (Ralphs et al. 1988, Pfister et al. 1994a). Other producers avoid grazing infested pastures with cattle entirely, or substitute sheep grazing for cattle, reason-

Resumen

Desde 1987 y hasta 1995 se condujeron una serie de estudios a pastoreo de verano con el objeto de evaluar el consumo de larkspur alto (*Delphinium barbeyi* [Huth] o *D. occidentale* [Wats.] Wats.) en prefloración por parte de bovinos en pasturas naturales de montaña distribuidas en Utah, Colorado, y Idaho. Antes de la elongación de los racimos de floración, los vacunos consumieron poco o nada de larkspur alto. El consumo de larkspur alto por parte del ganado vacuno también resultó bajo durante el estadio de floración temprana, con algunas notables excepciones en Salina y Manti, sitios de Utah. Los presentes estudios a pastoreo indican que el riesgo de perder vacunos por consumo de larkspur alto es bajo si las plantas no han florecido. Aunque la concentración de alcaloides tóxicos en larkspur alto es típicamente mucho mayor en plantas inmaduras que en plantas maduras, es improbable la ocurrencia de intoxicación debido a que el consumo por parte de vacunos es bajo. Temprano en la estación de pastores, muchas explotaciones de ganadería pueden ganar de 4 a 5 semanas de pastoreo con bajo riesgo de intoxicación en pasturas naturales infestadas por larkspur alto. Esto debiera ser considerado para el desarrollo de planes de manejo del pastoreo.

ing that the risk of cattle poisoning is not worth the grazing benefits. These adjustments have caused some ranches to relinquish their cattle grazing permits and leases on public lands, resulting in diminished ranch values.

The primary toxins in tall larkspur are the diterpenoid alkaloids, methyllycaconitine (MLA) and 14-deacetylnudicauline (DAN) (Manners et al. 1995). These toxins reversibly bind to acetylcholine receptors (Drasdo et al. 1992) at the neuromuscular junction, causing muscular fatigue, paralysis, and eventually death from respiratory paralysis. Lethality of a tall larkspur dose is determined by several factors, including concentration of toxic alkaloids in the plant, amount eaten, rate of consumption, and susceptibility of individual animals.

As tall larkspur matures, toxicity (i.e., concentration of toxic alkaloids) typically decreases (Ralphs et al. 1988, Pfister et al. 1994a). Previous grazing studies have found that cattle consumption appears to begin during the flower stage, and peak during late flower or pod stage (Pfister et al. 1988a, 1988b); the congruence of declining, but still substantial, plant toxicity with increas-

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ing plant palatability appeared to form a toxic window of risk during which many cattle deaths could be predicted (Pfister et al. 1988a). Our objective in this series of grazing studies was to determine when cattle graze tall larkspur in relation to plant phenology and toxicity, with specific emphasis on early flowering, i.e., transition between preflowering and full flowering. Our hypothesis was that cattle would eat no tall larkspur before elongation of flowering racemes. Consequently, risk associated with grazing tall larkspur-infested ranges before flowering may be low even though immature tall larkspur may be very toxic.

Methods

General

We defined early season grazing as grazing before tall larkspur elongated flowering racemes. Growth of tall larkspur is influenced by environmental conditions (e.g., snow cover, temperature, precipitation), but general patterns are apparent. Newly emergent tall larkspur shoots grow for several weeks in the vegetative stage. Visible bud clusters then develop for about 2 or 3 weeks, followed by rapid elongation of flowering racemes. Flowers on newly-elongated racemes generally require one to several weeks to open fully after stems have reached about 90% of their mature height. We designated the period before raceme elongation as the preflower stage, and the period after raceme elongation but before full flower opening as the early flower stage. In each trial, phenological stage was determined by the stage of growth of the majority of larkspur plants growing within the study pasture. Several hundred tall larkspur plants within each study area were visually examined on a daily basis, and dominant phenological stage was determined.

All pastures used in these trials were on National Forest land and enclosed with an electric fence. Grazing pressure in all trials was light to moderate. Daily bite counts were used to determine animal diets (Pfister et al. 1988a, 1988b; Pfister and Manners 1991). Beginning at about 0630 hours, individual animals were focally sampled (Altmann 1974) in a predetermined random

order. Each animal was observed in turn for 5 minutes. After all animals had been observed, the process was repeated during all active grazing periods until about 1900 hours, when cattle were generally placed in a corral for the night. Bites were categorized as grasses, shrubs, other forbs, and larkspur bud, flower, leaf, or leaf and stem. We defined an individual bite as a single cropping motion, always indicated by a head jerk, often accompanied by a visible sweep of the tongue, and independent of chewing motions.

The trials reported herein that were conducted from 1987 to 1991 constitute a reanalysis of data from control animals in previously published studies (Table 1). Trials from 1993 to 1995 report new data. Bite count methodology and manner of assessing larkspur phenology were the same for all trials.

Larkspur leaves and reproductive parts (i.e., bud, flower) were collected periodically for alkaloid analysis. Fresh plant material was harvested from at least 20 plants, composited, and frozen at -20° C. In Montrose, Colo. during 1995, individual plant samples were collected by harvesting all leaves from 20 randomly selected stems from 20 different plants, as recommended by Manners and Pfister (1996). Samples were freeze-dried and ground through a Wiley mill to pass through a 1-mm screen. Plant material was extracted and analyzed for methyllycaconitine (MLA) and 14-deacetylnudicauline (14-DAN) by high performance liquid chromatography (HPLC) methods (Manners and Pfister 1993). Since these 2 alkaloids account for > 80% of the toxicity of tall larkspur (Manners et al. 1993), and have a similar LD₅₀ in mice (4.0 to 4.5 mg/kg BW; K.E. Panter, personal communication), we summed their concentrations and expressed the sum as total toxic alkaloid (TTA) concentration (mg/g, dry wt basis). Typically, MLA constitutes ≥ 90% of the toxic alkaloid concentration (G.D. Manners, unpublished data).

Standing crop (kg/ha) was determined near the beginning of each trial by clipping ≥ 20, 0.25-m² plots to a 1-cm stubble height. Clipped material was separated into tall larkspur, grass, and other forbs, dried in a forced air oven at 60°C for 48 hours, and weighed. In all trials, other forages besides tall larkspur were abundant in the pastures (Table 1).

Table 1. Characteristics of each grazing study, including a literature reference if the data were extracted and reanalyzed from a previously published data set

Trial #	Location	Year	Larkspur spp.	Total non-toxic standing crop	Larkspur standing crop	Reference ^b
				(kg/ha) ^a	(kg/ha)	
1	Manti, Utah	1987	<i>D. barbeyi</i>	794	165	Pfister et al. 1988a
2	Oakley, Idaho	1988	<i>D. occidentale</i>	692	731	Pfister and Manners 1991
3	Yampa, Colorado	1990	<i>D. barbeyi</i>	1380	591	Pfister and Manners 1995
4	Yampa, Colorado	1991	<i>D. barbeyi</i>	1524	729	Pfister and Manners 1995
5	Yampa, Colorado	1993	<i>D. barbeyi</i>	1477	526	
6	Yampa, Colorado	1994	<i>D. barbeyi</i>	1112	524	
7	Salina, Utah ^c	1994	<i>D. barbeyi</i> and <i>D. occidentale</i> ^d	---	---	
8	Salina, Utah	1995	<i>D. barbeyi</i> and <i>D. occidentale</i>	538	440	
9	Montrose, Colorado	1995	<i>D. barbeyi</i>	646	212	

^aAvailability when the grazing trial began; total standing crop excludes tall larkspur; grazing pressure in all trials was light to moderate

^bData from previously published studies includes only control animals from experiments in which various treatments were applied

^cThis trial ended prematurely when all the experimental cattle escaped from the pasture

^dThis population of tall larkspur was a mix of *D. barbeyi* and *D. occidentale* and hybridized crosses

Trial 1: Manti, Utah 1987

Five yearling Hereford heifers (318 kg) grazed a 3-ha pasture at the head of Six Mile Canyon, 25 km east of Manti, Ut., at 3,250 m elevation (Pfister et al. 1988a). These heifers were familiar with tall larkspur as they had grazed this area as calves the previous summer. Observations were made during the preflower stage (2 to 11 July) and during the early flower stage (20 to 30 July). Major plant species were tall larkspur (*Delphinium barbeyi*), currant (*Ribes montigenum* McClatchie), slender wheatgrass (*Elymus trachycaulus* [Link] Gould ex Shinners), mountain brome (*Bromus carinatus* H. & A.), and sagewort (*Artemisia ludoviciana* var. *incompta* [Nutt.] Cronq.).

Trial 2: Oakley, Idaho 1988

Four yearling Hereford heifers (267 kg) grazed a 3-ha pasture 30 km west of Oakley, Ida. at 2,300 m elevation (Pfister and Manners 1991). These heifers grazed on mountain range as calves, but exposure to tall larkspur was unknown. Observations were made during the preflower stage (June 15 to 24) and during early flower (June 29 to July 8). Major plant species were tall larkspur (*Delphinium occidentale* [Wats.] Wats.), snowberry (*Symphoricarpos oreophilus* Gray), Great Basin wildrye (*Elymus cinereus* Scribn. & Merr.), slender wheatgrass, and Idaho fescue (*Festuca idahoensis* L.).

Trial 3: Yampa, Colorado 1990

Four Hereford X Angus X Charolais yearling heifers (286 kg) were grazed during the preflower stage (21 to 30 June) and the early flower stage (1 to 10 July). The trial was conducted near Dunkley Pass, 25 km west of Yampa, Colo. at an elevation of 2,650 m (Pfister and Manners 1995). These heifers grazed this allotment the previous summer. Dominant plants were tall larkspur (*Delphinium barbeyi*), false hellebore (*Veratrum californicum* Durand), cow parsnip (*Heracleum lanatum* Michx.), meadowrue (*Thalictrum fendleri* Engelm. ex Gray), sweet cicely (*Osmorhiza occidentalis* [Nutt.] Torr.), snowberry, and mountain brome.

Trial 4: Yampa, Colorado 1991

This grazing site was the same as used in Trial 3, and 2-yr old heifers (same animals as used in Trial 3; 372 kg) were grazed during the preflower stage (26 June to 5 July), and during the early flower stage (6 to 18 July) (Pfister and Manners 1995).

Trial 5: Yampa, Colorado 1993

Five, 2-yr old Hereford X Angus heifers (375 kg) grazed a 4-ha pasture on a site about 0.5 km from that used during Trials 3 and 4; site characteristics and vegetation were similar. These cattle had previously grazed a summer mountain range in Utah, but were naive to this allotment. Cattle grazed during the preflower stage (June 18 to July 5) and during the early flower stage (July 6 to 20).

Trial 6: Yampa, Colorado 1994

Five, 3-year old cows (same animals as used during Trial 5; 487 kg) grazed during the preflower stage (9 to 21 June) and during the early flower stage (22 June to 5 July) on a site adjacent and similar to that used during Trial 5.

Trial 7: Salina, Utah 1994

Five yearling heifers (300 kg) grazed a 4-ha site dominated by a mixed tall larkspur population (mostly *D. barbeyi* with some *D. occidentale* and hybrid crosses). Other major plant species were snowberry, mountain brome, meadowrue, and currant. Heifers had previous grazing experience on tall larkspur-infested rangeland about 35 km from this site. Cattle grazed during the preflower stage (18 to 30 June) and during the early flower stage (July 1 to 7). The pasture was located near the Salina Reservoir in the Fishlake National Forest about 40 km from Salina, Ut., at an elevation of 2,950 m.

Trial 8: Montrose, Colorado 1995

Five, 4-year old cows (574 kg) with previous experience grazing tall larkspur-infested rangeland in Utah were grazed during the preflower stage (5 July to 30 July) and early flower stages (1 to 12 Aug.). The 4-ha pasture was situated at 2,850 m elevation on the Umcompahgre Plateau about 38 km southwest of Montrose, Colo. Dominant plants under the aspen (*Populus tremuloides* Michx.) canopy were tall larkspur (*Delphinium barbeyi*), low larkspur (*Delphinium nuttallianum* Pritz.), lovage (*Ligusticum porteri* Coult. & Rose), meadowrue, currant, and mountain brome.

Trial 9: Salina, Utah 1995

Five, 3- and 4-yr old cows (499 kg) with previous experience grazing tall larkspur-infested rangelands grazed a 5-ha pasture during the preflower stage (6 to 21 to July 6 Aug.) and during the early flower stage (22 July to 6 Aug.). The pasture was located at the same site as used during Trial 7.

Statistical analysis

Each trial was analyzed separately for the dependent variable percent of bites of tall larkspur. In the general linear model (SAS 1988), animals were considered as blocks, and periods as treatments. The model also included the animal \times period interaction, days nested within periods, and animal \times day within period as the residual error term. The animal \times period interaction was first tested for significance. If the animal \times period term was significant ($P < 0.05$), then the animal \times period interaction was used to test for period differences; if this interaction was not significant, then the residual error term was used to test for period differences.

Relating Plant Toxicity and Consumption

The relationship between tall larkspur toxicity (i.e., toxic alkaloid concentration, mg/g) and consumption (% of diet as tall larkspur) was determined by calculating the amount of tall larkspur an animal would have to eat as a percentage of daily dry matter intake for toxicosis to occur (dose response) over a range of toxic alkaloid concentrations in tall larkspur. In all calculations we assumed a body weight of 600 kg and dry matter intake at 100 g/BW_{kg}^{0.75} (Cordova et al. 1978). We used 2 doses of TTA: 1) 21 mg/kg BW as a dose likely to cause overt clinical signs (muscular weakness, temporary sternal recumbency, and perhaps fatal bloat); and 2) 40 mg/kg BW as a plausible, but untested LD₅₀ in cattle. Originally we reported that an effective dose of TTA was 11 mg/kg (Pfister et al. 1994b), but recalibration and reanalysis of the same plant material by HPLC has established the correct effective dose in cattle to be 21 mg/kg body weight. We catego-

rized dose, and the resultant likelihood of poisoning, in each grazing trial as either high, medium, or low. The relative risk of losing cattle is primarily related to the amount of tall larkspur ingested, and understanding the relationship between plant toxicity and amount consumed can provide an indication of how risky a particular grazing situation may be.

Results

Trial 1. Manti, Utah 1987

Cattle ate no tall larkspur during the preflower stage, whereas total larkspur consumption increased ($P < 0.05$) during the early flower stage, and averaged 7% of bites (Table 2). The majority of the larkspur consumed during the early flower stage was flowers (5.7%). On the ninth day of the early flower period, cattle averaged 32% of bites as larkspur. One animal ate about 50% of her diet (Table 2) as flowers on day 9. She was probably approaching an intoxicating threshold (Pfister et al. 1997), but did not show clinical signs, presumably because tall larkspur was ingested gradually over an entire day and flowers were low in TTA concentration. Leaves were relatively high in toxic alkaloids (> 7 mg/g) early in the grazing season, and maintained relatively high concentrations (> 5 mg/g) after elongation of flowering stems (Fig. 1). The ingested larkspur dose, hence risk, was nonexistent during the preflower stage, because cattle ate no larkspur. The larkspur dose was low to medium during the early flower stage (Fig. 2), when maximal leaf consumption of about 19% (Table 2) in conjunction with leaf toxicity resulted in a potentially dangerous situation. Nonetheless, cattle showed no clinical signs of intoxication. Even though cattle ate a substantial amount of tall larkspur flowers on day 9 in the early flower stage, intoxication did not occur (Fig. 2) because flower toxicity was low.

Trial 2. Oakley, Idaho 1988

Cattle selected only a few bites of tall larkspur during the preflower stage; although consumption increased ($P < 0.05$) during the early flower stage, it remained very low (Table 2). Most ($> 90\%$) of the larkspur eaten during the early flower stage was leaf material. The concentration of TTA was relatively high (≥ 6.5 mg/g) in leaves and buds early in the growing season, but declined with maturity (Fig. 1). Although TTA concentration remained relatively high during 2 periods, the ingested toxic alkaloid dose (Fig. 2), and the risk of losing cattle, remained low because consumption was low.

Trial 3. Yampa, Colo. 1990

Cattle ate no tall larkspur during either the preflower or early flower stage. The concentration of TTA was high in immature leaves, but declined to relatively low concentrations when larkspur elongated flowering racemes (Fig. 1). Buds and flowers initially contained a high concentration of TTA, and although concentration declined with maturity, TTA concentration remained relatively high when larkspur began to flower. The risk of losing cattle was essentially zero during both grazing periods because cattle ate no tall larkspur.

Trial 4. Yampa, Colo. 1991

Cattle ate a small number of leaves ($< 0.1\%$ of bites) during both the preflower and early flower stages ($P > 0.05$; Table 2).

Table 2. Mean daily consumption of tall larkspur plant parts (% of bites (\pm SE) by cattle during the preflower and early flower stages of growth, and maximum amount of larkspur consumed by any individual animal on any day during each grazing period

Trial/Plant part	Larkspur Growth Stage			
	Preflower		Early Flower	
	Mean (SE)	Maximum	Mean(SE)	Maximum
----- (% of bites) -----				
#1				
Manti, UT 1987				
Leaf	0.0 (0.0)	0.0	0.9 (0.4)	19.2
Bud	0.0 (0.0)	0.0	0.0 (0.0)	0.0
Flower	0.0 (0.0)	0.0	5.7 (1.5)	50.8
Total	0.0 (0.0)	0.0	6.7 (1.6)	50.8
#2				
Oakley, ID 1988				
Leaf	0.1 (0.08)	2.0	0.6 (0.2)	4.1
Bud	0.0 (0.0)	0.0	0.0 (0.0)	0.0
Flower	0.0 (0.0)	0.0	0.1 (0.04)	1.5
Total	0.1 (0.08)	2.0	0.7 (0.2)	4.1
#3				
Yampa, CO 1990				
Leaf	0.0 (0.0)	0.0	0.0 (0.0)	0.0
Bud	0.0 (0.0)	0.0	0.0 (0.0)	0.0
Flower	0.0 (0.0)	0.0	0.0 (0.0)	0.0
Total	0.0 (0.0)	0.0	0.0 (0.0)	0.0
#4				
Yampa, CO 1991				
Leaf	0.03 (0.02)	0.4	0.1 (0.03)	2.5
Bud	0.0 (0.0)	0.0	0.0 (0.0)	0.0
Flower	0.0 (0.0)	0.0	0.0 (0.0)	0.0
Total	0.03 (0.02)	0.4	0.1 (0.03)	2.5
#5				
Yampa, CO 1993				
Leaf	0.2 (0.09)	5.6	0.6 (0.17)	8.3
Bud	0.0 (0.0)	0.0	0.06 (0.06)	4.5
Flower	0.0 (0.0)	0.0	0.0 (0.0)	0.0
Total	0.2 (0.09)	5.6	0.7 (0.18)	8.3
#6				
Yampa, CO 1994				
Leaf	0.0 (0.0)	0.0	0.0 (0.0)	0.0
Bud	0.0 (0.0)	0.0	0.0 (0.0)	0.0
Flower	0.0 (0.0)	0.0	0.0 (0.0)	0.0
Total	0.0 (0.0)	0.0	0.0 (0.0)	0.0
#7				
Salina, UT 1994				
Leaf	0.1 (0.02)	1.8	0.6 (0.14)	2.7
Bud	0.08 (0.03)	0.8	0.5 (0.2)	2.2
Flower	0.02 (0.01)	0.5	1.7 (0.5)	4.9
Total	0.2 (0.07)	1.8	2.7 (0.9)	8.7
#8				
Salina, UT 1995				
Leaf	0.07 (0.04)	2.9	0.9 (0.2)	11.8
Bud	0.0 (0.0)	0.0	0.0 (0.0)	0.0
Flower	0.02 (0.02)	1.9	3.2 (0.6)	20.2
Total	0.1 (0.1)	4.1	4.2 (0.7)	21.0
#9				
Montrose, CO 1995				
Leaf	0.1 (0.005)	0.6	0.04 (0.02)	0.6
Bud	0.0 (0.0)	0.0	0.0 (0.0)	0.0
Flower	0.0 (0.0)	0.0	0.02 (0.01)	0.7
Total	0.01 (0.005)	0.6	0.06 (0.03)	0.7

Leaf alkaloid concentration decreased with plant maturity, whereas bud TTA concentrations were initially low, and remained low as tall larkspur flowered (Fig. 1). The ingested toxic alkaloid dose and risk of losing cattle were very low as cattle ate only small amounts of tall larkspur (Table 2) during either the preflower or early flower periods.

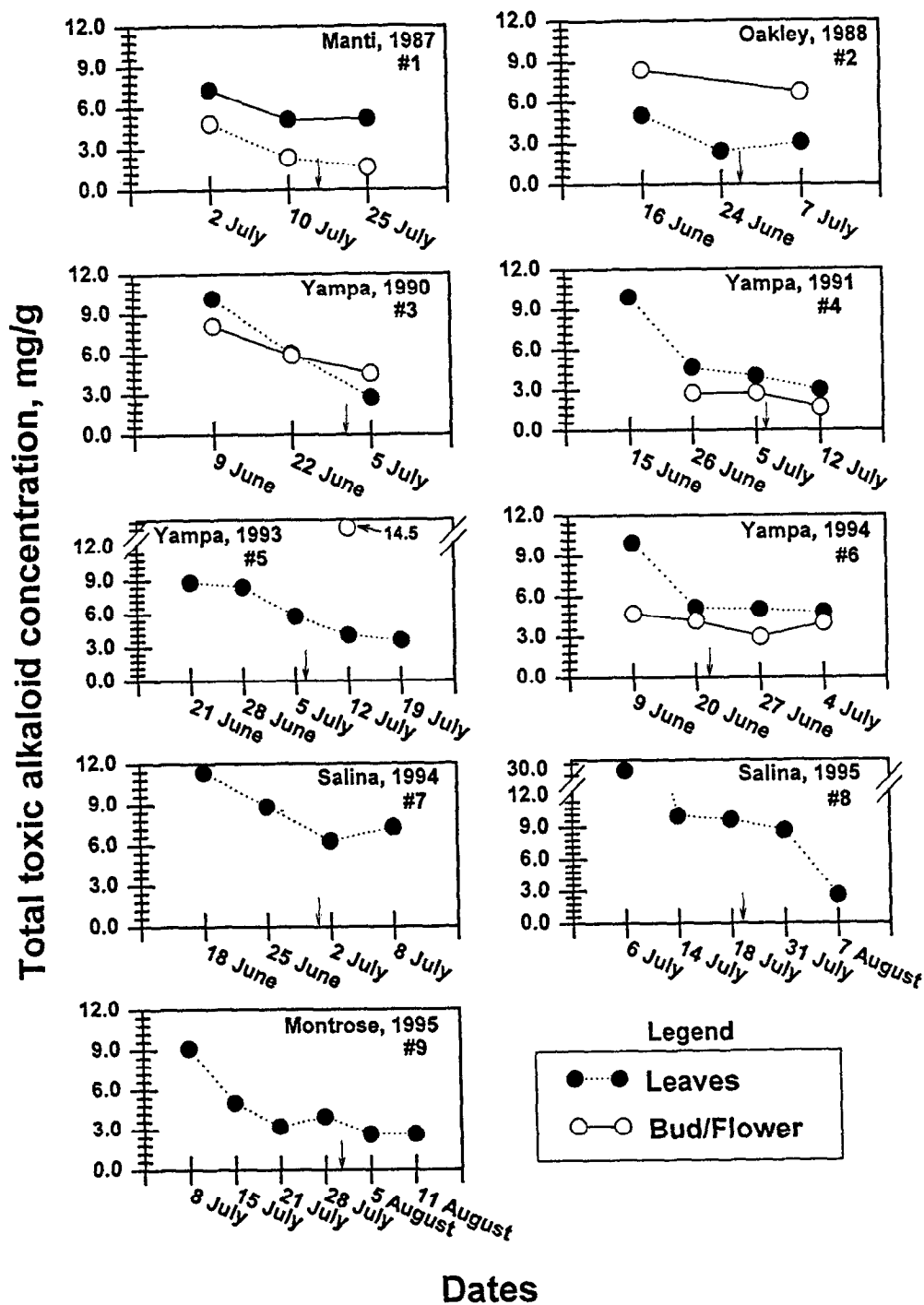


Fig. 1. Toxic alkaloid concentration (mg/g, dry wt basis) in tall larkspur leaves and reproductive parts (buds or flowers) during grazing studies conducted in various locations. The number refers to each grazing trial in sequence as detailed in the text, and the arrow shows the approximate date when the early flower period began.

Trial 5. Yampa, Colo. 1993

Cattle ate < 1% of their bites as larkspur during the 2 periods ($P > 0.05$). During the preflower stage, cattle consumed a few bites of leaves, and during the early flower stage they consumed some leaves and buds (Table 2). Leaves showed a typical decrease in the concentration of TTA with plant maturity. The

sole flower sample collected during the early flower stage had a very high TTA concentration (Fig. 1). The dose of toxic alkaloids was very low during the preflower stage because consumption was low; the ingested toxic dose remained low (Fig. 2) on day 17 when 1 cow ate 6% of her bites as larkspur leaves. During Day 2 of the early flower stage, 1 animal ate 8% of her bites as

larkspur leaves, while another animal ate 5% of her bites as buds on day 4. The toxic dose would have remained low (Fig. 2) when cattle ate leaves because TTA concentration in leaves was about 4.0 mg/g (Fig. 1), but the dose was higher when cattle ate substantial amounts of buds because the flower sample collected about this time was very toxic (> 14 mg/g). No clinical signs of intoxication were observed in cattle on that day.

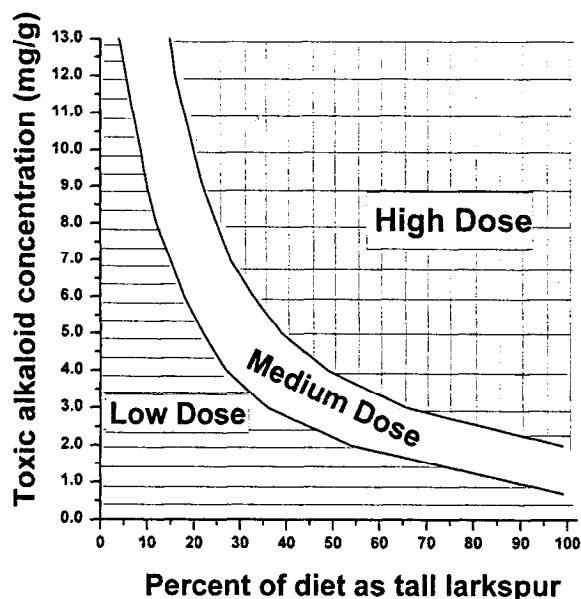


Fig. 2. Dose response of cattle to tall larkspur. The y-axis shows the toxic alkaloid (TTA) concentration (mg/g) in tall larkspur and the x-axis shows the amount of tall larkspur in cattle diets (% of dry wt). The risk of poisoning cattle increases as the toxicity of the plant increases and as animal consumption increases.

Trial 6. Yampa, Colo. 1994

Cattle ate no tall larkspur during the preflower or early flower stages. Concentrations of TTA in leaves showed a characteristic decline early in the preflower stage, but then did not decline thereafter (Fig. 1). Bud and flower concentrations of TTA remained relatively stable over time. The toxic dose, and risk of losing cattle, was essentially zero during both the preflower or early flower stages because of the lack of consumption.

Trial 7. Salina, Utah 1994

Cattle selected a few bites of tall larkspur leaves during the preflower stage, and increased consumption to about 3% of bites, primarily flowers, during the early flower stage ($P < 0.05$; Table 2). Cattle began consuming a substantial amount of larkspur (average of 5.7% flowers and 2.1% leaves) on day 3 of the early flower period, and 1 cow died during the night, presumably from tall larkspur intoxication (or resulting bloat). This cow consumed about 15% of her total bites as larkspur (mostly flowers) during the late afternoon grazing period; overall her daily larkspur consumption was about 5%. Immature leaves had a high concentration of TTA, and TTA concentration remained relatively high even after tall larkspur began elongating flowering racemes (Fig. 2). The toxic dose was low during the preflower stage because

consumption was low (Table 2). During the early flower stage, a fatal dose was ingested by 1 animal; the TTA concentration in leaves on the day previous was about 6 mg/g, but the full toxic dose was unknown as flower samples were not collected. On the other days during the early flower stage, the toxic dose and risk were correspondingly low.

Trial 8. Salina, Utah 1995

Cattle ate essentially no tall larkspur during most of the preflower stage, but on days 13 and 16 they increased leaf consumption to 1.8 and 0.7% of bites, respectively (Fig. 3). Cattle averaged 0.1% of bites as tall larkspur during the preflower stage, compared to 4.2% during the early flower stage ($P < 0.05$); cattle generally preferred flowers over leaves during the early flower stage (Fig. 3). One cow rapidly ate about 18% of her diet as larkspur leaves in the late afternoon of day 6 of the early flower stage. She died sometime during the night, presumably from tall larkspur intoxication. Leaves were very toxic early in the grazing season, and retained a relatively high concentration of TTA (> 9 mg/g) into the beginning stages of flowering (Fig. 2). The toxic dose ingested by cattle was low during the preflower stage because consumption was generally low. The toxic dose and risk increased greatly (Fig. 2) when larkspur elongated flowering racemes. Although means were not alarmingly high (Table 2), maximal daily amounts eaten during this period were about 12 and 20% of bites for leaves and flowers, respectively.

Trial 9. Montrose, Colo. 1995

Cattle ate a few bites of tall larkspur during both the preflower and early flower stages ($P > 0.05$; Table 2). During the preflower stage, cattle ate a few leaves on 3 different days. During the early flower stage, cattle ate a few leaves on numerous days, but the maximum number of bites taken in a single day by any animal was very low (Table 2). Leaves were relatively consistent in TTA concentrations with values of 2.6 to 5.0 mg/g during most of the grazing season (Fig. 1). The ingested toxic dose was low (Fig. 2) during both the preflower and early flower stages because of low levels of consumption and relatively low plant toxicity.

Discussion

Cattle generally ate little or no tall larkspur during the preflower stage before larkspur elongated flowering racemes. Therefore, these data strongly support our hypothesis that cattle do not eat tall larkspur before elongation of flowering racemes. Consumption of tall larkspur was also generally low during the early flower stage of growth, except periodically at the 2 Utah sites. These grazing studies indicate that risk of losing cattle to tall larkspur is low if plants have not flowered. Even though concentration of toxic alkaloids is typically high in immature larkspur, cattle are unlikely to eat these plants in sufficient amounts for toxicosis to occur. When tall larkspur does comprise a major portion of an animal's diet, risk of intoxication may still remain low if plant toxicity is low. A good example is the heifer that ate 50% of her diet as larkspur flowers at Manti, Ut. during 1 day in 1987, yet was not overtly intoxicated because flowers were not very toxic.

It is unclear why tall larkspur growing at the Salina site, and to a lesser extent at Manti, was apparently more palatable to cattle

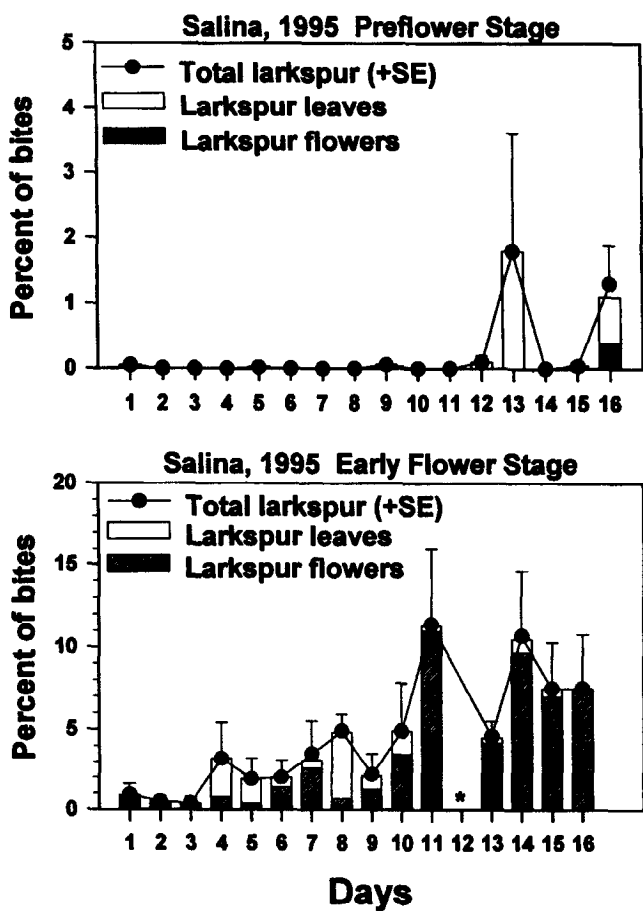


Fig. 3. Consumption of tall larkspur (% of bites) by cattle during the preflower (July 6-21) and early flower (2 July-6 Aug.) stages of growth during 1995 in Salina, Ut. (*indicates missing data for that day).

shortly after elongation of flowering racemes in comparison to the other grazing locations. There were 2 fatalities in the grazing studies at Salina when individual cows began eating large amounts of flowers or leaves. In general, cattle ate more flowers at Salina or Manti than at the other sites, and higher flower consumption seems to indicate a higher risk to cattle from more palatable larkspur during the early flower stage. There were not any obvious major differences in leaf toxicity for the Salina population compared to the other sites; unfortunately flowers were not collected at Salina for alkaloid analysis. We have shown that acceptability of tall larkspur to cattle is not influenced by the toxic or total alkaloid concentration (Pfister et al. 1990, Pfister et al. 1996), nor were storms a factor (Ralphs et al. 1994), and we speculate that consumption was driven by other individual plant or plant community factors unrelated to toxicity.

Consumption of tall larkspur leaves and (or) flowers during the early flower stage probably indicates that consumption levels will increase later in the grazing season (Pfister et al. 1988a). On the other hand, lack of consumption during the early flower stage does not necessarily mean that cattle are less likely to eat tall larkspur later in the grazing season (J.A. Pfister, personal observations). Thus, preflower consumption should be used cautiously in attempts to predict postflower consumption. Postflower consumption can begin suddenly and accelerate quickly (Pfister et al. 1988b, Pfister and Manners 1995).

A major consideration in determining risk is the likelihood that cattle will consume a given amount of tall larkspur, as we have previously presented in the context of a toxic window (Pfister et al. 1988a). Our studies have shown that cattle generally ingest low doses of toxic alkaloids before tall larkspur begins flowering. Once tall larkspur elongates flowering racemes, producers are much more likely to lose cattle to tall larkspur poisoning. Actual death losses are influenced by both plant and animal factors. The major animal factor is individual animal susceptibility, whereas major plant factors include concentration of toxic alkaloid and palatability of tall larkspur, which determine dosage and rate of consumption of toxic alkaloids (Pfister et al. 1988b).

If consumption is low or nil, then risk of losing cattle will also be low regardless of toxic alkaloid concentration. As cattle begin to consume increasing amounts of tall larkspur, toxic alkaloid concentration becomes critical in making grazing management decisions. In particular, consumption of flowers during the early or full flower period should warn of potential high risk situations. For a crude indication of tall larkspur consumption, livestock producers can quickly note defoliation of flowers (perhaps even leaves) without seeing cattle actually eat tall larkspur. Figure 2 can provide general guidelines to help producers determine the toxic alkaloid dose that animals may ingest. Grazing management decisions can be improved if information on plant toxicity and possible dose response is considered along with the probability that cattle will eat injurious amounts of tall larkspur at a particular phenological stage (i.e., toxic window).

Although we have not studied the ecological consequences of early grazing, grazing early followed by a rest period is probably benign or even beneficial for other forbs and perennial grasses (Richards and Caldwell 1985, Lacey et al. 1994), and thus is unlikely to increase larkspur populations. If cattle numbers are reduced after flowering, decreased grazing pressure on tall larkspur may increase larkspur density over long periods of time (e.g., 40 years, Ellison 1954). On the other hand, flowering tall larkspurs are probably important vectors for hummingbird and bee populations (Inouye et al. 1991, Inouye and McGuire 1991), and reducing cattle grazing during flowering may benefit livestock producers by reducing cattle deaths while benefitting other organisms.

Management Implications

Much of the productive forage on tall-larkspur infested rangeland is underutilized because cattle grazing is deferred or curtailed due to perceived risk of cattle deaths caused by tall larkspur. Our studies indicate that many livestock operations can typically gain 4 to 5 weeks of grazing on these infested ranges early in the grazing season. Since cattle can graze tall larkspur-infested ranges before elongation of flowering racemes with little risk of death losses from tall larkspur toxicosis, management of tall larkspur-infested rangeland should be evaluated to determine if it is feasible to take advantage of this low-risk period. When feasible within a multiple use setting, cattle should be grazed on these ranges as soon as sufficient forage is available; livestock producers should also consider removing cattle or reducing cattle numbers when tall larkspur flowers. The transition in tall larkspur phenology from the preflower to flowering state can be easily distinguished by simply noting whether the majority of racemes

have elongated. Fully developed tall larkspur buds often "nod" or droop to one side when raceme elongation begins, and this is another visual clue that the transition is occurring. If cattle remain on tall-larkspur infested rangeland after plants have flowered, and cattle eat significant quantities of tall larkspur, relative risk of losing cattle may be high until tall larkspur toxicity declines with maturation. Our results do not apply to low larkspurs (e.g., *D. nuttallianum*) or to plains larkspur (*D. geyeri*) as specific grazing recommendations have not been developed for these species.

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Structure and causes of vegetation change in state and transition model applications

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Abstract

State and transition (ST) descriptions of rangeland vegetation dynamics provide information on current perceptions of explicit causes of change in dominant vegetation. Structural attributes of ST applications allow an evaluation of the complexity of the ST model and comparisons with the organization of the traditional succession-retrogression model of secondary succession. An analysis of 29 applications of the ST model revealed consistent trends. The number of transitions connecting states showed a less-than-expected increase with the size of the application. This is probably associated with limitations to interpret complex relationships and a need to produce relatively simple applications. Larger applications exhibited a shift towards stable states with pivotal positions within structures less connected (i.e., with fewer transitions) than expected by chance for a given number of states. Thus, some stable states assume key intermediary roles as the number of states considered increases. It is debatable whether this is a property of larger systems or an effect of modeling bias. The analysis of causes of vegetation change confirmed current perceptions about the importance of man-related sources of disturbance. Grazing, fire, and control of woody plant species are visualized as the most relevant man-related agents of change. Some ST applications retain autogenic behaviors embedded in transitions in spite of the event-driven nature of the approach. However, the ST model removes autogenic processes from their central role as general causes for vegetation change. This approach is theoretically very limited because no general properties or attributes of the components (e.g., plant species assemblages, individual species) or processes (e.g., growth, reproduction, mineralization) of the system are used in any comprehensive way to generate predictive rules of wider than local relevance. Alternative approaches are suggested that would allow ecological generalizations and comparisons across systems.

Key Words: alternative stable states, climax, fire, grazing, retrogression, secondary succession

Resumen

Descripciones de la dinámica de la vegetación natural del tipo "estados y transiciones" (ET) proveen información sobre percepciones actuales acerca de causas explícitas de cambio en vegetación dominante. Las características estructurales de aplicaciones del modelo ET permiten una evaluación de su complejidad y comparaciones con la organización del modelo tradicional de sucesión secundaria, basado en secuencias de deterioro-sucesión. Un análisis de 29 aplicaciones del modelo ET reveló tendencias consistentes.

El incremento en el número de transiciones asociado a un aumento en el número de estados fue menor del esperado. Ello se debería, probablemente, a limitaciones en la interpretación de relaciones complejas y a la necesidad de producir aplicaciones relativamente sencillas. Las aplicaciones de mayor tamaño tendieron a incluir estados estables centrales inmersos en estructuras menos conectadas (i.e. con menos transiciones) que lo esperable por azar para un cierto número de estados. Ello implicaría que algunos estados estables tienden a asumir roles intermedios claves en aplicaciones que incluyen un elevado número de estados. Es discutible que ésta sea una propiedad de sistemas extensos o simple sesgo inducido en el uso del modelo.

El análisis de causas de cambio en la vegetación confirmó actuales percepciones acerca de la importancia de los disturbios antropogénicos. El pastoreo, el uso del fuego, y el control de especies leñosas aparecen como los más importantes agentes de cambio antropogénico. A pesar de ser dinámicamente controladas por eventos, algunas aplicaciones del modelo ET conservan elementos autogénicos. Los procesos autogénicos, sin embargo, aparecen desplazados de su rol central como causas universales de cambio en la vegetación. El valor teórico de esta propuesta es muy restringido porque no hace uso de propiedades o atributos de los componentes (e.g. especies, grupos de especies) o procesos (e.g. crecimiento, reproducción, mineralización) del sistema en alguna manera abarcadora que permita formular reglas predictivas de aplicación amplia. Se sugieren propuestas alternativas que permitirían generalizaciones ecológicas y comparaciones entre diferentes sistemas.

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The state and transition (ST) model, named by Westoby et al. (1989a), has recently become a popular tool for communicating ideas and hypotheses about vegetation change in rangelands. For systems in which it may be meaningful to define ecological objects at a certain scale of perception, the ST model facilitates the capture of relevant system-driving events/processes. It also

forces the suggestion or indication of explicit causes to justify transitions among states. Although the ST model lacks a spatial component, some of its most recent applications include statements about time frame, confidence, and expected probability of transitions (e.g., Ash et al. 1994).

Despite suggestions to the contrary (e.g., Borman and Pyke 1994), the ST model does not represent new ecological theory (Westoby et al. 1989b, Walker 1993). It has been used to describe vegetation dynamics that do not fit within the traditional succession-retrogression (SR) frame of vegetation change in rangelands described by Sampson (1917, 1919) and Dyksterhuis (1949, 1958a, 1958b) and this has probably generated some confusion. Applications of the ST model are frequently associated with "community" as opposed to "continuum" theories because of their structure, particularly the splitting of change processes into discrete states when systems are evaluated at pre-selected scales of time and space. This does not necessarily imply support for community-unit ecological theories; rather, it reflects an effort to simplify the translation of the supposedly complex operation of ecological objects into understandable diagrams amenable for management decisions. In particular, the dynamics of models presumably containing alternative stable states (for a theoretical view, see Law and Morton 1993) are usually depicted using this tool. This may be justified when the presence of alternative stable states, the occurrence of irreversible changes relative to the selected time scale, or the action of non-linear processes, are hypothesized.

A structural analysis of ST applications may provide an opportunity to evaluate differences and similarities between these "alternative stable state" schemes and traditional linear (Clements 1916, 1936) or star-like (Dyksterhuis 1949) representations of "climax-seral stage" models. The explicit implication of particular factors used to explain transitions between states offers a unique opportunity for cataloging and evaluating the relative frequency of causes of vegetation change and relationships among such causes. Sources of change of widespread apparent importance can be identified that may be relevant to consider when confronting the task of understanding range dynamics in similar vegetation types.

The objectives of this work were: (1) to identify causes of vegetation change of perceived widespread importance in rangelands, and (2) to assess the potential complexity of the state and transition model through an analysis of 29 applications of this approach. Some structural comparisons with the traditional succession-regression model were possible using regression techniques and graphical representations of a stage version of the SR model as the null hypothesis for the ST model.

Materials and Methods

Twenty nine published and unpublished applications of the state and transition model were analyzed (Table 1). Details on unpublished applications are available from the authors upon request. These studies represented the most complete set available and were not subjected to any selective process other than checking for "state and transition" structure and explicit indication of causes of transitions. Some of the studies (Whalley et al. 1978, Wilson et al. 1988, Silcock et al. 1988) predate the publication of the paper that is usually referred to as the original source for the scheme (Westoby et al. 1989a). Most of the models origi-

nated in Australia, with some examples from Argentina, South Africa, Spain, and the US. These applications cover a fairly broad range of rainfall regimes and vegetation types, but most of them were developed for semi-arid grasslands/shrublands.

Clarification of some terms is required to interpret the analyses performed. A state and transition model contains 2 types of objects: *states* and *transitions*. States are physiognomically characterized ecological entities and are usually described by botanical composition of dominant vegetation. Transitions are not always clearly defined and may be classified as *simple* or *complex*. Simple transitions involve the action of only 1 possible *cause* (although it may have more than 1 component; chemical treatment of woody plants *and* grazing, for example) that may involve 1 or more single *factors* (e.g., chemical treatment of woody plants, grazing, rainfall, fertilization). Complex transitions may be provoked by more than one cause (grazing *or* rainfall and summer fire) each of which may involve 1 or more factors. Factors may be additionally characterized by some *attribute* (e.g., intensity, season) that completes their description. Complex transitions were distinguished from complex causes (those including more than 1 factor) by means of identifying 3 of the basic connectives of sentential logic in the model descriptions: negation (\neg , i.e., *no*), conjunction (\wedge , i.e., *and*) and disjunction (\vee , i.e., *or*). Stylistic variants of these connectives (e.g., both, although, as well as, unless) were interpreted and translated into 1 of the 3 logic equivalents (Allen and Hand 1992). Some examples follow.

Example 1: transition provoked by summer fire.

1 cause: fire

1 factor: fire (qualified by season)

Transition 1: (simple) provoked by factor A

1 cause: A (simple)

1 factor: A

Example 2: transition provoked by *no* chemical control *and no* rain *and* heavy grazing.

Transition 2: (simple) provoked by $\neg A \wedge (\neg B \wedge C)$ 1 cause: $\neg A \wedge (\neg B \wedge C)$ (complex);

3 factors: A, B, and C

Example 3: transition provoked by fire *and no* grazing *or* above average rainfall and seeding *and no* competition.

Transition 3: (complex) provoked by $(A \wedge \neg B) \vee (C \wedge D \wedge \neg E)$

2 causes: $A \wedge \neg B$ (complex) or $C \wedge D \wedge \neg E$ (complex);

5 factors: A, B, C, D, E

The classification of factors and attributes causing vegetation change required many iterations. The classification developed is obviously not unique.

Causes of Vegetation Change

An analysis of causes of transitions was performed on the set of factors involved as qualified by attributes (a total of 50) and then grouped into 6 main factors determined from this preliminary general classification. Main factors identified were labeled as grazing, fire, rainfall, woody plant control, other man-related management practices, and endogenous factors. Causes identified as the "absence" or "lack" of single factors (e.g., fire, grazing) or combinations thereof (e.g., rainfall and grazing and no fire) were classified as endogenous based on the rationale that "absence of ..." or "lack of ..." implied that the system was left to its own spontaneous dynamics involving recruitment of new (possibly woody) plants, aging of perennial species, exhaustion of seed banks, and similar autogenic processes. It is recognized that, in some cases (e.g., purposive fire suppression), this assumption

Table 1. Overview of main characteristics of models included in the data base of state and transition applications.

Type of vegetation	Country/ region	Number of stable states	Annual rainfall regime ¹ (mm)	References
Perennial sown pasture	Sub-tropical eastern Queensland, Australia	2	1100	Jones 1992
Chenopod shrubland	Riverine Plain, Australia	3	300–400	Westoby et al. 1989b
Mulga woodlands	Southeastern Australia	3	253–483	Hodgkinson 1991
Chenopod shrubland	South Australia	3	200–300	Hunt 1992
Monsoonal tallgrass woodland	Northern Territory, Australia	3	-	Ash et al. 1994
Semi-arid grassland/ woodland	Eastern Australia	4	-	Westoby et al. 1989a
Mediterranean savanna- woodlands	California and Spain	4	-	Huntsinger and Bartolome 1992
Low forest/ scrub	Argentina	4	800–1200	De Pietri 1992
Tropical woodlands	Northern Queensland, Australia	4	-	Scanlan 1994
Perennial grassland	Central/southern Queensland, Australia	4	500–700	Hall et al. 1994
Eucalypt woodland with grass understory	Queensland, Australia	4	600–1200	Orr et al. 1994
Chenopod shrubland	Northern Territory, Australia	5	200	M. Friedel (personal communication)
Perennial grassland	Queensland, Australia	5	-	McIvor and Scanlan 1994
Perennial grassland	Victoria River District, Northern Territory, Australia	5	500–700	Stockwell et al. 1994
Herbaceous layer in caldén forest	Argentina	5	555	Llorens 1995
Temperate semi-arid rangelands	Argentina	5	-	Distel and Bóo 1995
Tall grassveld	South Africa	6	-	Westoby et al. 1989b
Sagebrush grassland/shrubland	Great Basin, USA	6	-	Laycock 1991
Perennial grasslands	Northern Slopes and Tablelands, NSW, Australia	7	-	Lodge and Whalley 1989, Whalley 1994
Annual grassland	California, USA	7	675–875	George et al. 1992
Monsoonal tallgrass woodland	Northern Territory, Australia	7	-	T.G.H. Stockwell (personal communication)
Tallgrass periennial grassland	Northern Australia	7	(semi-arid)	Ash et al. 1994
Perennial grassland	Northern Australia	7	200–800	McArthur et al. 1994
Semi-arid woodland	NSW and Queensland, Australia	8	200–500	J. Noble (personal communication)
Perennial grassland	Victoria River District, Northern Territory, Australia	8	500–700	Stockwell et al. 1994
Perennial grasslands ²	Northern Tablelands, NSW, Australia	9	-	Whalley et al. 1978
Mulga shrubland	Queensland, Australia	9	400–500	Silcock et al. 1988
Chenopod shrubland	NSW, Australia	9	125–350	Wilson et al. 1988
Mulga open woodlands	Southwestern Queensland, Australia	9	250–550	Jones and Burrows 1994

¹If indicated in the original documentation.

²Model is an integrated view of 3 different perennial grasslands that were arbitrarily considered as a whole to avoid artificial replication of causes of vegetation change.

might introduce some bias. However, in an overwhelming majority of cases, the correct interpretation was that lack of fire, for example, implied the absence of conditions to apply prescribed burning when indicated. References to "climatic conditions" or "weather" (a total of 4 instances) were grouped under the "rain-fall-general" label.

Causes involving 1, 2, and 3 or more single factors were classified independently and then pooled to obtain overall estimates of occurrences. A classification was also performed on complex causes involving exactly 2 or exactly 3 factors. This latter proce-

dure allowed us to ascertain relationships between factors that are frequently cited in association. Results are expressed as occurrences (i.e., the number of times a particular factor or combination of factors was cited as involved in transitions) and/or frequencies (i.e., occurrences in relation to the total number of occurrences and expressed as percentages).

Structural Analysis

An analysis of some structural attributes of state and transition applications was implemented to study relationships involving

the number of transitions, the degree of connection among states, and the distribution of transitions among states. Regression techniques and graphical representations of null hypotheses were used for these purposes. The rationale for this type of analysis was to evaluate the structural complexity of ST applications relative to a linear or star-like traditional stage-based "succession-retrogression" structure. This rationale requires clarification to avoid possible misinterpretations. Dyksterhuis' approach to range condition assessment (Dyksterhuis 1949, 1958a, 1958b) is based upon the succession-retrogression (SR) concept, but implemented in the context of a continuum in the vegetation space, i.e., no stages or states are distinguished (Dyksterhuis 1949, 1985). The widespread idea that Dyksterhuis' condition-relative-to-climax scheme is, somehow, "Clementsian" orthodoxy, is incorrect. However, and only for the purpose of comparing structural characteristics, SR was represented as linear or star-like sequences of states, more in line with a "traditional" view (e.g., Clements 1916, 1936; Sampson 1917, 1919).

For the representation of expected values and null hypotheses, the following results were used. The minimum number of transitions (t) required to maintain the integrity of an application with s states is $s-1$ (otherwise at least 1 state will be disconnected from the rest) and corresponds to a linear model (or some topologically equivalent structure) with only one transition linking consecutive states. The maximum number of transitions for an s -sized application of any possible structure is $s(s-1)/2$. Thus, an application with 3 states can have a maximum of up to 6 transitions that will connect each state to the rest through two-way links. The equivalent maximum possible number of transitions for an s -sized application with linear or topologically equivalent structure is $s-1$. This is because links are only allowed between contiguous states. The degree of connectance (c) among states was calculated as the number of indicated transitions (t) relative to the maximum number of possible transitions for a given size, i.e., $c = t / (s(s-1)/2)$, which has a maximum of 1 (when all states are connected through two-way transitions) and a minimum of $1/s$ (i.e., when the number of transitions is just enough to keep all states integrated). An estimate of connectance provides a way to evaluate the potential intricacy of the behavior of the system for a given nominal size. The null hypothesis for the expected value of connectance as a function of number of states required the calculation of a probability distribution for every possible number of stable states. For $s = 2$, the maximum number of possible transitions is 2. These 2 transitions can be different or the same with the same probability (0.5) only by chance. In the first case, $c = 1/(2(2-1)) = 0.5$ while in the second one $c = 1.0$, so the weighted (connectance values weighted by the probability of occurrence) mean outcome $(0.5 \times 0.5 + 1.0 \times 0.5)$ would be 0.75. The process can be visualized as a random assignment of the maximum number of possible transitions for a given application size (of any possible structure, not necessarily linear) to the possible slots that transitions can occupy among states. A Monte Carlo approach, involving 10 replicates of 20,000 simulations for each nominal size (number of stable states) was used to estimate expected values of connectance.

The distribution of transitions, a measure of the concentration or dispersion of transitions among states, was estimated using an *ad hoc* equitability index (e) derived from Shannon's information index (Shannon and Weaver 1949):

$$e = (H - L) / L$$

where H is Shannon's index calculated as: $H = - \sum_{i=1}^s (p_i \ln p_i)$;

where $p_i = t_i / \sum t_i$, t_i represents transitions as defined above, i is i^{th} state and L is H calculated for a model with completely reversible linear structure, i.e., one in which there would be 2 states (those located at both ends of the linear structure) connected to the rest by 2 transitions and $(s-2)$ other states each connected by 4 transitions. This equitability index can be used as an indicator to detect structural shifts in the distribution of transitions which are indicative of certain states playing key "intermediary" roles in the dynamics of the system. Maximum equitability will vary with the number of stable states but can be easily calculated from configurations in which each state is connected to every other state by the same number of links, either 1 or 2. Comparative minimum values of equitability were calculated using the following approach. For each nominal size, all possible configurations of linear and star-like reversible systems were determined and their frequencies and equitabilities calculated taking into account topologically equivalent configurations. A weighted (by frequency) average was then obtained for every possible number of stable states from 3 to 9 (equitability is fixed and equal to zero for a 2-state configuration).

Results

Causes of Vegetation Change

The 29 applications contained a total of 162 stable states (Table 1; mean: 5.6 states / application, range: 2-9). They provided a total of 310 transitions among states, 369 instances of causes of transitions, and 604 instances of factors involved in causes. In 1.2% of these latter instances (7/604) the ultimate factor involved was unknown to the author(s) or the corresponding transition was deemed improbable and the factor involved not identified. Table 2 shows occurrences and relative frequencies of main factors and individual factors within main factors, classified by causes involving one (192), two (264), or three or more (141) single factors. Only individual factors with at least 1.5% of overall frequency are shown in Table 2.

Grazing was the main factor most frequently cited (over 30% overall relative frequency) although its relative contribution decreased from over 40% to less than 20% as the number of factors involved in causes increased from 1 to 3 or more (Table 2). Endogenous factors were the second most frequently cited; they approached and finally exceeded the frequency of grazing factors as the number of factors considered increased. Rainfall was the third most frequently cited main factor and showed a trend to increase in relative frequency of citation as the number of factors involved in causes increased. The involvement of fire, woody plant control, and other man-related practices was lower and seemed to be less dependent on the number of factors included in causes although woody plant control increased up to 17% relative frequency when 3 or more factors were considered.

Grazing. A "within main factor" calculation of frequencies for grazing (Table 2) indicated a consistently high relative frequency of citation for intensity of grazing (either alone or interacting with season or system of grazing) that was not associated with the number of factors considered. Trampling, system of grazing, and an interaction factor between system of grazing and animal

Table 2. Individual and main factors most frequently cited. Values are frequencies (occurrences) classified according to the number of factors involved in causes of transitions.

Main Factor	Number of factors involved in causes							
	One		Two		Three or more		All	
Grazing	43.2	(83)	33.0	(87)	19.9	(28)	33.2	(198)
by intensity	51.8	(43)	66.7	(58)	75.0	(21)	61.6	(122)
by system x intensity	18.1	(15)	12.6	(11)	0.0	(0)	13.1	(26)
by season x intensity	14.5	(12)	3.4	(3)	0.0	(0)	7.6	(15)
general	7.2	(6)	8.0	(7)	7.1	(2)	7.6	(15)
by season	1.2	(1)	6.9	(6)	10.7	(3)	5.1	(10)
Endogenous	19.8	(38)	25.4	(67)	24.1	(34)	23.3	(139)
seed bank	0.0	(0)	32.8	(22)	50.0	(17)	28.1	(39)
absence of fire	26.3	(10)	17.9	(12)	20.6	(7)	20.9	(29)
absence of grazing	23.7	(9)	13.4	(9)	14.7	(5)	16.5	(23)
soil fertility	5.3	(2)	11.9	(8)	0.0	(0)	7.2	(10)
absence of woody plant control	10.5	(4)	7.5	(5)	0.0	(0)	6.5	(9)
Rainfall	11.5	(22)	14.0	(37)	21.3	(30)	14.9	(89)
above average	27.3	(6)	24.3	(9)	50.0	(15)	33.7	(30)
below average	50.0	(11)	43.2	(16)	6.7	(2)	32.6	(29)
general	9.1	(2)	13.5	(5)	20.0	(6)	14.6	(13)
Fire	12.0	(23)	12.9	(34)	12.1	(17)	12.4	(74)
general	43.5	(10)	61.8	(21)	88.2	(15)	62.2	(46)
by season	21.7	(5)	8.8	(3)	5.9	(1)	12.2	(9)
Woody plant control	6.3	(12)	5.7	(15)	17.0	(24)	8.5	(51)
chemical	50.0	(6)	40.0	(6)	45.8	(11)	45.1	(23)
mechanical	25.0	(3)	53.3	(8)	50.0	(12)	45.1	(23)
Other man-related factors	7.3	(14)	9.1	(24)	5.7	(8)	7.7	(46)
seeding	21.4	(3)	54.2	(13)	62.5	(5)	45.7	(21)
fertilization	21.4	(3)	29.2	(7)	0.0	(0)	21.7	(10)

Endogenous. The "endogenous" main factor had the largest number and variety of individual factors included. Availability of seed/propagules was the individual factor most frequently referred to within this group although it was never mentioned as the only factor responsible for any transition (Table 2). Other, less frequently mentioned individual factors were insect outbreaks, absence of various complex causes, establishment of exotics/invasers, competition and absence of competition, plant diseases, increased above ground primary production, plant dieback, soil surface conditions, and absence of cultivation. The absence of a factor (e.g., no fire, no grazing) was the most frequently invoked cause of change within this group, accounting for over 50% (72/139) of all instances. When this uninformative composite factor was removed from calculations, the frequency of citation of seed bank status increased to 54.2% (39/72) with similar incidences when 2 (22/41) or 3 or more (17/22) individual factors were considered.

Rainfall and Fire. These main factors were cited a similar number of times (Table 2) although the internal distribution within main factors was remarkably different. Most frequent references involving rainfall mentioned lack of rain (or drought) and above average precipitation (or some stylistic variants) with rainfall as a general event mentioned less frequently (Table 2). Also, opposite trends with the number of individual factors involved were observed for above and below average precipitation. Season, timing of rain, timing of rain interacting with amount of rainfall, and season interacting with amount of rainfall accounted for the rest of the occurrences within this main factor.

Fire was rarely qualified as dependent on the usual attributes of season, frequency, and intensity (Table 2) and interactions

between those attributes were only mentioned in 3 instances of fire involvement. Wildfires or wildfire control, intensity of fire, and an interaction between frequency and intensity of fire complete the list of individual fire-related factors.

Woody Plant Control and Other Man-related Factors. Patterns of relative frequency within the "woody plant control" and "other" groups are probably much less reliable because of the reduced number of instances involved. Nevertheless, similar frequencies of chemical and mechanical control of woody plants were observed (Table 2), with biological control and plant control as a general factor, less frequently considered. Man-related factors other than those indicated in Table 2 were overharvest of propagules, soil reclamation, cultivation, and weeding.

Pairs of Factors. Main factors most frequently mentioned together included grazing and endogenous factors, grazing and fire, and grazing and rainfall (Table 3). Marginal frequencies (last column in Table 3) differ slightly from the distribution of two-factor causes in Table 2 because contributions from pairs constituted by the same factor count double in Table 3. Results from the occurrence of three-factor causes (117 instances) followed similar trends with grazing, rainfall, and endogenous as the most important groups of factors (59.0, 56.4, and 51.3%, respectively), followed by woody plant control (46.1%), fire (38.5%), and other man-related practices (12.8%).

Frequency of main factors varied among applications, and for those with 3 or more states, there was no apparent pattern of change associated with the number of states (Fig. 1). Frequency of endogenous factors tended to follow an inverse trend relative to grazing factors. Rainfall and grazing were the only factors mentioned in the 2-state application included in the analysis (Fig. 1).

Table 3. Occurrence (frequency) of different pairs of factors as causes of transitions. Individual factors are grouped under endogenous, fire, grazing, rainfall, woody plant control (WPC), and other man-related main factor labels.

	Grazing	Endogenous	Fire	Rainfall	Other (man)	WPC	Overall Frequency ¹
Grazing	1 (0.8)	34 (25.8)	22 (16.7)	20 (15.1)	2 (1.5)	7 (5.3)	65.1
Endogenous		11 (8.3)	3 (2.3)	7 (5.3)	1 (0.8)	0 (0.0)	42.4
Fire			0 (0.0)	4 (3.0)	0 (0.0)	5 (3.8)	25.8
Rainfall				2 (1.5)	2 (1.5)	0 (0.0)	26.5
Other (man)					8 (6.1)	3 (2.3)	12.1
WPC						0 (0.0)	11.4

¹Last column shows the overall frequency of occurrence of each main factor relative to the total number of pairs (132).

Structural Analysis

Results from structural analyses are summarized in Figs. 2 to 4. As expected, the number of transitions increased with the number of states although 2 of the applications only exhibited enough transitions to exactly keep the integrity corresponding to their nominal size (Fig. 2). A linear regression of number of transitions against number of states in log-log scale was found to adequately describe this relationship ($P < 0.001$, $r = 0.73$) and attenuated an increase in variance associated with the number of states. Non-linear alternatives did not improve this fit significantly. The slope of this relationship in the linear scale (1.82 ± 0.322 ; $b \pm SE$) was compared to the expected value for applications with linear or topologically equivalent structure (i.e., 2) and found not significantly different ($t = 0.56$; 27 d.f.). The theoretical intercept (i.e., -2) was within the standard error of the calculated intercept (0.04 ± 1.921) and consequently not significantly different from it ($t = 1.06$; 27 d.f.). Points corresponding to applications with minimum numbers of transitions for their nominal size (Fig. 2) showed up as potential outliers in many diagnostic plots, even in log-log scale. Removing those data, however, did not change any result so they were retained.

Average connectance among states tended to decrease with an increase in the number of states (Fig. 3). Average connectance was close to theoretical expected values for applications with few states but declined, approaching minimum connectance, as the

number of states increased. The equitability index (Fig. 4) showed similar behavior. Applications with 4 or fewer stable states exhibited null or positive deviations (i.e., more uniform distribution of links than with a linear or topologically equivalent reversible structure) except for 1 case, while applications with 5 or more states showed increasingly negative deviations.

Discussion

Although the set of state and transition applications analyzed does not represent any particular ecological system or region, some general structural features can be characterized and applied for developing other applications. The relative frequency of factors cited as causes of vegetation change in this collection of ST applications does not necessarily apply in general to rangelands, but does reflect current main-stream range management ideas (Stafford Smith and Pickup 1993). The high relative frequencies with which certain factors and groups of factors were cited is a

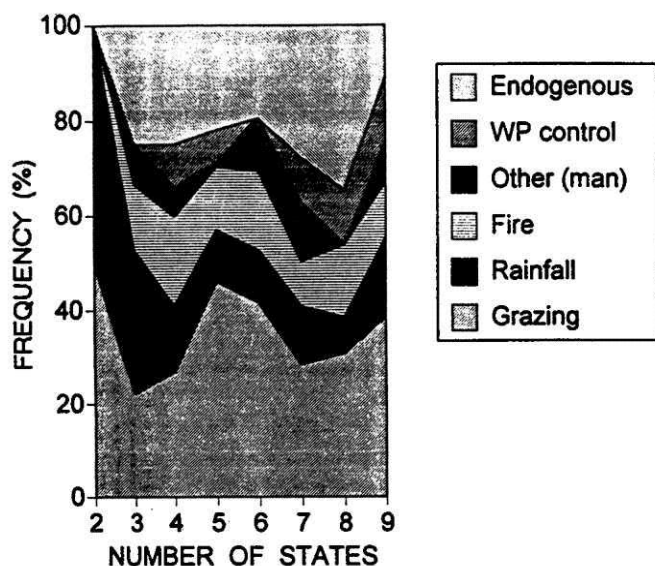


Fig. 1. Relative frequencies of main factors involved in transitions as a function of the number of stable states.

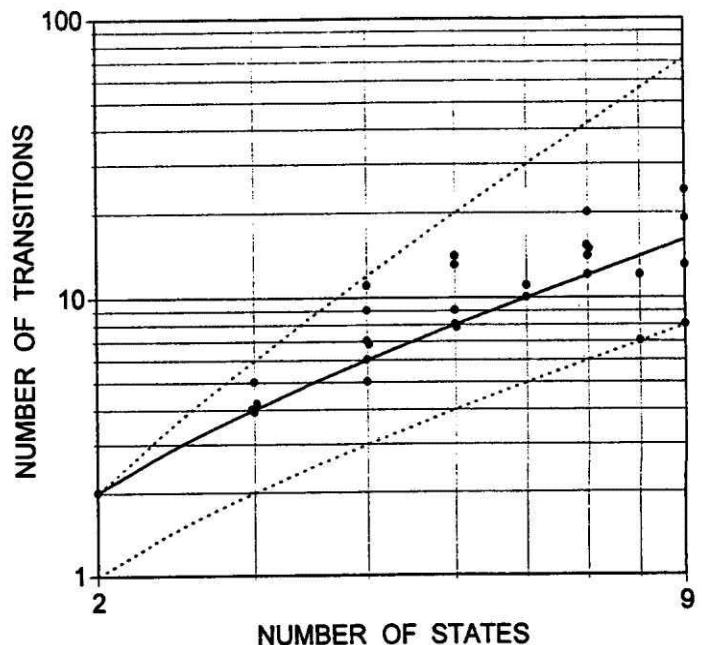


Fig. 2. Observations (black symbols) and expected relationship (solid line) describing the number of transitions as a function of the number of stable states under the assumption of linear (or topologically equivalent) structure. Dotted lines indicate allowable maxima and minima for the observations. Clumped observations (number of states 3, 4, 5, and 7) were jittered by adding random noise to improve visualization.

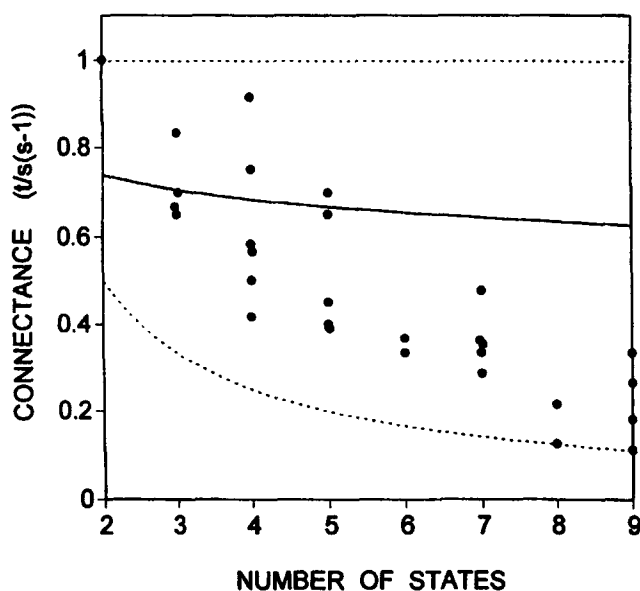


Fig. 3. Observed (black symbols) and expected (solid line) values for connectance. Maximum and minimum values allowable are indicated by the dotted lines. Clumped observations (number of states 3, 4, 5, and 7) were jittered by adding random noise to improve visualization.

consequence of their perceived widespread importance across a variety of rangeland types (see Fig. 1). In this sense, sources of change frequently mentioned in these applications should be considered when evaluating the dynamics of similar types of rangelands.

Causes of Vegetation Change

Among the factors that can be controlled by management, intensity of grazing is obviously considered the most important single cause of vegetation change followed by the use of fire. Other management practices like chemical or mechanical woody plant control and seeding account for a much reduced relative frequency of citation. However, when considered as a whole, man-related factors justify more than 60% (364/597) of the total number of instances of identified factors. Rainfall (15%) and endogenous factors (23%) account for the rest. Although this partition depends on a non-unique classification of individual factors, it is surprising that about 20% (38/192) of simple instances of transitions and 23% of the total were attributed to the action of auto-genic factors. This is hardly expected for system components that are supposed to remain relatively stable when external forces are not operating (Laycock 1991). Some of the endogenous "factors" cited (e.g., availability of propagules) may well be considered conditions required for the operation of other factors, rather than genuine and ultimate causes of change. However, almost half (68/139) of the instances included in the "endogenous" group of factors corresponded to cases of "absence of ...", particularly of grazing or fire. This is a clear indication that certain spontaneous behavior still remains embedded in the structure of some ST applications, even if not explicitly modeled.

Two trends were observed relative to the number of factors considered. The overwhelming frequency of citation of grazing when only single factors are considered was moderated by an

increasing relevance of factors such as seed bank dynamics (Table 2) up to a point in which grazing was no longer the most frequently cited main factor. Above and below average rainfall regimes exhibited opposite trends associated with the number of factors considered (Table 2). This probably reflects the fact that droughts can severely modify the botanical composition of a site by themselves while a good rain needs to be accompanied by other factors or conditions, like availability of propagules or a reduction of stocking rate, to produce similar effects.

The analysis of pairs of factors (Table 3) was in general agreement with the trends discussed above. Additive, interactive or sequential effects involving grazing seem to be the most common instances of complex factors.

Structural Analysis

The structural analyses revealed an economy of transitions between states remarkably similar to what would be expected for linear or star-like succession-retrogression models of comparable dimensions (Fig. 2). Accordingly, the likelihood of transition from a given state towards any other possible state was proportionally lower for larger state and transition applications (Fig. 3). A similar phenomenon is usually observed in ecological webs (Yodzis 1980, Warren 1994), although in this latter case it may well be due to defective sampling. In our case, the observed decrease in connectance may indicate a real trend associated with an increase in the complexity of the applications. Alternatively, and more probably, it reflects human limitations to visualize complex systems. The decrease in connectance was associated with a shift in the distribution of transitions (Fig. 4) from applications with states more evenly connected than expected for a reversible linear structure towards applications with a more biased distribution of transitions among states. This indicates that some stable states tend to assume central or key roles as the number of states considered increases. With climax removed from its central role as the reference state in succession-deterioration sequences, more equitability among states would be expected. A

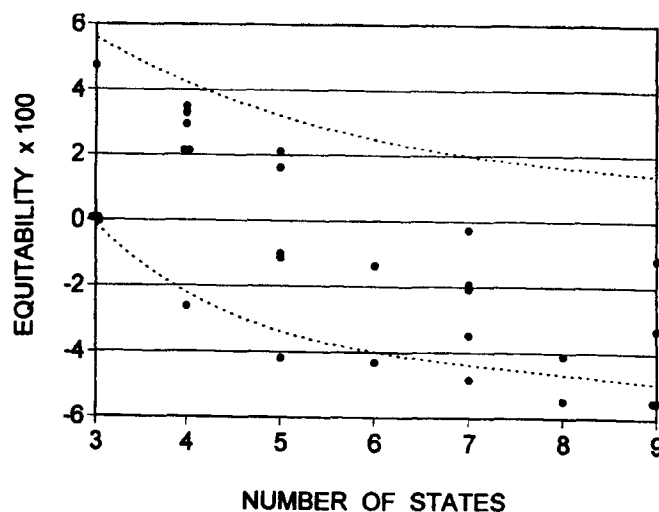


Fig. 4. Observed values for the equitability index as a function of the number of stable states. Maximum and minimum values allowable for linear or topologically equivalent structures are indicated by dotted lines. Clumped observations (number of states 3, 4, and 5) were jittered by adding random noise to improve visualization.

possible explanation is that those central intermediary states are the best known or the ones most frequently observed under current management conditions. Familiarity with a certain common state of the vegetation may bias the general picture of the system. Again, it is difficult to ascertain to what extent a decreased equilibrium is a real property of larger systems or simply an effect of the way human minds look at the world. Some of the structural properties observed may be more related to the psychology of perception than to any real characteristic of increasingly complex systems.

Two striking outcomes from these analyses are the elementary nature of causes of change and the structural simplicity of the applications. More than half of the instances of transitions for which some explanation was provided involved only 1 factor (206/359), possibly modified by the attachment of some attribute. In 90% of the instances (324/359), transitions were associated with at most 2 factors. In only 2% of the cases were transitions justified by the action of complex causes involving 4 factors. In addition, wording of complex causes involving 2 or more factors generally corresponded to a mental image of additivity or sequential effects rather than of interactions among factors. This is in sharp contrast with the generally acknowledged complexity of vegetation dynamics (Roberts 1987, Wiegand 1989) and reveals the equivalent of a statistical "main effects" linear model operating at each node (stable state) in state and transition applications. The reasonableness of this approach may well be justified in the necessity of providing unsophisticated management-level predictions and/or in the lack of a consistent ecological theory about the spontaneous behavior of complex ecological objects.

The dynamic represented in Fig. 5 is a good example of how spontaneous and "external" causes of change are weighted in ST applications. Fig. 5 is a modification of Fig. 5 from Westoby et al. (1989b) in which all man-related causes of change have been removed. According to what is left from the original ST application, in a hands-off scenario and given enough time, the system would tend to reach a unique stable state that would persist unless the system were put under some disturbance stress. Many ST applications can be reduced to similar schemes by means of removing identifiable "non-spontaneous" causes of change. What is usually left, in turn, is very similar to traditional succession schemes in which a certain sequence of seral stages, terminating in a unique stable state, was hypothesized to represent the sponta-

neous behavior of the system when freed from disturbances. Thus, compared to traditional seral stages-climax ideas, the ST approach shifts the relative importance of causes of change by means of overweighing identifiable man-caused factors and down-playing autogenic factors like modifications of soil properties and competition. In doing this, however, the power of an all-encompassing theory of ecological system behavior is lost and replaced by *ad hoc* local shifts that fit previously observed vegetation changes under the influence of local prevailing disturbance forces. This may be realistic, but it is also theoretically very limited because no general properties or attributes of the components (e.g., plant species assemblages, individual species) or processes (e.g., growth, reproduction, mineralization) of the system are used in any general way to generate prediction rules of wider than local relevance. The cohesive nature contributed by processes involved in autogenic succession is removed from its central role of providing a coherent general reason for vegetation change but no alternative comprehensive properties are invoked to fill the gap.

The closest thing to a theoretical support for favoring state and transition representations of ecological systems is provided by the hypothesized existence of alternative stable states in those systems (Lewontin 1969, Sutherland 1974). A thorough discussion of this subject is out of the scope of the present paper but a brief comment on it is worthwhile. The existence of alternative stable states in very simple *mathematical* systems (see, for example, Noy-Meir 1975) has been widely invoked as evidence favoring the possible occurrence of alternative stable states in complex ecological systems (see, for example, Scheffer et al. 1993). This is a misleading assumption. No general principle can be invoked to justify any similarity between the behavior of a closed isolated mathematical system and the functioning of an open real complex adaptive system with diffuse boundaries. There is no evident reason to assume that more complex entities than those usually represented by Lotka-Volterra equations or similar predator-prey dynamics would behave in a similar way. In fact, empirical evidence frequently shows that the opposite may be true due to compensating effects induced by interactions with other systems within a common local landscape. Thus, general equilibrium conditions may emerge asymptotically at certain spatial scales (DeAngelis and Waterhouse 1987).

The correct interpretation of Noy-Meir's graphical exercise (Noy-Meir 1975) is that simplicity does not preclude the possible existence of alternative stable states in grazing systems if the assumptions and strong simplifications embedded in the mathematical abstraction are tenable. However, what is a "state" and what is "stable" depends primarily on our perception of change; i.e., on the temporal and spatial scale at which abstractions of reality are being produced. In this sense, it may be fruitful to dissect a system's behavior into discrete states, if looking at its functioning at such a scale facilitates interpretation and management decisions. This procedure does not require theoretical justification.

Producing theoretical support in the form of unifying ecological principles with predictive capability, based upon the concept of discrete states, is a different, yet unsolved problem (Stafford Smith 1992). Some examples of possibly alternative stable states have been reported in various ecosystems (Barkai and McQuaid 1988, Dublin et al., 1990, Scheffer et al. 1993) but the question still remains whether the nature of those states is dependent upon the intrinsic dynamic of the ecological objects or, in contrast, whether they are produced by some "external" forces alien to the

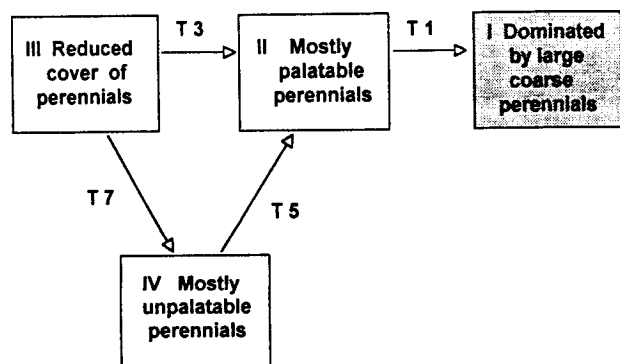


Fig. 5. ST application from Westoby et al. (1989b, Fig. 5), modified by removing transitions provoked by man-related causes of vegetation change.

alien to the undisturbed or unexploited system (Connell and Souza 1983). Thus, Dublin et al. (1990) considered elephants (apparently a true component of the system) as agents able to maintain the grassland state in the Serengeti-Mara woodlands ecosystem but they claimed that such a state was only produced by fire, an "external" perturbation according to the authors.

Summary and Conclusions

The set of state and transition applications analyzed revealed the following general characteristics:

- 1) ST applications are structurally similar to traditional linear "climax-seral stages" succession-retrogression models. However, other important differences are the rejection of complete reversibility embedded in the traditional view of secondary succession and the explicit treatment of other causes of vegetation change, in addition to grazing.
- 2) The lack of an expected more-than-proportional increase in transitions in response to an increased number of states may be due to some yet unknown property of the type of systems studied, a consequence of the necessity to keep models simple, or the result of human intellectual limitations to elucidate complex relationships.
- 3) Bigger applications tended to be centered around stable states that would play key roles as a consequence of their pivotal position within structures less connected than expected by chance for a given number of states.

The analysis of causes of change confirmed current perceptions concerning the apparent overwhelming importance of man-related sources of vegetation change in rangelands. In particular, grazing, fire, and woody plant control are visualized as the most relevant man-related agents of change. Some spontaneous behavior, not explicitly modeled, remains hidden in the definition of transitions in many ST applications.

If we are going to produce meaningful and comparable observational evidence regarding vegetation change, the nature of the boundaries between spontaneous and induced (by "external" forces) behaviors of ecological objects needs to be defined for previously selected scales of time and space. Those boundaries are blurred in the ST model by a lack of underlying support in the form of a general explanatory theory (*sensu* Hempel and Oppenheim 1948) that would link and generalize what otherwise is a collection of *ad hoc* site-specific hypotheses. Alternative approaches, based upon comprehensive properties of the elements or processes involved in rangeland systems, are required for updating currently unsatisfactory paradigms. Response and assembly rules based upon ecologically meaningful species traits (Keddy 1990, 1992a, 1992b) are probably the most promising alternatives. Response rules to the major disturbance factors discussed in this paper may be derived from currently available expert knowledge and generalized for application in similar ecosystems by means of relating responses to adaptive species profiles (Rodríguez Iglesias 1996). The challenge is to integrate models of autogenic behavior with management-level models driven by disturbance events/regimes and inputs. The ST model may provide phenomenological background for local applications, but truly explanatory models will require the integration of autecological information on individual species and processes involved in the observed responses to disturbance agents.

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Biomass and carbohydrates of spotted knapweed and Idaho fescue after repeated grazing

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Abstract

Spotted knapweed (*Centaurea maculosa* Lam.), an aggressive Eurasian forb, is replacing many native perennial grasses such as Idaho fescue (*Festuca idahoensis* Elmer.) on foothills of the Northern Rocky Mountains. We assessed biomass allocation, carbohydrate reserves (total nonstructural carbohydrate concentrations - TNC), and carbohydrate pools (TNC \times biomass) as indicators of cumulative effects of 3 summers (1991–1993) of repeated sheep grazing on spotted knapweed and Idaho fescue. In early May 1994, we excavated 30 spotted knapweed and Idaho fescue plants previously exposed to repeated grazing and 30 ungrazed plants of each species. On grazed Idaho fescue plants, shoot ($P < 0.02$) and root ($P < 0.06$) biomass were 38 and 27% less than on ungrazed plants. In contrast, shoot ($P = 0.26$) and root biomass ($P = 0.85$) of grazed and ungrazed spotted knapweed plants were similar. Although grazing resulted in some minor differences in total nonstructural carbohydrate concentrations and carbohydrate pools of shoots, total nonstructural carbohydrate concentrations and pools of crowns and roots were similar for grazed and ungrazed plants of each species. Thus, carbohydrate concentrations or pools were not sensitive indicators of the response of Idaho fescue or spotted knapweed to the cumulative effects of repeated grazing. In contrast, aboveground biomass could be used to indicate the response of Idaho fescue to repeated grazing. By reducing shoot and root biomass of Idaho fescue but not spotted knapweed, repeated grazing may reduce the ability of Idaho fescue to compete with spotted knapweed when both species are grazed.

Kelsey and Locken 1987), although some livestock producers have observed sheep grazing the plant (Cox 1989). In a greenhouse study, a single defoliation did not affect spotted knapweed, whereas monthly defoliations reduced root and crown weights, and carbohydrate concentrations of roots, crowns, and stems (Kennett et al. 1992, Lacey et al. 1994). In 1991, we began a 3-year field study to assess cumulative effects of repeated sheep grazing on spotted knapweed and associated perennial grasses (Olson et al. 1993).

Herbage production, height and number of stems, and other physical characteristics have been used as indicators of plant vigor (Cook and Stubbendieck 1986). Carbohydrate reserves have also been used to indicate a plant's ability to regrow following defoliation and their overall vigor (e.g. McIlvanie 1942, Buwai and Trlica 1977), although this approach towards grasses has been challenged (Caldwell et al. 1981, Richards and Caldwell 1985). Carbohydrate reserves have also been considered important indicators of the status of native and introduced forbs (e.g. Donart 1969, Brummer and Bouton 1992). Our objective was to assess the biomass and carbohydrate status of spotted knapweed and Idaho fescue after 3 summers of repeated grazing by sheep.

Methods and Materials

Our study site was 14 km south of Bozeman, Mont. (111° 4' 45" 36'). Elevation is 1,570 m. Soils are of the Typic Argiboroll class, Beaverton series. They are shallow to moderately deep, silty clay loams over sand and gravel on an alluvial fan. The 30-year precipitation average for the nearest weather station (Bozeman, Mont.) was 487 mm. Precipitation for 1991–1993 in Bozeman was 99%, 115%, and 123% of the 30-year average, respectively. The summer (June–August) of 1991 was drier and warmer than the 30-year average, whereas the summers of 1992 and especially 1993 were wetter and cooler than the long term average (Table 1).

In the summers of 1991–1993, three 0.1-ha pastures were grazed repeatedly by 5 yearling Targhee sheep each summer. Pastures were grazed for 5 to 7 days in mid-June, 2 to 6 days in mid-July, and 1 to 5 days in early September depending on the available forage. Our intent was to graze the pastures intensively when Idaho fescue was in summer dormancy to minimize the impact on this native grass. Utilization of permanently marked plants of spotted knapweed and Idaho fescue was usually high, ranging from 56 to 99% based on grazed plant frequency (Olson

Key Words: reserves, allocation, weed, sheep, *Centaurea maculosa*, *Festuca idahoensis*

Spotted knapweed (*Centaurea maculosa* Lam.), an aggressive introduced perennial forb, has replaced many native perennial grasses in the foothills of the Northern Rocky Mountain region (Tyser and Key 1988, Lacey et al. 1992). Herbicides, insects, pathogens, and fire either have not contained the spread of this noxious weed, or may not be cost-effective in some situations. Most herbivores rarely graze this plant, possibly because it contains cnicin, a bitter tasting compound (Watson and Renny 1974,

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

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

et al., unpublished data), and 43 to 86% based on volume removed (Table 2).

On 2 May 1994, 1 to 2 weeks after spring growth began, we established one 30-m diagonal transect within each pasture [$n = 3$ pastures (blocks)], and four 10-m transects parallel to, but outside, the pasture in ungrazed areas. Ten grazed and 10 ungrazed spotted knapweed and Idaho fescue plants were located systematically at intervals along these transects. These plants, including their entire root systems, were excavated with a narrow blade shovel. By shaking and then rinsing each plant several times over a screen in cold water, soil and intermingling roots were separated from the plant. These plants were separated into shoots, crowns, and roots, placed on ice in a cooler, and transported to the laboratory. Crown biomass of Idaho fescue plants included stem bases. Plant materials were dried for 48 hours at 60°C, weighed, and ground to pass a 1-mm screen. Total nonstructural carbohydrates concentrations were determined at Colorado State University (AOAC 1965).

We analyzed biomass, TNC concentrations, and carbohydrate pools (TNC concentrations \times mass) of shoots, crowns, and roots

Table 2. Estimated percent canopy removed of spotted knapweed and Idaho fescue during mid-June, mid-July, and early September of 1991–1993. Means \pm 1 S.E.

	1991		1992		1993	
	Spotted knapweed	Idaho fescue	Spotted knapweed	Idaho fescue	Spotted knapweed	Idaho fescue
	(%)					
Jun.	79 \pm 11	79 \pm 6	45 \pm 10	73 \pm 4	57 \pm 3	57 \pm 7
Jul.	75 \pm 5	61 \pm 2	62 \pm 8	72 \pm 2	56 \pm 2	64 \pm 4
Sep.	58 \pm 8	86 \pm 3	43 \pm 4	77 \pm 3	58 \pm 3	60 \pm 2

with ANOVA as a randomized-complete-block design ($n = 3$; GLM, SAS 1988). Main effects of treatment (grazed, ungrazed) and species (Idaho fescue, spotted knapweed), and the treatment by species interaction were tested with ANOVA. Residuals from ANOVA were normally distributed. P-values less than 0.15 are presented (Gill 1981). We present least square means and standard errors.

Results

Shoot and root biomass were less on grazed than ungrazed Idaho fescue plants, whereas shoot and root biomass of grazed and ungrazed spotted knapweed plants were similar (species \times treatment, shoot $P < 0.02$, root $P < 0.18$, Fig. 1). Grazing did not reduce crown biomass of either species. Crown and root biomass of Idaho fescue plants were greater than crown and root biomass of spotted knapweed plants ($P < 0.1$, $P < 0.001$).

Based on biomass, root:shoot ratios of grazed spotted knap-

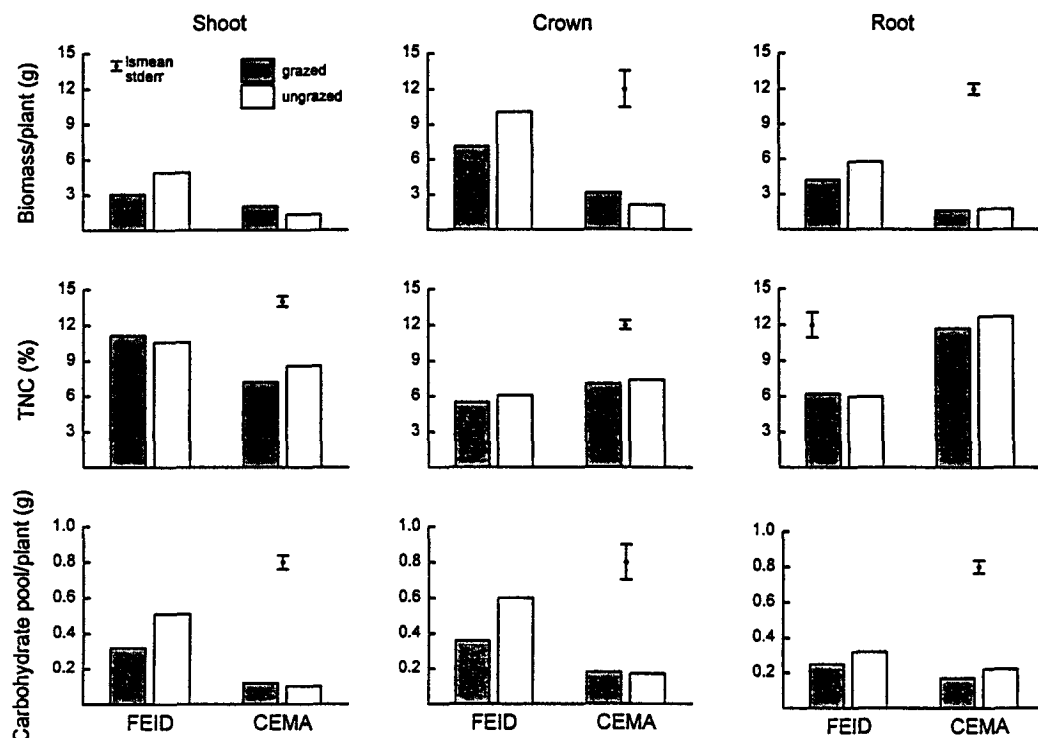


Fig. 1. Biomass, total nonstructural carbohydrate concentrations, and carbohydrate pools of shoots, crowns, and roots of Idaho fescue (FEID) and spotted knapweed (CEMA) after 3 summers (1991–1993) of repeated grazing. Plants were excavated 2–4 May 1994 ($n = 3$ blocks). Least square means and standard errors are presented.

weed plants averaged 0.9 ± 0.1 S.E., whereas ratios of ungrazed spotted knapweed plants averaged 1.5 ± 0.4 . Root:shoot ratios of grazed Idaho fescue plants averaged 1.6 ± 0.3 , whereas ratios of ungrazed Idaho fescue plants averaged 1.3 ± 0.1 .

Total nonstructural carbohydrate concentrations were similar in shoots of grazed and ungrazed Idaho fescue plants, whereas they were higher in shoots of ungrazed than in grazed spotted knapweed plants (species \times treatment, $P < 0.07$, Fig. 1). Grazing did not affect carbohydrate concentrations of crowns and roots of either species. Carbohydrate concentrations of crowns ($P < 0.1$) and roots ($P < 0.001$) of spotted knapweed plants were higher than those of Idaho fescue.

Shoot carbohydrate pools (TNC \times biomass) of grazed Idaho fescue plants were less than shoot carbohydrate pools of ungrazed plants, whereas shoot carbohydrate pools of grazed and ungrazed spotted knapweed were similar (species \times treatment, $P < 0.03$, Fig. 1). Grazing did not affect crown and root carbohydrate pools of either species. Crown ($P < 0.02$) and root ($P < 0.05$) carbohydrate pools of Idaho fescue plants were greater than those pools of spotted knapweed plants, reflecting differences in biomass not carbohydrate concentrations.

Discussion

Biomass

Three years of repeated sheep grazing reduced shoot and root biomass of Idaho fescue, indicating that the ability of Idaho fescue to compete may have been compromised. Reductions in root growth, length, or biomass were measured in several short term studies (Crider 1955, Hodgkinson and Baas-Becking 1977, Richards 1984, Brown 1985), whereas long term responses are measured less often (Cook et al. 1958). Effects of a single extreme defoliation of Idaho fescue that reduced herbage volume 85% and eliminated flower stem production were still evident after 5 years (Mueggler 1975). Presumably, the lengthy recovery time of Idaho fescue in his study was related to concomitant reductions in root biomass following defoliation. In contrast, 3 years of repeated grazing did not reduce crown or root biomass of spotted knapweed. Shoot biomass was actually greater on grazed than ungrazed plants. Natural and simulated herbivory increases shoot and root biomass of another tap-rooted forb, scarlet gilia (*Ipomopsis aggregata* Pursh Spreng.; Paige and Whitham 1987). Changes in biomass of thick, woody roots of forbs may be less responsive to environmental perturbations, unlike fibrous roots of grasses which turnover rapidly (Sims and Singh 1978). Further, fine roots of grasses represent minimal investment and are readily decomposed, whereas taproots of forbs represent greater investment by the plant, and are not readily decomposed. Decomposition of roots of certain forbs such as spotted knapweed may be further slowed by presence of secondary compounds (Locken and Kelsey 1987).

Although shoot, crown, and root biomass of Idaho fescue were greater than counterparts of spotted knapweed, grazing reduced shoot and root biomass of Idaho fescue indicating a lower tolerance to repeated defoliation than spotted knapweed. Our intent was to intensively graze pastures primarily when the cool season Idaho fescue should have been dormant. However, Idaho fescue may have remained physiologically active and thereby more sensitive to defoliation during cool wet summers of 1992 and 1993. Reduced biomass of shoots, crowns, and roots of Idaho fescue

after repeated defoliation may not be critical when plants are growing with other native species. However, it may be especially critical when competing with introduced species that avoid, or are more tolerant of grazing, or both (Briske 1990).

On an individual plant level, grazing negatively affected Idaho fescue but not spotted knapweed, although the response at the community level is less conclusive (Olson et al. 1997). Repeated sheep grazing altered the age distribution of spotted knapweed, resulting in fewer 1 to 3 year-old plants in the population. In contrast, basal areas of Idaho fescue plants from grazed and ungrazed areas were similar, although grazed plants had shorter leaves and flower stems than ungrazed plants (Olson et al. 1997). These non-destructive measures agree with reduced biomass of grazed Idaho fescue plants measured in this study.

Based on lower root:shoot ratios, grazed spotted knapweed plants allocated more biomass aboveground than ungrazed plants, possibly to increase reproductive effort (Paige and Whitham 1987). Similar root:shoot ratios of grazed and ungrazed Idaho fescue plants indicates Idaho fescue does not allocate additional resources to reproductive effort. Idaho fescue produces few, if any, flower stems when grazed heavily (Mueggler 1975). With plants maintaining a relatively constant root:shoot ratio, such as Idaho fescue, reduced aboveground biomass after repeated defoliation will reflect reduced belowground biomass (Cook et al. 1958).

Carbohydrate Concentrations

Similar total nonstructural carbohydrate concentrations of roots, crowns, and shoots of grazed and ungrazed Idaho fescue plants indicates this was not an appropriate measure of plant response to grazing 3 consecutive years. We sampled plants only once, early in the growing season when carbohydrate concentrations are usually lowest (Menke and Trlica 1981). We expected to detect the greatest differences at this time. However, warming soil and air temperatures 1 to 2 weeks before we excavated the plants could have maximized photosynthetic rates, restoring carbohydrate concentrations. Other bunchgrasses replenish carbohydrate pools within 1 to 3 days (Richards and Caldwell 1985), which is one reason to challenge using carbohydrate concentrations to predict response to grazing.

The higher nonstructural carbohydrate concentrations in ungrazed spotted knapweed shoots could reflect accumulation of photoassimilate in rosette leaves, whereas previously grazed plants may have allocated photoassimilate to depleted root and crown materials at the expense of shoot carbohydrate concentrations. In the rosette stage, Canada thistle (*Cirsium arvense* L. Scop.) rapidly moves photoassimilate to roots even without defoliation (Tworkoski 1992). Allocation and storage patterns of non-structural carbohydrates have been used to manage alfalfa (*Medicago sativa*; e.g. Brummer and Bouton 1992), although others have found taproot carbohydrate concentrations are not correlated with yields in the subsequent year or with winter survival of this species (Reynolds 1971, Boyce and Volonec 1992). Similarly, our results indicate carbohydrate concentrations of spotted knapweed are not correlated with growth or survival.

In our study, carbohydrate pools of Idaho fescue plants were reduced by grazing, but this reflected changes in biomass, not carbohydrate concentrations. Carbohydrate pools have been suggested as a more appropriate indicator of the amount of nonstructural carbohydrates mobilized or used to support various metabol-

ic processes (Caldwell et al. 1981, Richards and Caldwell 1985), although neither changes in carbohydrate concentrations nor pools explain the differential response of bluebunch (*Pseudoroegneria spicata* [Pursh] A. Love) and crested wheatgrass (*Agropyron desertorum* Fischer ex Link, Schultes) to defoliation (Caldwell et al. 1981, Richards and Caldwell 1985). Other factors, including meristematic limitations, different storage compounds, residual leaf material, and changes in allocation or growth patterns, may better explain short and long-term responses of grasses and forbs to defoliation than carbohydrate status (Crider 1955, Richards 1984, Brummer and Bouton 1992).

Conclusions

Three years of repeated sheep grazing reduced shoot and root biomass of Idaho fescue, whereas shoot and root biomass of spotted knapweed were not reduced. Chronic reductions in above- and belowground biomass would reduce the competitiveness of Idaho fescue. Carbohydrate concentrations or pools did not appear to be sensitive indicators of the response of Idaho fescue and spotted knapweed to cumulative effects of repeated grazing.

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In vitro regeneration of fourwing saltbush [*Atriplex canescens* (Pursh) Nutt.]

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Abstract

A successful, in vitro regeneration system for fourwing saltbush [*Atriplex canescens* (Pursh) Nutt.] has potential use for mass propagation and genetic engineering of this important range species. This system could be used as a vehicle for gene transfer and for genetic modification of forage quality, stress tolerance, and biomass. The objectives were to develop an in vitro system for shoot production from both leaf discs and axillary buds, and induce root production. Shoot organogenesis (265 shoots) from leaf disc explants was accomplished at rates of 12.3 shoots/disc or 1.7 shoots/mm² of leaf disc explants. Root organogenesis was induced in 63% (168) of the shoots, using indolebutyric acid (IBA, 0.5 mg liter⁻¹) and gibberellic acid (GA₃, 0.1 mg l⁻¹ liter) in a Murashige and Skoog (MS) medium. Roots were also induced on shoots placed in soil. Survival of both shoots and plantlets transferred to soil was 65%. Plantlets transferred to a hydroponic solution were twice the height of plantlets grown in soil. For axillary bud multiplication, the number of shoots generated ranged from 0.7 to 9.1 per explant. Roots were induced on 63% of the shoots, and 58% survived transfer to soil. The successful production of plantlets using both leaf-disc and axillary-bud methods demonstrates that this important range species can be mass propagated in vitro.

Key Words: tissue culture, organogenesis, leaf disc, axillary bud

Atriplex (saltbush) species are a valuable component of rangelands and are used for forage (Ueckert et al. 1988, Barrow 1989, Rehman et al. 1991), regeneration of disturbed sites (Plummer 1970, Aldon 1978, 1984; Booth 1985), and energy production (Van Epps et al. 1982, Goodin 1984, Newton and Goodin 1985). Progress has been made in the asexual propagation of *Atriplex* species by cuttings (Weisner and Johnson 1977, Richardson et al. 1979, McArthur et al. 1984) and adventitious shoot production via tissue culture (Wochok and Sluis 1980, Barrow 1989, Wurtele 1989, Tripathy and Goodin 1990). Although Barrow (1989) alluded to root production from shoots, data were not provided. Therefore, root initiation data from in vitro-produced shoots coupled with plantlet production has not been reported. In addition,

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Resumen

Se estableció un sistema eficiente para la regeneración in vitro de atriplex [*Atriplex canescens* (Pursh) Nutt.] con uso potencial en la propagación masiva e ingeniería genética de esta importante especie forrajera. Este sistema puede ser usado como vehículo en la transferencia de genes y para la modificación genética de la calidad de forraje, tolerancia a estrés y biomasa. Los objetivos fueron desarrollar un sistema in vitro para la producción de brotes a partir de discos de hoja y yemas axilares, así como la inducción de raíces en los brotes. La organogénesis de brotes se logró (265 brotes) a partir de discos de hoja en un rango de 12.3 brotes por disco o 1.7 brotes/mm². Se logró un 63% de enraizamiento de los brotes (168) usando ácido indolbutírico (AIB, 0.5 mg l⁻¹) y ácido giberélico (GA₃, 0.1 mg l⁻¹) en medio de cultivo Murashige y Skoog (MS). Igualmente se indujo enraizamiento de brotes que fueron directamente transplantados a suelo. El porcentaje de sobrevivencia de las plantas producidas in vitro así como de aquellas transplantadas a suelo fue del 65%; sin embargo, después de ser transplantadas a un sistema hidropónico, las plantas producidas in vitro alcanzaron el doble de altura. Para la multiplicación de yemas axilares, el número de brotes regenerados varió de 0.7 a 9.1 por explante. Se logró un 63% de enraizamiento de los brotes, y 58% sobrevivieron el trasplante al suelo. El éxito en la producción de plantas usando ambos métodos: disco de hoja y yemas axilares, demuestra que esta importante especie forrajera puede ser propagada in vitro.

regeneration by axillary bud multiplication has not been reported for *Atriplex*.

With the in vitro technique of tissue culture, shoots can either be produced from leaves or from axillary buds. To produce adventitious shoots from leaves, small discs are cut out of the leaf, surface sterilized, and then placed on a solid nutrient medium where they are subjected to a hormone treatment which differentiates the disc tissue first into a callus and with subsequent hormone treatment the callus produces shoots. The shoots are then subjected to an additional hormone treatment to produce roots. The rooted shoot is then referred to as a "plantlet." Shoots can also result from buds located within the axillary angle between the leaf petiole and the stem. When the bud is induced to elongate with a hormone treatment, a small branch with several shoots is produced. The shoots are excised and placed on a solid medium with hormones to induce root formation. Again when roots are formed, the rooted shoot becomes a plantlet.

As indicated by Wochock and Sluis (1980), a successful regeneration system for *Atriplex canescens* using tissue culture has potential use in the genetic engineering of this very important rangeland species. Recently, new biotechnologies have been developed to isolate drought-induced genes (Newton et al. 1991, Adair et al. 1992, Funkhouser et al. 1993, Cairney et al. 1995, Chen et al. 1995) and several ozone-induced genes (No 1994) from *A. canescens*. These have a possible use for gene transfer and genetic modification of saltbush for improved resistance to environmental stresses. However, application of gene transfer technology requires an appropriate tissue culture system. Its use in gene transfer would allow researchers to better understand functions of stress-induced genes in *A. canescens*, and provide a rapid means for improving its stress tolerance, biomass production and forage quality. The objectives of this study were to: (1) develop an in vitro system for shoot production from leaf tissue and subsequent root production, and (2) develop a shoot production system from axillary buds.

Materials and Methods

Plant Material and Media

Atriplex canescens cv. "Rincon" (McArthur et al. 1984) seedlings were grown in pots and maintained in the greenhouse. Leaves and stem sections of those seedlings were used as explants. To prevent browning of tissues, half-strength Murashige and Skoog (1962) medium (MS) plus sucrose 30 g liter⁻¹ and Gelrite 4 g liter⁻¹ (gellan gum, Merck & Co.) were used as the basal medium for shoot initiation. For rooting, the basal medium was full-strength MS medium with sucrose 30 g liter⁻¹ and Gelrite 4 g liter⁻¹.

Organogenesis from Leaf Discs

Young leaves, 5 nodes or less from the seedling apex, were soaked with 100% commercial bleach for 20 min, rinsed with sterilized water 6 times (all the sterilization procedures mentioned in other protocols follow the same method), then aseptically cut into small discs and cultured on the appropriate media protocols. Four leaf discs, 3 mm in diameter, were placed in a petri dish; 8 discs were used for each protocol. Several protocols modified from Barrow (1989) and Tripathy and Goodin (1990) were tried. In contrast to the shoot initiation procedures of Tripathy and Goodin (1990), we used: half-strength MS media, a lower concentration of 2,4-D, and a different nitrogen source. Whereas Barrow (1989) used a modified B5 media amended with picloram and auxin to induce shoots, we used MS media amended with auxin, but not GA₃. Our 2 successful protocols are shown in Table 1. The means \pm S. E. for each protocol were compared with the t-test at a 0.05 level of significance (Ott, 1988).

Two rooting experiments were conducted. First, 2 different rooting protocols were compared (Protocols 1 and 2, Table 2). Thirty shoots were used in both the IBA-GA₃ and the IAA-BA-GA₃ protocols, respectively. Second, the optimal rooting media composition was determined by comparing rooting performance as affected by various concentrations of GA₃ in a basal MS media with IBA after 30 days (Protocol 3, Table 2). Arc-sine transformations of the rooting percentages for the three GA₃ treatments were compared using the comparison test for 2 binomial proportions (Ott 1988).

Table 1. Protocols for shoot organogenesis from leaf discs

Protocol	Step	Time (days)	Media Composition
1	Callus induction	30	1/2 MS; kinetin (KT), 1 mg l ⁻¹ ; 2,4-D, 0.2 mg l ⁻¹
	Shoot induction	30	1/2 MS; KT, 0.2 mg l ⁻¹
	Shoot elongation	30	1/2 MS; KT, 0.1 mg l ⁻¹
	Proliferation	15	1/2 MS; BA, 0.5 mg l ⁻¹ ; gibberellic acid (GA ₃), 0.1 mg l ⁻¹
	Separation of Shoots		
	Elongation & Subculture	15 each	1/2 MS; thymine (B1), 1 mg l ⁻¹ ; BA, 0.01 mg l ⁻¹ ; and NH ₄ Cl, 450 mg l ⁻¹
	Root Initiation		See Table 2
2	Callus induction	30	1/2 MS; IAA, 0.1 mg l ⁻¹ ; benzyladenine (BA), 0.5 mg l ⁻¹ ; NH ₄ Cl, 450 mg l ⁻¹
	Shoot Induction &	60	1/2 MS; 2,4-D, 0.01 mg l ⁻¹ ; KT, 0.5 mg l ⁻¹ ; NH ₄ Cl 450 mg l ⁻¹
	Elongation		
	Proliferation	15	Same as Protocol 1 above
	Separation of Shoots		
	Elongation	15	Same as Protocol 1 above
	Root Initiation		See Table 2

Organogenesis from Axillary Buds

Young shoots from greenhouse-derived shrubs containing dormant axillary buds, were surface sterilized, cut into one-bud segments, and placed on 4 different media protocols (Table 3). Each protocol was divided into 2 stages: Stage I for breaking dormancy of the axillary buds and Stage II to enhance shoot extension. For each protocol, 8 stem-segment explants were used. The means \pm S. E. of regenerated shoots per axillary bud for the 4 protocols were compared using analysis of variance (Ott, 1988). After Stage II of organogenesis, the elongated shoots were transferred to the rooting medium (MS; IBA, 0.5 mg liter⁻¹ and GA₃, 1.0 mg liter⁻¹) for a period of 30 days.

Transferring Shoots and Plantlets to a Soil Medium

Shoots without roots and the rooted plantlets were then transferred to a soil medium [perlite, vermiculite and peat moss (2:2:1)]. Three days prior to transfer, test-tube caps were taken off plantlets and shoots, and they were exposed to air and high intensity artificial light (photon flux density, 240 μ mol m⁻²) to harden-off. Before transfer, the rooting rate was recorded. The test-tubes were then soaked in distilled water at room temperature for 20 min to loosen the attachment of plantlets to the gelrite. Plantlets and shoots were taken out of test-tubes and planted in soil. Fungicides (0.59 ml gal⁻¹ of Subdue, 1.6 g gal⁻¹ of Benlate) were sprayed on plants after planting. The containers were covered with a piece of thin plastic film and placed into a growth chamber with a relative humidity of 85%, a temperature cycle of 25°C day/22°C night, and a photoperiod of 16 hours light/8 hours dark with a light intensity of 240 μ mol m⁻². Three days later, the plastic film was removed. The transplants were irrigated daily and liquid fertilizer was dispensed 15 days after transfer at an interval of once per week. One month after transfer, survival rates were recorded.

Table 2. Protocols for root organogenesis

Protocol	Time (days)	Media Composition
1	30	MS; indolebutyric acid (IBA), 0.5 mg l ⁻¹ ; GA ₃ , 0.1 mg l ⁻¹
2	30	1/2 MS; indoleacetic acid (IAA), 0.2 mg l ⁻¹ ; BA, 0.1 mg l ⁻¹ ; GA ₃ , 0.5 mg l ⁻¹
3	30	MS; indolebutyric acid (IBA), 0.5 mg l ⁻¹ ; GA ₃ , 0 ⁻¹ , 0.5 and 1.0 mg l ⁻¹

Survival percentages for the 3 GA₃ treatments (Table 2) were compared using arc-sine transformation and the comparison test for 2 binomial proportions (Ott 1988).

Plantlet Hydroponics

Plantlets derived from leaf discs were potted in soil and grown in the greenhouse for 1 month. From those that survived the transplanting, about 80 were randomly selected and placed in pots (15 cm high and 15 cm in diam. with a volume of 2 liters) containing a nutrient solution (Bethke and Drew 1991). In hydroponics, the top and the sides of the pots were covered with aluminum foil to prevent light penetration and growth of algae. Plantlet size (mean \pm S.D.) was recorded at the start of hydroponics and 1 month later. Plantlet size increase in hydroponics and soil culture was further compared for a period of 1 month. Four round holes, 2 cm diam., were made in the top of each container. Plantlets with roots, 3 cm or larger, were wrapped with a piece of foam and each held fast to a hole on the top of the container. Air, driven by an aquatic pump, was introduced into the solution via small plastic tubes (3mm diam.) capped with an injection needle. The nutrient solution was changed every week. The pots were placed in the same growth chamber with the same physical environment as the soil treatment.

Table 3. Protocols for shoot organogenesis from axillary buds

Protocol	Stage Number	Time (days)	Media Composition
1	I	30	1/2 MS; 2,4-D, 0.01 mg l ⁻¹ ; KT, 0.5 mg l ⁻¹ ; and NH ₄ Cl, 450 mg l ⁻¹
	II	30	MS without hormones
2	I	30	1/2 MS; IAA, 0.1 mg l ⁻¹ ; BA, 2 mg l ⁻¹ ; and NH ₄ Cl, 450 mg l ⁻¹
	II	30	1/2 MS; NAA, 0.01 mg l ⁻¹ ; BA, 2 mg l ⁻¹ ; and NH ₄ Cl, 450 mg l ⁻¹
3	I	30	1/2 MS; B1, 1 mg l ⁻¹ ; BA, 2 mg l ⁻¹ ; NAA, 0.01 mg l ⁻¹ ; GA ₃ , 1 mg l ⁻¹ ; and NH ₄ Cl, 450 mg l ⁻¹
	II	30	Same as Stage I.
4	I	30	1/2MS; IAA, 0.1 mg l ⁻¹ ; BA, 0.5 mg l ⁻¹ ; and NH ₄ Cl, 450 mg l ⁻¹
	II	30	MS without hormones

Table 4. Shoot organogenesis* from leaf explants of *Atriplex canescens*

Protocol**	shoots/disc***	shoots/mm ²
1	8.6 \pm 1.2 ^b	1.2 \pm 0.2 ^b
2	12.3 \pm 1.7 ^a	1.7 \pm 0.2 ^a

*Mean number of shoots \pm S. E. per leaf disc or mm² of leaf surface

**See Table 2 for protocol descriptions

***8 leaf discs, 3mm diam.; 4 leaf discs per petri dish; 2 petri dishes per protocol

^aMeans \pm S. D. in columns followed by the same letter are not significantly different at the 0.05 level using the t-test (Ott 1988)

Results

Organogenesis from Leaf Discs

Shoot organogenesis from leaf discs using 2 different protocols (Table 1) was achieved (Table 4). With the first protocol, using small leaf discs on a medium containing KT and 2,4-D, a thin layer of loose, white to translucent, callus appeared at the midrib and the edge of the leaf disc after 3 days. Subsequently, the callus extended to lateral veins, and then to the whole surface. Callus was more copious at the midrib and the edge of the leaf disc than the other parts. After approximately 1 month's culture and subsequent transfers to shoot induction media, half of the green callus underwent a slow process of change in which its color turned deeper and its texture turned solid (Fig. 1A). On the third medium and while the dominant white callus turned brown and died, the localized, deep green callus turned into a firm and tumor-like structure, from which small shoot clumps eventually differentiated (Fig. 1B). Using this protocol, organogenesis occurred on about 5% of the leaf disc surface after 3 months' culture. More than 8 shoots per leaf disc resulted (Table 4).

With the second protocol (Table 1), both white and light-green calli were induced from leaf discs cultured on medium containing IAA, BA, and NH₄Cl. Both white and light-green calli were induced on the first medium. One month later, the calli were transferred to a shoot-induction media and after more than 2 months, shoot clumps began to appear from grain-like, green calli, which were evenly scattered among the rest of the white or brown calli. After an overall period of 3 months, organogenesis occurred on about 20% of the leaf surface, resulting in more than 12 shoots per leaf disc (Table 4).

Calli with the attached shoots were transferred to a shoot proliferation medium (Table 1), and shoot bud number increased two-fold after a culture period of 15 days. Over 4000 healthy and vigorous shoot clumps (Fig. 1B) were produced by separating larger clumps into several small ones and subculturing them onto fresh proliferation medium every 15 days. When shoots were separated and transferred to the shoot elongation medium, most of them grew to approximately 1 cm after 15 days of culture (Fig. 1C).

Of 2 different protocols tested (Table 2), the best root induction from shoots was accomplished with the medium containing IBA. Sixteen of 30 shoots rooted when treated with IBA, and only 7 of 30 rooted in the presence of IAA. It was also observed that those shoots whose roots were induced using IBA exhibited a more vigorous growth than those induced with IAA (data not shown). Therefore in the second experiment where the effects of GA₃ on rooting were addressed, IBA was the hormone used (Protocol 3, Table 2). The IBA treatment in combination with 3 different GA₃ concentrations resulted in more than 60% of the shoots producing roots and resulting in 168 plantlets (Table 5) as shown in Fig. 1D.

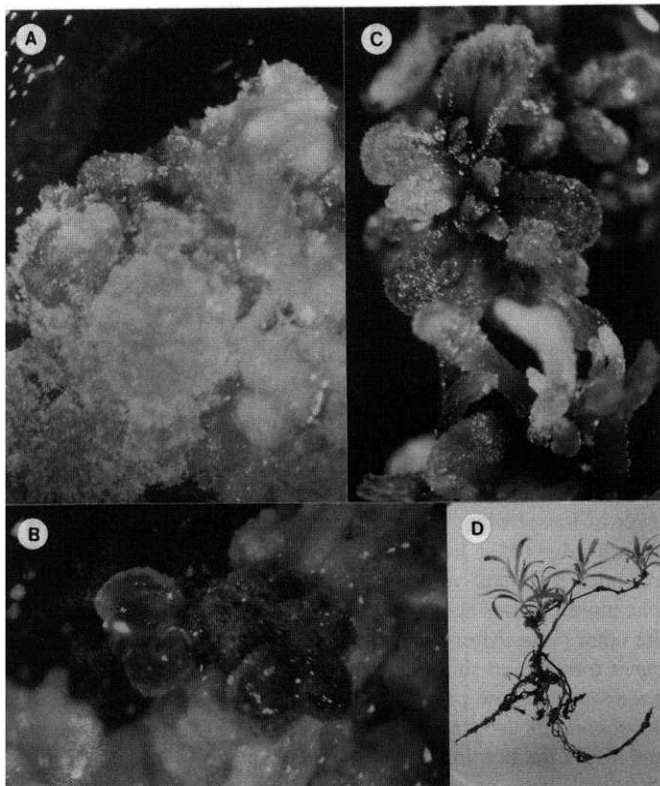


Fig. 1. Organogenesis from leaf disc explants of *Atriplex canescens*. (A) A localized green organogenic callus obtained from leaf explants from one-year old greenhouse grown seedlings, and undergoing solidification on 1/2 MS medium plus KT for one month ($0.2 \text{ mg liter}^{-1}$) (10 X). (B) Shoots derived from organogenic callus on the third medium: 1/2 MS medium plus KT ($0.1 \text{ mg liter}^{-1}$) for one month (10X). (C) A single shoot derived from organogenic callus on 1/2 MS as basal medium plus B1 (1 mg liter^{-1}), BA ($0.01 \text{ mg liter}^{-1}$) for one month (10X). (D) Plant derived via organogenesis (0.5 X).

IBA in combination with the lower GA_3 treatment ($0.1 \text{ mg liter}^{-1}$), induced 85% of the shoots to root (Table 5). Those shoots which had not yet produced roots after 1 month on induction medium were transferred to soil along with the rooted shoots. The rooting percentage ranged from 49 to 85% with more than 60% of the combined shoots plus plantlets surviving after transfer to soil (Table 5), indicating that several shoots eventually produced roots when introduced into the soil. This was estimated to be about 40% of those nonrooted shoots that had been induced in the presence of 0.5 and $1.0 \text{ mg liter}^{-1}$ GA_3 . Those induced with lower GA_3 ($0.1 \text{ mg liter}^{-1}$) did not survive when transferred to soil, presumably because they did not form roots.

Organogenesis from Axillary Buds

Using 4 different protocols consisting of 2 stages each (Table 3), shoot multiplication from axillary buds was initiated by first breaking their dormancy and then inducing shoots with a cytokinin (Fig. 2A). In some cases the initiated shoots died; however, a second round of shoots grew out from the axillary bud and survived. A single axillary bud could be multiplied into a small compact clump with several shoots (Fig. 2B). The mean number of regenerated shoots per explant ranged from 0.74 to 9.11 (Table 6). During Stage II, shoots were cultured on media with or without hormones (Table 3) and allowed to elongate. One hundred

and 12 of 178 shoots (63%) derived from axillary bud multiplication were rooted after 1 month's subculture in rooting medium. One hundred rooted plantlets derived from axillary-bud multiplication were transferred to soil and after one month, 58 plantlets survived (58%). A total of 4 months was required from initiation of axillary buds to the establishment of plantlets in soil.

Hydroponics of Plantlets

Eighty-eight plantlets with an average height of $4.8 \pm 1.3 \text{ cm}$ and placed in hydroponic culture for 1 month, increased to a mean height of $23.5 \pm 6.3 \text{ cm}$. However, it was still not clear whether the rapid growth of these plants was due to the favorable physical conditions of the growth chamber or the combined effect of the growth chamber plus the hydroponic medium. Therefore, growth of the plantlets in hydroponic and soil culture was compared. Plantlets in hydroponics increased in size from 4.0 cm to 20.4 cm in 4 weeks, while plantlets in soil culture increased from 4.6 to 11.0 cm in the same period (Fig. 3). In addition, plantlets transferred to hydroponic culture resumed their regular growth sooner (1 week) than did the plantlets in soil culture (2 weeks) (Fig. 3), and hydroponically-grown plantlets had more well-developed root systems (data not shown).

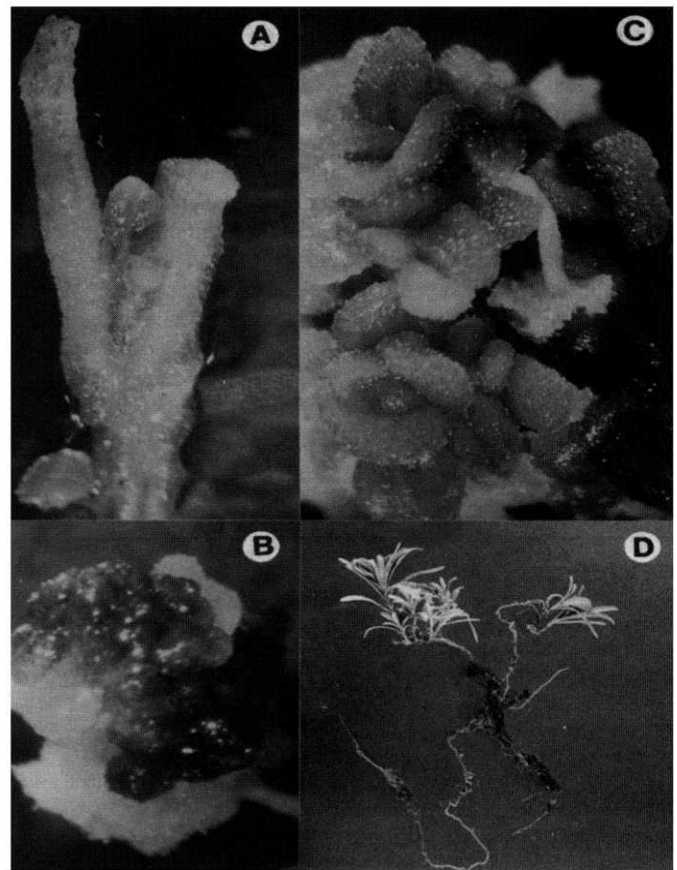


Fig. 2. Initiation and elongation of shoots derived from axillary-bud stem explants of *Atriplex canescens*.

(A) A single shoot derived from a single axillary bud on 1/2 MS plus IAA ($0.1 \text{ mg liter}^{-1}$), BA ($0.5 \text{ mg liter}^{-1}$) and NH_4Cl ($450 \text{ mg liter}^{-1}$) for one month (10 X). (B) Proliferation of shoots from a single axillary bud on the same medium as in Fig. A for one month (10X). (C) Elongation of shoots derived from axillary buds on MS basal medium without hormones added for one month (10X). (D) Plant derived from axillary bud (0.5 X).

Table 5. Effects of IBA and GA₃ on root induction from shoots of *Atriplex canescens* derived from leaf disc explants and survival after transfer to soil.

Protocol*	Number of Shoots	Rooting Number	Rooting	Total Number of Shoots and Plantlets Planted**	Total Survival Number***	Total Survival
	(%)	(No)	(%)			(%)
1	78	66	85 ^a	78	30	38 ^b
2	84	41	49 ^c	84	60	71 ^a
3	103	61	59 ^b	103	81	79 ^a
Total	265	168		265	171	
Mean Percent			63			65

*See Table 2 for protocol descriptions

** Shoots grown in vitro with no visible roots as well as rooted shoots were planted in soil

***Included shoots that produced roots after transfer to soil

^{a,b}Percentages in columns followed by the same letter are not significantly different at the 0.05 level after arc sine transformation and using the comparison test for two binomical proportions (Ott 1988)

Discussion

This is the first data report of root organogenesis from adventitious shoots of *Atriplex canescens* and resulting in intact plantlets. Shoot induction took at least 3 months and only 2 out of several different protocols tested were successful. Green callus production, followed by callus solidification appeared to be essential for the differentiation of shoots. Several other variations in the media were tried but they were not successful. Protocol 2 may be more effective than Protocol 1 in terms of the number of shoots induced per unit area of leaf surface perhaps as a result of the higher cytokinin concentration (Table 4), whereas shoot buds

induced with Protocol 1 grew faster and more vigorously. Because Tripathy and Goodin (1989) used whole leaves and Barrow (1989) used hypocotyl sections as explant sources for callus initiation and we used leaf discs, comparison of efficiencies of shoot production between our method and theirs is not possible. It appears that all methodologies, regardless of their slight differences, were conducive to shoot production. However, it appears that the specific conditions in which the shoots were produced by Barrow (1989) and Tripathy and Goodin (1989) may have subsequently contributed to the recalcitrance of these shoots to root, or the rooting response may be genotype-specific. Another explanation for our success in rooting could be the lower 2,4-D concentration or the nitrogen source (NH₄Cl) that we used in shoot establishment. Nevertheless, as many as 85% of the shoots produced using our methodology rooted when placed on the appropriate induction medium.

Previous workers have reported shoot induction from *Atriplex canescens* explants, but root establishment data from these shoots were not provided. We have shown that rooting can be established, on average, on more than 60% of the adventitious shoots using IBA in combination with GA₃. Hence, plantlet production via leaf disc organogenesis is possible with fourwing saltbush with as much as 80% of them surviving transfer to soil. This is also the first report of saltbush plantlet production from axillary buds with over 60% of the elongated shoots subsequently producing roots and resulting in plantlets in which nearly 60% survived. The time required to produce adventitious shoots from leaf callus

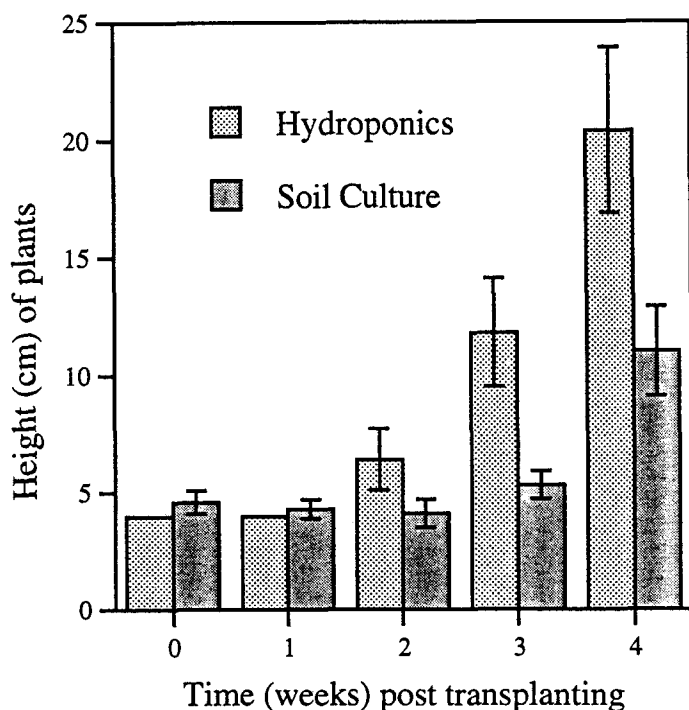


Fig. 3. A growth comparison in hydroponics and soil of plantlets of *Atriplex canescens*. Eight plantlets per treatment; soil culture with perlite, vermiculite and peatmoss (2:2:1). Potted plantlets were irrigated every other day and fertilized once a week. Bars represent the mean with S.D.

Table 6. Shoot organogenesis and elongation from axillary-bud explants* of *Atriplex canescens*.

Protocol**	Number Regenerated Shoots/Axillary Bud	Length of Regenerated Shoots
		(mm)
1	0.76 ± 0.17b	0.6-4.0
2	9.11 ± 3.71a	1.8-6.0
3	0.74 ± 0.84b	3.9-7.7
4	1.80 ± 0.70b	1.5-3.9

*Each stem explant segment contained one axillary bud. For each protocol, 8 stem segment explants were used.

**See Table 3 for protocol descriptions

^{a,b}Means + S.D. followed by the same letter within columns are not significantly different at the 0.05 level using analysis of variance (Ott 1988).

was longer than that required for axillary-bud shoot production (2 versus 3 months). Another additional benefit of axillary-bud shoot production is that this regeneration process bypasses the callus induction stage needed in adventitious shoot production, thus greatly reducing the initiation of mutations that lead to deviation from the true genotype.

However, both of these techniques could be used for mass propagation of this important range species, particularly with hydroponic culture. Hydroponically-grown plantlets displayed a more vigorous growth and a more developed root system than did soil-grown plantlets. It has the potential to enhance growth, and therefore shorten the holding time before plantlets are incorporated into commercial use.

Conclusions

Mass micropropagation of *Atriplex canescens* using both shoot and root organogenesis resulting in the production of intact plantlets has been accomplished. In addition, this is the first report of saltbush plantlet production from axillary buds. Shoots established in the presence of kinetin (callus culture) or cytokinin (axillary bud culture), 2,4-D and NH_4Cl , subsequently rooted when induced with IBA and GA_3 . Hydroponic culture of plantlets was successful. These propagation techniques can be used to mass produce *A. canescens* as well as for gene transfer, using either the leaf-disc (Horsch et al. 1985) or the shoot apex (Gould et al. 1991) method of transformation. A well-established regeneration system plus a successful gene transfer system would allow for improvement of saltbush as a forage, and would contribute to better understanding of the genetic basis of this species in terms of stress resistance and protein production.

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Effect of seed moisture on Wyoming big sagebrush seed quality

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Abstract

Seed germination and seedling vigor of Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis*) were evaluated following manipulation of seed moisture, a practice benefiting many species. At the time of harvest, seed moisture ranged from 2.3 to 9.0% for 5 collections tested and seeds with moisture between 5 to 6% had the highest and most rapid germination. Seed moisture changed during storage, but germination percentage was not affected by post-harvest seed moisture change, indicating that germination is related more to habitat or genetic variations than the initial moisture content. Seedling vigor increased after storage, suggesting that after-ripening may be required. Seeds of 2 commercial collections were subsequently humidified at 2, 5, 10, and 15°C for up to 15 days, or to 60% moisture content. Seed moisture increased most gradually at 2°C and seeds held at 10°C attained a higher moisture level than at other temperatures. Germination percentage, germination rate, and seedling vigor were similar between treatments and controls regardless of seed moisture change. Imbibition temperature did not affect germination percentage or seedling vigor, but the time to 50% germination decreased with increasing imbibition temperature. We conclude that artificial seed moisture management did not affect germination percentage, germination rate, or seedling vigor of this species when tested under optimum moisture conditions. Germination is more related to habitat or genetic variables than initial seed moisture content.

Key Words: *Artemisia tridentata* ssp. *wyomingensis*, germination percentage, germination rate, seedling vigor, seed weight, seed dispersal

Restoring native shrubs to post-mining plant communities in a cost-efficient manner has remained a challenge to western reclamationists. The inherent low seedling vigor of shrubs generally makes direct seeding difficult. A better understanding of the seed

physiology before planting can provide a basis for improving restoration technology. Advances in seed physiology, particularly in the area of seed rehydration, suggest that managing seed moisture and imbibition can enhance the transition from seed to seedling. Controlled imbibition has been used to improve seedling vigor and synchronize seedling emergence in a variety of species (Coolbear and McGill 1990, Heydecker and Coolbear 1977, Khan 1992, Roos et al. 1976, Taylor and Harman 1990). The early imbibition processes are generally considered reversible and seeds are desiccation tolerant as long as the radicle has not emerged (Bewley and Black 1985, Koller and Hadas 1982). During that time many changes, such as macromolecular repair, will occur in seeds (Bray 1995).

The influence of seed moisture on seed germination and seedling vigor of sagebrush is unknown. Given the studies discussed above, we hypothesized that increasing sagebrush seed moisture would improve germination percentage, germination rate, and/or seedling vigor. The purpose of this study was to test the effect of humidification on germination and seedling vigor of Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young), and relate this to initial seed moisture. Our objectives were to determine: 1) the relationship between initial seed moisture after harvest and seed germination or seedling vigor; 2) the rate of seed water uptake under humidification treatments as a function of temperature, and; 3) the effect of humidification treatment and the consequent imbibition temperature on seed germination and seedling vigor of Wyoming big sagebrush.

Materials and Methods

Experiment 1: Effects of seed moisture at harvest on seed quality

Seeds of Wyoming big sagebrush were collected from 5 locations in Wyoming in February 1994, when air temperature was below 0°C (Table 1). Twenty plants were selected randomly at each location and 7 seeds from each plant were sealed in an aluminum container in the field at the time of harvest. The seed moisture content of sealed seeds and the seed weight per 100 seeds were determined on a dry weight basis after drying for 24 hours at 80°C. The remaining seeds were put in paper bags, hand cleaned, and stored in the laboratory for approximately 2 weeks before the first germination test.

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Table 1. Site descriptions and seed characteristics for the 5 seed collections of Wyoming big sagebrush.

Collection	Date	Site	Moisture Seed weight	
			(%)	(g 100 ¹ seeds)
1	10 Feb. 94	S. of Hanna, Wyo.	9.0 a ¹	0.024 bc
2	11 Feb. 94	E. of Ft. Steele, Wyo.	5.6 b	0.027 b
3	10 Feb. 94	S. of Rock River, Wyo.	5.2 b	0.032 a
4	4 Feb. 94	Med. Bow Forest, Wyo.	3.3 c	0.022 c
5	4 Feb. 94	Roger Canyon Rd., Wyo.	2.3 c	0.022 c
Mean			5.3 *** ²	0.025 ***

¹Means with the same letter within a parameter are not significantly different at $P \leq 0.05$.

²The probability of significance among collections ≤ 0.005 .

Twenty seeds from each collection were placed on 1 mm thickness germination paper on slant boards. Seeds were imbibed at 5°C in an incubator for 4 days, then incubated under 12-hour light for 14 days at 20°C because seedling vigor of some sagebrush seeds tends to be enhanced by low imbibition temperatures (Booth and Bai 1996). Germinated seeds were counted daily and were considered germinated if the radicle length was ≥ 1 mm. Germination rate was determined by the time required to reach 50% germination based on total germinated seeds. Seedling vigor was determined by measuring the axial length at the end of the germination test using a digitizing tablet (Booth and Griffith 1994). A completely randomized design with 4 replicates was used to test germination, germination rate, and vigor for each collection. Seed moisture content, seed weight, germination percentage, germination rate, and seedling vigor were analyzed with a one-way ANOVA to test differences among seed collections (Snedecor and Cochran 1980). Means were separated using LSD (Snedecor and Cochran 1980). Seed germination was also tested at 6 months and 2 years after seed harvest with seed moisture measured as described above.

Experiment 2. Seed water uptake during humidification and its influence on seed germination and seedling vigor

Two different seed collections were obtained from a commercial supplier. These lots were collected in late October 1993, from Lincoln County, Wyo., at 2,044 m elevation (Collection 1) and from a site near Casper, Wyo., at 1,624 m (Collection 2). Seed weight was 0.022 ± 0.001 and 0.023 ± 0.001 g per 100 seeds (mean \pm S E) for Collections 1 and 2, respectively. After harvest, seeds were put in large woven polypropylene bags and stored in an unheated warehouse for approximately 4.5 months before being processed with a 48" Simon-Day debarker for 10 min (for details see Booth et al. 1997).

Twenty seeds from each of the above 2 collections were put in 0.25 ml tin capsules weighing 0.16163 g. A pill plate with 4 columns and 22 rows (88 cells) was filled with 4 seed-containing capsules per cell. The columns served as blocks. Two of the 4 capsules in each cell were sealed as controls while the remaining 2 were left open for humidification. A $32 \times 19 \times 18$ cm plastic box was filled to 10 cm depth with distilled water and a pill plate was placed 1 cm above the water surface. These boxes were then sealed inside clear plastic bags and placed in incubators at 2, 5, 10, or 15°C. This was a split-plot design within randomized complete blocks. Four replications were arranged over time as blocks.

Samples of both humidified and untreated seeds were collected at 0, 2, 4, 6, 8, 16, and 24-hour and 2, 5, and 15-day intervals. Immediately after being removed from incubators, open capsules

were sealed to prevent seed moisture loss. These capsules were left for 1 hour at room temperature to allow the evaporation of surface water from the capsule exterior before weighing. Seed moisture content was measured with a CAHN-31 microbalance (6-place digital) after 24 hours of drying at 80°C. Seeds from all treatment intervals were imbibed and incubated immediately after humidification as described in Experiment 1, and seedling axial length was measured at the end of the germination test. Data were analyzed with ANOVA corresponding to the experiment design and means were separated with LSD (Snedecor and Cochran 1980).

Experiment 3. Effects of imbibition temperature

The same 2 seed collections used in Experiment 2 were humidified at 10°C for 0, 8, 24, 48, or 96 hours and seed moisture content was determined as described above. After humidification, seeds were imbibed at 2, 10, or 20°C in darkness for 4 days. Seeds were incubated for an additional 14 days at 20°C under 12-hour light. Seedling axial length was measured at the end of germination test. This was also a split-plot design within randomized complete blocks. Four replications were arranged over time as blocks and data were analyzed with ANOVA accordingly.

Results

Experiment 1: Effects of seed moisture at harvest on seed quality

The moisture level of seeds harvested in February ranged from 2.3 to 9.0% and seed weights ranged from 0.022 to 0.032 g per 100 seeds (Table 1). Germination percentage was highest and seeds germinated most rapidly (or required the least time for 50% germination) for Collections 2 and 3 (Table 2), which had the highest seed weight and intermediate moisture content. Seedling vigor was similar among collections.

Seed moisture content of the 5 collections ranged from 4.9 to 5.9% after 6 months of storage and from 3.9 to 4.5% after 24 months (data not shown). Interactions between storage duration and collection were significant for germination percentage and time to 50% germination, but not for seedling vigor.

Germination percentage increased after 24 months of storage for Collection 4, decreased after 6 months for Collections 2 and 3, and did not change for Collections 1 and 5 (Table 2). Time to 50% germination increased after 24 months of storage for Collections 2 and 3 with no change for the other 3 collections. Seedling vigor increased after 6 months, but decreased after 24 months.

Experiment 2. Seed water uptake during humidification and its influence on seed germination and seedling vigor

Seed moisture before humidification was similar for the 2 seed collections (Fig. 1). Seed water uptake during humidification was also similar. However, interactions among humidification, temperature, and time were significant. Seed moisture increased with humidification time at all temperatures. Significant moisture increase occurred after 16 hours at 2°C, after 4 hours at 5°C, and after 2 hours at 10 and 15°C; and seed moisture did not increase significantly after 5 days. Seed moisture was higher under 10°C humidification than under other temperatures after 5 days of humidification. There was no difference in moisture change for

Table 2. Germination percentage, time to 50% germination (T50), and seedling vigor of 5 collections of Wyoming big sagebrush at 3 testing times after harvest.

Collection	Germination (%)	T50 (day)	Seedling vigor (mm)
----- 0.5 months after harvest -----			
1	23 c ¹ A ²	6.5 a A	15.1 a B
2	87 a A	1.0 c B	16.2 a B
3	89 a A	1.0 c B	17.9 a A
4	43 b B	3.3 b A	16.7 a B
5	16 c A	4.5 ab A	20.8 a A
Mean	52 *** ³	3.3 ***	17.3 NS
----- 6 months after harvest -----			
1	26 c A	2.8 b A	22.9 a A
2	76 a A	1.5 b B	22.3 a A
3	61 ab B	1.3 b B	21.6 a A
4	48 b B	2.5 b A	22.4 a A
5	25 c A	5.3 a A	24.8 a A
Mean	47 ***	2.7 ***	22.8 NS
----- 24 months after harvest -----			
1	32 c A	3.8 b A	21.1 ab A
2	52 b B	3.3 a A	14.2 c B
3	53 ab B	2.0 a A	19.4 b A
4	70 a A	2.8 a A	23.6 a A
5	30 c A	3.5 a A	24.7 a A
Mean	47 ***	3.0 NS	20.6 ***

¹Means with the same letter within a testing time are not significantly different at $P \leq 0.05$.

²Means with the same letter within a collection are not significantly different at $P \leq 0.05$.

³The probability of significance among collections is ≤ 0.005 .

non-humidified seeds sealed in capsules during humidification except after 15 days.

Germination percentage, germination rate, and seedling vigor were not affected by humidification and temperature (data not shown). Germination percentage was higher for Collection 2 than Collection 1 throughout the experiment, averaging 77 versus 65% (data not shown). The time to 50% germination was similar for the 2 collections, averaging 1.9 days. Vigor was higher for Collection 1 than Collection 2, averaging 23.5 vs. 22.5 mm.

Experiment 3. Effects of imbibition temperature

Seed moisture content after humidification was similar between collections. It was 4.1 ± 0.1 , 19.8 ± 2.4 , 33.3 ± 1.0 , 41.8 ± 2.3 , and $47.6 \pm 1.2\%$ after 0, 8, 24, 48, and 96 hours of humidification at 10°C , respectively, for Collection 1; it was 4.2 ± 0.2 , 17.4 ± 0.4 , 34.9 ± 1.2 , 44.8 ± 1.9 , and $49.4 \pm 2.2\%$ for Collection 2. Germination percentage was similar among humidification treatments and among imbibition temperatures, but it was higher for Collection 2 than Collection 1, averaging 73 and 78% (data not shown). Seedling vigor was higher for Collection 1 than for Collection 2, averaging 24.1 and 23.2 mm, but was similar among imbibition temperatures. The time to 50% germination decreased with increasing imbibition temperature (Fig. 2).

Discussion

The moisture content of Wyoming big sagebrush seeds in February varied among sites. Differences in seed moisture among collections were not the effect of weather conditions immediately before collection because temperatures were near or below 0°C and there was no snow on the plants at the time of harvest. Some

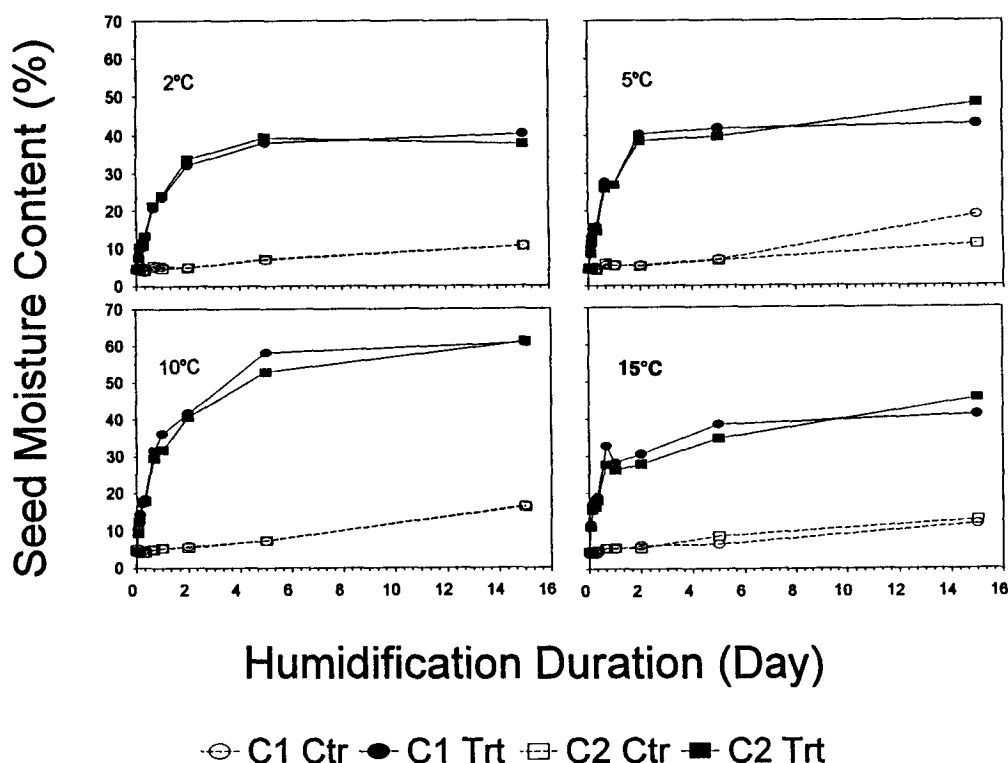


Fig. 1. Seed moisture content of humidified (Trt) and non-humidified (Ctr) Wyoming big sagebrush seeds of Collection 1 (C1) and Collection 2 (C2) at different temperatures and treatment durations.

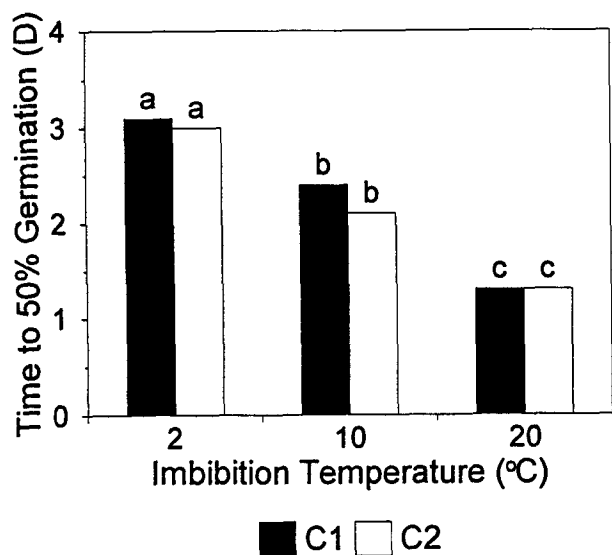


Fig. 2. Time to 50% germination for Wyoming big sagebrush seeds of Collection 1 (C1) and Collection 2 (C2) imbibed at 2, 10, and 20°C. Means with the same letter within a collection are not significantly different at $P \leq 0.05$.

other environmental factors such as topography, wind, relative humidity, and air temperature, as well as genetic variability and seed maturity, may have contributed to the varying seed moisture.

Seed moisture content near 5% at harvest was related to high and rapid germination when seeds were tested shortly after harvest. Germination percentage and germination rate, but not seedling vigor, were positively correlated with seed weight. The fact that germination percentage was not affected by post-harvest seed moisture change during storage indicates that germination is related more to habitat or genetic variations than the initial moisture content and that manipulating seed moisture of this species may not be beneficial. Germination percentage and seedling vigor increased in some seed collections during storage, reflecting a possible after-ripening requirement of Wyoming big sagebrush seeds as observed by Booth et al. (1997).

We observed during seed harvest in February that at least a portion of seeds were capable of staying on mother plants during the winter. Previous studies suggest that basin big sagebrush (*Artemisia tridentata* ssp. *tridentata* L.) generally shed seeds rapidly and completed dispersal before winter (Young and Evans 1989). However, there are large variations in the dispersal phenology of seeds among individuals within a population of fringed sagebrush (*A. frigida* Willd.) (Bai and Romo 1997). Therefore, variations in seed dispersal among and within populations of Wyoming big sagebrush should be considered in studies on seed dispersal phenology.

Seeds of Wyoming big sagebrush absorbed water quickly during humidification, hydrating faster at 10°C than at higher or lower temperatures, indicating an optimal temperature for maximum water uptake. Even though the seed moisture content reached as high as 60% after humidification, total germination percentage, time to 50% germination, and seedling vigor did not change. This is inconsistent with results from legume species such as soybean and snap bean, in which germination was enhanced by seed moisture manipulation (Roos et al. 1976, Obendorf and Hobbs 1970, Hobbs and Obendorf 1972). The dif-

ference may be due to seed size, because larger seeds are known to suffer mechanical stress as tissues hydrate (Spaeth 1989). In addition, germination in the present study was conducted under optimal water condition (no water stress). Germination percentage and germination rate of Lehmann lovegrass (*Eragrostis lehmanniana* Nees.) and side-oats grama (*Bouteloua curtipendula* (Michx.) Torr.) were not affected by increased seed moisture through priming when germinated at optimal conditions, but performance was improved when germinated under water stress (Hardegree and Emmerich 1992). Whether increasing moisture will affect seed germination or seedling vigor of Wyoming big sagebrush under environmental stress is unknown and will be addressed in future studies.

We conclude that seedling vigor of Wyoming big sagebrush is not influenced by increasing seed moisture before sowing. Seed moisture content at harvest reflects the plant environment, but environmental influences on seed quality can not be separated from those of ecotype. Seed weight is an important seed quality variable in sagebrush as in other species, and further study on this aspect may produce guidelines to help seed collectors select high quality seed lots.

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Ownership and management changes on California hardwood rangelands: 1985 to 1992

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Abstract

Results of a 1985 survey of California hardwood rangeland landowners were used to develop a multi-agency research and extension program known as the Integrated Hardwood Range Management Program. In 1992, the same properties were re-surveyed. Although the results cannot prove the program is the sole or direct agent of change, program-sponsored education and research aimed at encouraging oak rangeland owners to change oak management practices is reflected in changes in key landowner behaviors. Program-sponsored research showed that intermediate levels of oak canopy cover did not significantly reduce forage production. Concurrently, landowners have significantly reduced the clearing of oaks for forage production. Other significant changes are reduction of cutting of living oaks for any reason, reduced cutting of oaks for fuelwood, increased use of oak promoting practices, and a growing awareness of the need to be concerned about the status of oaks. Landowners who were aware of the resource benefits of having oaks, or who believed oaks were threatened, or who had been in contact with a natural resource advisory service were significantly more likely to carry out oak-promoting practices. Between 1985 and 1992, many properties changed hands: 24% of parcels were sold but remained intact, while an additional 11% were subdivided. As was found in 1985, owners of smaller properties manage for different and more diverse goals than those of larger properties. The changing pattern of hardwood rangeland land ownership will have an impact on education and conservation programs.

Key Words: oak woodlands, *Quercus*, landowners, land use, management, values

A 1985 statewide survey of the goals, characteristics, and management practices of California hardwood rangeland landowners was instrumental in developing the research and extension components of the multi-agency "Integrated Hardwood Range Management Program" (IHRMP) (Huntsinger and Fortmann 1990). As coordinated among the University of California Cooperative Extension, the California Department of Forestry and Fire Protection, and other agencies, program goals included reducing the loss of oaks in the state, researching ways to encour-

Resumen

Una encuesta, hecha en 1985, de las opiniones de aquellos terratenientes californianos cuyas tierras producen maderas nobles, dio resultados que fueron utilizados para desarrollar un programa de extensión e investigación, compuesto de varias agencias gubernamentales, conocido por el nombre de "Integrated Hardwood Range Management Program." Las mismas tierras fueron sondeadas en 1992. Aunque no se puede comprobar que la índole de los nuevos datos tenga una relación directa o de causa y efecto con dicho programa, parece ser que la educación y las investigaciones llevadas a cabo (para fomentar que los propietarios de robledos cambiaran sus modos de administración) se ven reflejadas en el comportamiento de ciertos propietarios claves. Investigaciones patrocinadas por el programa indican que niveles medios de población arbórea y, por consecuencia, de sombra no reducen significativamente la producción de forraje. A la vez, los propietarios han aminorado notablemente la práctica de despoblar robles para producir forraje. Otros cambios importantes han sido la reducción del corte de robles vivos—bien sea para leña o para cualquier propósito—, el aumento de prácticas que ascienden la supervivencia del roble, y mayor conciencia del valor del mismo. Los propietarios que eran conscientes de los beneficios del cultivo del roble, los que creían que el roble se encontraba en peligro, o los que habían estado en contacto con un servicio de asesoramiento de recursos naturales, estaban notablemente más dispuestos a llevar a cabo prácticas que beneficiaban el roble. Muchas propiedades cambiaron de manos entre los años 1985 y 1992: el 24% se vendieron y quedaron intactas, mientras que el 11% fueron parceladas. Igual que en 1985, los propietarios de terrenos pequeños exhiben modos de administración encauzados por objetivos distintos y más diversos que los de propietarios de terrenos grandes. La cambiante parcelación de terrenos con maderas nobles tendrá un impacto sobre programas dedicados a la educación y conservación de recursos naturales.

age appropriate management of the woodlands by landowners, and researching the causes of oak regeneration failure. The vast majority of California's hardwood rangelands are privately owned, providing about a third of the state's total rangeland live-stock forage. In order to develop effective research programs and education materials, it was necessary to discern who the owners of hardwood rangelands were, what their goals were, and to what incentives they would be most receptive. In 1992, the current owners of the same random selection of properties from 1985

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were re-surveyed, regardless of changes in ownership or land use. Because selected properties were surveyed at 2 different times, results offer opportunity to answer at least 2 kinds of questions central to the conservation of hardwood rangelands: What is the rate and nature of rangeland land use change? Since program implementation, have landowner practices and values changed? This paper compares results of the second survey to those of the first and addresses these questions for the years from 1985 to 1992.

A variety of surveys have been conducted in California's hardwood rangelands in recent years (McClaran and Bartolome 1985, Stewart 1991, Johnson 1996, Richards and George 1996), but none has been based on a randomly selected, statewide sample of hardwood rangeland ownerships. Nevertheless, they generally support the results of the 1985 survey showing that the majority of landowners value at least some oaks on their property for a variety of reasons and are often actively managing them. Field-based inventory and monitoring projects examining land use and oak management practices also supported the results of the 1985 survey (Bolsinger 1988, Ewing et al. 1988, Holzman 1993, Swiecki and Bernhardt 1993), finding, for example, that about three-quarters of hardwood rangelands are grazed by livestock and that conversion and fragmentation are serious problems. However, field inventories only indirectly and inferentially reveal landowner goals, practices, and values.

The 1985 survey identified groups of landowners with quite different interests and characteristics, indicated that ownership of the woodlands was fairly fluid, and showed fragmenting of parcels by subdivision to be a growing problem in the woodlands (Fortmann and Huntsinger 1989, Huntsinger and Fortmann 1990). Two archetypal hardwood rangeland landowner classes were described, each owning at least a third of the woodlands (Table 1). These archetypes were used to develop education packages targeted to landowners statewide. This re-survey allows examination of trends in land ownership, land uses, and management practices since 1985, and offers insight into the effectiveness of the IHRMP. The objectives of the 1992 survey were to:

1. contribute to the further development of the Integrated Hardwood Range Management Program's (IHRMP) education and research activities, and provide information for legislators;
2. examine demographic characteristics, attitudes, management practices, and land uses of hardwood rangeland landowners in 1992;
3. examine changes between 1985 and 1992, including change in land ownership and landowner behavior; and,
4. do a preliminary exploration of water quality-related landowner practices and land uses, because water quality policy and regulation is an important issue for California rangeland landowners.

Study Area

The 3 million ha of California hardwood rangeland (also referred to as oak woodland or foothill woodland) (Ewing et al. 1988) intermix with valley annual grasslands at low elevations, and with montane forest at upper elevations. Characterized by an oak (*Quercus* spp.) overstory and annual grass (*Bromus* spp.,

Table 1. The hardwood rangeland archetypes identified as characterizing respondents in the 1985 and 1992 surveys.

Owner of Small Property	Owner of Large Property
doesn't sell products from land	sells products, most often livestock
more often absentee	resident owner
more recent arrival	long term owner
relatively amenable to oak use regulation	anti-regulation
less than half cut living oaks	most cut living oaks
growing in numbers	relatively stable in number

Avena spp., *Hordeum* spp., *Festuca* spp., *Vulpia* spp., *Medicago* spp., *Trifolium* spp.) understory, they occupy coastal and valley foothills throughout most of the state in the Mediterranean climate zone (James 1966) from sea level to about 2,000 m elevation. Canopy cover varies from complete closure in the dense thickets found in canyons to open savanna woodlands characteristic of foothill slopes. The type and its many variations are described thoroughly by Griffin (1978). More than 80% of the woodlands are in private ownership (Ewing et al. 1988).

Hardwood rangelands can be thought of as an ecosystem at risk. Much of the value and character of this woodland has to do with its being large and contiguous. Unsited to crop or forest production, the foothill woodlands remain a vast, often interconnected acreage running through 38 of California's 52 counties — home to more wildlife than any other major habitat type in the state (Mayer et al. 1986). Migratory and resident mule deer, mountain lions, raptors, and a host of species can maintain viable populations in the unfragmented, acorn-producing woodlands. Stock grazing has been the dominant use of these lands since the European settlement of California (Burcham 1982), and mid-elevation woodlands often are a key component of California's traditional transhumant grazing practices.

There are 2 major forces that most threaten the extensive hardwood rangeland. In the early decades of the century millions of hectares of hardwood rangeland in valley bottoms were converted to cropland. Today, conversion for residential use is gobbling up woodland (Bolsinger 1988). Planners, confronted with a choice of steering development to prime farmland or forest, often settle on the woodlands as marginal in economic value and attractive to prospective residents. Land values in many woodland areas are far higher than those justifiable by range livestock production (Hargrave 1993, Johnson 1996). Property tax reduction incentive programs like the California Land Conservation Act (CLCA or Williamson Act) have been shown to be effective when firm land use zoning designations support them, but these are often lacking (McClaran et al. 1985).

The second major risk to hardwood rangelands is a perceived lack of recruitment of oaks in the woodlands (Muick and Bartolome 1987). Scientists and lay people alike have noted an absence of mid-sized oak trees in many areas. Seedlings can be found, older trees are obvious, but mid-sized or sapling-sized trees may be surprisingly sparse or absent. Concerns that some parts of the woodland will eventually disappear due to attrition are exacerbated by the harvest of oaks for fuel and for increasing forage production. In 1985, when the Integrated Hardwood Range Management Program (IHRMP) was conceived, it was believed that this kind of oak removal was a serious problem in the woodlands.

Methods

In spring of 1985 and 1992, after pre-testing with selected landowners not part of the study sample, private owners of hardwood rangeland throughout the state were surveyed by mail, using the standard four-wave technique described by Dillman (1978) to achieve a high response rate. The greater the response rate, the less "self-selection" influences responses and hence the greater the representativeness of the sample.

Questionnaires were sent to the owners of land containing the Forest Inventory Assessment plots previously used to assess hardwood volume in California (Bolsinger 1988). The plots were established at the intersection points of a randomly established eleven-square-kilometer grid overlaid on the state. Plots designated as "Hardwood Woodland Type," (USDA, Forest Service 1981) were selected for this study if an overstory of 10% or greater canopy cover was predominately *Quercus* spp. and the plot was on private land. By definition, these lands do not show evidence of ever having had 10% or more cover of trees of industrial roundwood species and quality. Usable plots occurred in 38 of the state's 58 counties, at elevations ranging from 80 to 1,800 m.

Usable questionnaires were returned by 126 of 166 eligible respondents for a response rate of 76% in 1985 and 121 of 151 eligible respondents for a response rate of 80% in 1992. Of the properties successfully surveyed in 1985, 87% were successfully re-surveyed in 1992. More than 10% of California's total hardwood rangelands were owned by the respondents to each survey. In 1992, every effort was made to locate and survey moved or new owners of properties in the sample. This involved travel to the county assessor's office and an examination of plat maps and title transfers. The 1992 respondents include those who purchased, inherited, or took over management of a family property since 1985, some who did not respond to the 1985 survey, as well as those maintaining ownership of the property since 1985. As a result, only about 30% of the respondents in 1992 reported that they participated directly in the 1985 survey. For all survey questions, no significant differences were found in the responses of the 30% who participated in the 1985 study and those of new respondents.

The grid method used to establish Forest Inventory Plots means that larger properties have a greater probability of being selected for the sample (Wensel 1983). While this resulted in a sample with good representation of landowners of each property size, it means that responses about land use practices cannot be directly extrapolated to the hardwood rangeland as a whole. For this reason, responses to each question were evaluated in 2 ways. First, contingency table analysis was used to make comparisons of the mean responses and responses by 3 property size categories of landowners between 1985 and 1992. The 3 property size categories were those used in the 1985 study (under 80 ha, 80 to 2,008 ha, and greater than 2,008 ha). Changes by property size category are mentioned when they are of interpretive value and significant at $P < 0.1$. The Chi-square statistic was used to determine significance for categorical variables, while a t-test was used to compare grouped continuous variables (Spicer 1972).

Second, in order to estimate the amount of hardwood rangeland potentially affected by certain landowner management practices or demographic characteristics, responses were weighted in inverse proportion to size of ownership relative to Forest Inventory Plot grid size (weight=grid size/property size) up to the

size of the grid as described in Wensel (1983). This adjusts the distribution of ownership sizes in the sample to make it comparable to that of ownerships in the hardwood rangeland as a whole, so estimates of the proportion of total hardwood rangeland owned by landowners who claim certain practices and particular demographic characteristics can be developed (Wensel 1983). Analyses using the weighted sample are identified in the tables.

Landowners were asked about their demographic characteristics, attitudes, land tenure, land use, and management practices. Questions are condensed in the tables presenting results.

Results

Overall, landowners still fall into the archetypes described as a result of the 1985 study (Huntsinger and Fortmann 1990) (Table 1). The relationships between property size and landowner goals, attitudes, and practices remain consistent with those of the results of the 1985 survey (Huntsinger and Fortmann 1990). However, since 1985 there have been changes in land status, owner characteristics, management, and attitudes about oaks.

Sample Histories and Characteristics

In the 7 years between 1985 and 1992, about 1% of the owners of parcels in the original sample moved and could not be re-located for survey purposes. One parcel was donated to a public park agency. A little less than two-thirds of the parcels, 63%, remained

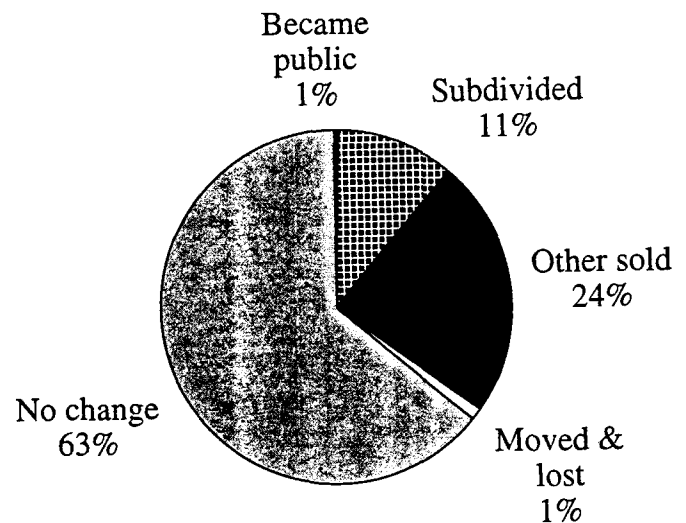


Fig. 1. Land ownership change in the original sample, 1985 to 1992 (n = 194).

in the same ownership (Fig. 1). During the same period, 24% of the parcels in the original sample were sold but remained intact. An additional 11% were subdivided into smaller parcels, with about half sold to new owners. Altogether an average of about 4% of hardwood rangeland parcels were sold each year.

The characteristics of the 1992 sample, when compared to the sample in 1985, reveal a similar distribution of land ownership sizes (Table 2). The weighted sample shows almost a halving of the mean property size among the smallest category of landown-

Table 2. Comparison of the weighted and actual sample of hardwood rangeland landowners in California: percent of owners, land, and average property size in 1985 and 1992.

Parcel size Year n ¹ =	Under 80 ha		80 to 2,008 ha		Over 2,008 ha	
	1985	1992	1985	1992	1985	1992
	36	38	54	54	25	23
Percent of owners in sample	31	33	47	47	22	20
Percent of owners, weighted sample	98	99	2	1	0.05	0.03
Percent of land in sample	0.3	0.3	12	14	88	86
Percent of land, weighted sample	29	32	42	44	29	23
Average property size in sample (ha)	26	20	668	662	10,231	11,181
Average property size, wtd. sample (ha)	4	2	302	299	6,256	6,116

¹n varies slightly with each questions.

ers ($P < 0.01$) (Table 2), while changes in other property size categories were not significant. Overall, using the weighted sample, mean property size declined from a mean of 13 ha in 1985 to 7 ha in 1992 ($P < 0.01$).

Owner Characteristics and Rangeland Use

There has been no significant change in landowner demographic characteristics such as residence on property, age, education, income, or length of ownership since 1985 (Table 3). Apparently

Table 3. Characteristics of hardwood rangeland landowners in 1985 and 1992.

Landowners with the following characteristics	% Land-owners, 1985 n = 126 ¹	% Land-owners, 1992 n = 115 ¹	P (X ²)	Est. ² % ha
	(%)	(%)		
College graduate	50	54	ns	58
Mean age	57	59	ns ³	
Income 75,000 and over	37	37	ns ⁴	24
Land in family 21 years or more	52	57	ns	64
Major source of income:				
ranching	27	22	ns	28
other	73	78	ns	72
Absentee owner	25	26	ns	21
Member wildlife or environmental group	25	30	ns	34
Member livestock association or farm bureau	58	49	ns	39
Contact with advisory service about oaks, last 2 yrs.	24	26	ns	38
Female	18	24	ns	20
Have a manager	21	16	ns	28

¹n varies slightly with each question.

²estimate of % oak woodland owned by landowners with the characteristic, calculated using the weighted sample.

³P > 0.1, t-test.

⁴adjusted to 1985 dollars.

the rate of ownership turnover did not change much between 1985 and 1992. Although the pattern of results here and in Table 4 suggests a general decline in ranching and agricultural pursuits among hardwood rangeland landowners, most of these were not statistically significant changes.

Since 1985, significantly fewer owners graze livestock on their land, although livestock still graze on 71% of the woodlands (Table 4). Although for the whole sample there has been no sta-

tistically significant change in the proportion of landowners carrying out practices to improve wildlife, among landowners with mid-size properties improving wildlife habitat has gone from 38% of owners in 1985 to 56% in 1992 ($P < 0.1$), and in absolute numbers more landowners in every category in 1992 reported improving wildlife habitat.

Significantly more hardwood rangeland landowners live less than 9 km (5 miles) from a subdivision in 1992 (Table 4), another indication of the on-going fragmentation of the woodlands. The owners of an estimated 7% of the hardwood rangelands report having subdivided part of their land within the 5 years previous to 1992 (Table 4).

Table 4. Land use of California woodland landowners, 1985-1992.

Percent of landowners	% Land-owners, 1985 n = 126 ¹	% Land-owners, 1992 n = 115 ¹	P (X ²)	Est. ² % ha
	(%)	(%)		
Sells products from land	86	79	ns	70
Produces livestock	65	58	ns	56
Livestock graze property	76	66	0.07	71
Fee hunting	10	9	ns	15
Land in Williamson Act	51	54	ns	44
Improves wildlife habitat	37	44	ns	52
Subdivided in last 5 years	9	9	ns	7
Less than 5 miles to subdivision	49	69	0.08	56
Used for hunting	66	57	ns	62
Used for recreation, vacation home	16	23	ns	18

¹n varies slightly with each question.

²estimate of % oak woodland owned by landowners with each use, calculated using the weighted sample.

Oak Values and Cutting Practices

In both 1985 and 1992, oaks were highly valued for wildlife habitat, shade, and natural beauty (Table 5). In 1992, oaks were valued significantly more for browse, for erosion control, and for conserving water (Table 5).

Changes in values are apparently reflected in changes in behavior. There has been a strong and significant reduction in cutting or thinning living oaks for any purpose. The number of owners engaged in the sale of firewood, whether standing or down, has also declined (Table 5).

The reasons and relative importance of reasons for cutting oaks have changed (Table 5). Cutting oaks for home firewood and removal for increased forage production significantly declined

Table 5. Oak values and practices of California hardwood rangeland landowners, 1985 to 1992.

	Land-owners, 1985 n = 126 ¹	Land-owners, 1992 n = 115 ¹	P (X ²)
	(%)	(%)	
<i>The respondent values oaks for:</i>			
Property value	54	61	ns
Shade	77	79	ns
Erosion control	73	83	0.07
Wildlife habitat	80	84	ns
Natural beauty	82	88	ns
Fuelwood	63	57	ns
More forage underneath	29	37	ns
Browse	51	67	0.02
Conserving water	46	58	0.07
<i>Landowners who:</i>			
Thin oaks	35	26	0.09
Cut any living oaks	70	50	0.04
Sell firewood	20	11	0.06
<i>Agrees an important reason to cut oaks is:</i>			
Removing dead or diseased oaks	87	93	ns
Improving access	43	33	ns
Home firewood	48	30	0.01
Increasing forage production	45	28	0.01
Increasing waterflow	23	15	ns
Clearing for development	20	16	ns
Firewood income	14	11	ns
<i>Oak management practices:</i>			
Burn scrub oaks	12	11	ns
Seasonally graze oaks	43	47	ns
Protect oak sprouts	12	19	0.09
Thin softwoods to promote oaks	12	9	ns
Spray, poison, girdle oaks	7	2	0.05
Plant oaks	6	14	0.03
Maintain oak stocking rate	18	15	ns
Cut mistletoe out of trees	21	20	ns

¹n varies slightly with each question.

(Table 5). Landowners with larger properties have most severely reduced harvest for increased forage production, from 62% to 38% of owners ($P < 0.1$). Clearing oaks to improve access for livestock or vehicles is now the most frequent reason the owners of large properties report for cutting oaks (besides cutting dead and diseased oaks), while increasing forage production, which used to be the major reason, now trails.

The most dramatic reduction in harvest for home firewood use was among landowners in the smallest property size category, from 64% to 36% ($P < 0.1$). Among owners of small properties, cutting firewood for home use was once the most frequently reported as an important reason to cut oaks (besides removing dead and diseased oaks), while today it is improving access.

There has been no significant change in number of landowners who clear oaks for development, or who remove dead and diseased oaks, regardless of property size. Cutting oaks for firewood sales continues among a small proportion of landowners. Using the 1992 weighted sample, an estimated 49% of the woodlands were owned by those who cut any living oaks, 37% by people who thinned oaks, and 25% by those who sold firewood from their property. While in 1985, landowners with greater than 50% oak canopy cover on their land were significantly more likely to remove living oaks, in 1992 the great reduction in number of landowners who cut oaks obscured any possible statistical significance to this relationship.

Promoting Oak Growth

Perhaps more indicative of how landowner values bear upon behavior is to examine whether or not landowners actively promote the maintenance of their oak stands (Table 5). In 1992, landowners are significantly more likely to plant oaks and to protect oak re-sprouts (Table 5). Using a scale developed by summing the frequency of carrying out 4 oak-promoting management practices, we can compare the behavior of those who value oaks for certain purposes to those who do not. The 4 practices are planting oaks, protecting oak sprouts, maintaining a fixed oak stocking level, and cutting mistletoe out of trees. Landowners who value oaks for wildlife habitat, browse, soil protection, and beauty are more likely to carry out oak promoting activities ($P < 0.001$), as are those who value oaks for shade ($P < 0.1$). Valuing oaks for fuelwood, property values, or water conservation did not show this relationship.

Also using the scale of oak-promoting practices, landowners receiving advice about oaks from University of California advisory services within the last 2 years, and in fact from any public advisory service, were significantly more likely to carry out oak promoting practices ($P < 0.1$).

Finally, those who agree with the statement that "oaks are being lost in California" (Table 6) were significantly more likely to carry out practices that benefit oaks ($P < 0.001$).

Attitudes About Regulation

In both 1985 and 1992, some standard questions about regulation were included in the survey. In 1985, landowners in all property size categories were unresponsive to the idea of regulation of resource use and regulations in general. This sentiment has continued over the last 7 years, with the overwhelming majority of landowners agreeing that regulation leads to a loss of liberties and freedom (Table 6). However, a vast majority of landowners agreed in both 1985 and 1992 that protection of water quality should be a state responsibility.

Landowner perception that oaks are declining has significantly increased (Table 6). This pattern persists throughout property size categories, as in absolute numbers, more landowners in each category agreed that oaks are being lost in California in 1992. Despite

Table 6. California oak woodland landowner attitudes toward regulation, 1985–1992.

	Land-owners, 1985 n = 126 ¹	Land-owners, 1992 n = 115 ¹	P (X ²)
Respondents agree that:	(%)	(%)	
State regulation means a loss of liberties and freedom	83	88	ns
State can regulate private land resources	22	25	ns
State can regulate private land with compensation	46	53	ns
Oaks are being lost in California	59	79	0.01
Should regulate California oak use	32	39	ns
Protecting water quality should be a state responsibility	88	85	ns
The state consults adequately with citizens before regulating resources	21	22	ns

¹n varies slightly with each question.

this, change in receptivity to possible regulation of oak use has not occurred (Table 6).

Water Management and Riparian Grazing Practices

Questions about water and riparian management were asked only in the 1992 survey. About two-thirds of private hardwood rangelands (estimated from the weighted sample) are in parcels with perennial sources of surface water. Less than a fifth is in parcels with only intermittent surface water sources, and about 8% of the woodland is comprised of properties with no surface water. Most livestock producers get some forage from riparian areas, but the majority reported getting less than 10% of their forage from riparian grazing lands, although whether that is in terms of days of use, or forage weight, or some other unit of measure used by the landowner is unknown. A full valuation of these forage resources is not possible without considering seasonal demand.

Owners of large properties in particular are active managers of their water resources (Table 7). More than half divert some water and stabilize streambanks. About a third channelize streams. More than two-thirds of the owners in the largest property size class report that they graze riparian areas seasonally; almost half claim to fence and manage riparian areas separately from the rest of their woodlands (Table 7).

Table 7. Water management and oak woodland landowners, 1992.

Parcel size	Under 80 ha;	80 to 2008 ha;	Over 2008 ha;
Percent of landowners who:	n = 38 ¹	n = 54	n = 23
	----- (%) -----		
Graze riparian areas seasonally	16 ^{a2}	61 ^b	70 ^b
Fence riparian areas	3 ^a	19 ^b	41 ^c
Put erosion control structures in streams	8 ^a	17 ^a	17 ^a
Divert water	11 ^a	39 ^b	61 ^c
Graze riparian areas separately	11 ^a	35 ^b	78 ^c
Stabilize streambanks	11 ^a	35 ^b	60 ^c
Channelize streams	11 ^a	21 ^{ab}	31 ^b

¹n varies slightly by question.

²different superscripts within rows mean significantly different at $P < 0.05$.

Discussion

Since 1985, significant changes have occurred in the hardwood rangelands and in the goals and practices of those who own them.

Fragmentation is occurring

During the period between surveys, an average of almost 4% of hardwood rangeland properties were sold each year. In general, hardwood rangeland property ownerships are becoming smaller. According to database and assessor records, about 11% of ownerships in the original sample were subdivided during the 7 years between sampling periods, coinciding well with respondent reports that 9% had subdivided some part or all of their land in the 5 years previous to 1992, or about 7% of all hardwood rangelands as estimated from the weighted sample (Table 4). Eventually, the fragmentation of properties results in the conversion of some land from woodland to housing or other intensive uses. Results of various field surveys conducted in the woodlands

show an exponential decline in the amount of woodland (Huntsinger and Hopkinson 1996). Holzman (1993) found that conversion rates over the last 60 years varied regionally, with more than a third of the woodlands developed in one region, and an average conversion loss of 20% among the 5 regions studied. Ranchers interviewed in a Central Sierra study tended to believe that high land values and the estate and property taxes that go with them, coupled with irregular and low investment return from ranching, are major obstacles to the long term future of ranching in areas where development pressures are high (Johnson 1996). Hargrave (1993) found that in El Dorado County, investment returns from land appreciation often exceeded that from livestock production. Landowners report that subdivisions are closer than ever to their own properties, and with subdivision, management conflicts between agricultural producers and urban refugees also become part of the scene (Huntsinger and Hopkinson 1996).

Values and practices targeted by the IHRMP were affected

Although this type of survey cannot "prove" that the program caused people to act differently, changes in values and behavior reflect program goals. Considerable Integrated Hardwood Range Management Program (IHRMP) research was targeted to finding out how wildlife management could offer incentives to landowners to keep oaks through the marketing of hunting opportunities and habitat management, and in 1992, significantly more landowners were aware of the value of oaks as wildlife browse and more of those with mid-size properties in particular were actively engaged in improving wildlife habitat.

Research testing overstory-understory relationships in hardwood rangelands was sponsored by the IHRMP. Results showed that most notably in drier parts of the state, an oak canopy of 50% or less does not reduce forage production, and in some cases, can extend the availability of green feed by increasing the species and phenological diversity of the grassland (Frost and McDougald 1989, McClaran and Bartolome 1989). This information was promoted through educational materials and workshops, and while removing oaks for increased forage production was the major reason large landowners gave for removing healthy oaks in 1985, today it is one of the least important reasons and is seldom done. Program efforts directed at smaller property owners have also apparently paid off. Owners of small properties tend not to cut oaks for economic reasons such as increasing forage production, but instead cut them for home use and landscaping. Since 1985, the frequencies of these practices have declined significantly, especially on small properties. Landowners are also much less likely to sell firewood than they were in 1985, perhaps reflecting program efforts to increase awareness that oak harvest may not always be sustainable. In fact, a landowner in 1992 is far more likely to agree that "oaks are being lost in California" than they were in 1985.

The effects of these changes in practices are more widespread than it appears from the relative proportion of landowners in Table 5. Clearing oaks for increased forage, to increase water-flow, or to sell firewood typically takes place over greater area per owner than removing a few oaks to put in a road or trail for better access. On the other hand, experts advise that in many cases where oak densities are greater than 50%, or where the oaks are mostly evergreen species such as *Quercus agrifolia* Nee, *Q. chrysolepis* Liebm., or *Q. wislizeni* A.DC. (California, canyon, and interior live oak), thinning of oaks for enhanced forage production, wildlife habitat, and amenity values can be part of a con-

servation-based resource management program (Standiford 1996).

Grazing is still the major land use

The data show a statistically significant reduction in the use of hardwood rangelands for grazing. Results consistently suggest less participation of landowners in livestock groups and economies, with fewer landowners in all land ownership size categories reporting ranching as a major income source, or belonging to a livestock-related association or group, although these changes are not statistically significant. In fact, livestock production remains an important activity and major underlying goal for the owners of most of the hardwood rangelands. This is especially true for larger parcels—in both 1985 and 1992, more than half of the owners in the largest property size category reported ranching as their major income source, and more than 85% produced livestock on their properties. Other studies have also indicated that about three-fourths of California's hardwood rangelands are grazed by livestock (Bolsinger 1988, Holzman 1993, Swiecki and Bernhardt 1993), and that although less than half of ranches are solely supported by ranching (Richards and George 1996), ranching is the most important source of household identity for the majority of ranchers (Richards and George 1996, Bartlett et al. 1989). Conservation of hardwood rangelands on any large scale will require the participation of the livestock industry.

Landowners are not receptive to regulation

As also indicated by other studies, ranchers and hardwood rangeland landowners are not fond of regulatory options (Ellickson 1991, Huntsinger and Hopkinson 1996). However, the results suggest that they are receptive to education and information programs, as well as to incentive programs like the California Land Conservation Act or "Williamson Act," that reduce the costs of high land values for producers. A dramatic increase in landowner perception of the loss of California's oaks has occurred in the last seven years and landowners have reduced cutting and increased protection of oaks. Stewart (1991) indicates that ranchers are more willing to accept "carefully crafted oak related ordinances" than is revealed in the general response to oak use regulation presented in this study.

Hardwood rangeland landowners are shown here to be active managers of water on their lands, just as they are of oaks, and it seems possible that research, education, and information programs directed toward improvement of water quality could be quite effective.

Conclusions

Landowner behavior and attitudes can apparently be changed through applied research and extension. Several of the behaviors targeted by the Integrated Hardwood Range Management Program (IHRMP), including cutting of oaks for forage production enhancement and home firewood use, have shown especially dramatic reductions. Selling of firewood is also less common. Landowners more often value oaks for diverse reasons, including for wildlife habitat, and they are aware that oaks are losing ground. This change in values is linked to increased landowner implementation of oak-promoting activities. These changes in

values and behavior have occurred among ranchers and other owners of large properties, as well as the owners of small properties whose goals do not include livestock production. Landowners who have been in contact with University of California and other public advisory services about oaks are more likely to carry out management practices that promote oaks. A multi-agency program like the IHRMP may influence landowners through a variety of advisory contacts, as well as word of mouth from peers.

The results of this study have shown that ranchers and other owners of large properties have changed their management behaviors in ways encouraged by the IHRMP. Because ranching and livestock production, by maintaining large open space areas in private, productive ownerships, can play a critical role in conserving California's natural resources, changes in the attitudes and practices of these landowners are important. By linking reserve areas and parks, the privately owned woodlands can magnify reserve effectiveness in protecting wildlife populations. Landowners, however, tend to be adamant about protecting their own rights to use their land as they see fit, including selling the land at a profit for real estate development (Huntsinger and Hopkinson 1996). Often the land represents the majority of a family's financial assets and they feel threatened by any public tendency to view the state's remaining open space as having an implicitly "public" character, particularly when government regulation is the result. Working through this dilemma will challenge Californians in decades to come.

While a program of research and extension can help reduce land use change by contributing to the economic well-being of ranchers through better or more diverse management, and the enjoyment of hardwood rangelands by small property owners through enhanced wildlife and aesthetic values, it cannot hope to prevent massive land use change as California's population continues to expand into rural areas (Teitz 1990). There continues to be a fairly rapid turnover of properties in the woodlands, and an increase in small parcel sizes. The fragmentation of the woodlands is by all accounts haphazard, the result of development opportunities that do not take into consideration conservation biology principles such as the protection of migration corridors and critical habitat, much less the imperatives of rangeland livestock production. Livestock grazing for fire hazard reduction, as is common in many California urban-rural interface areas, may become infeasible if land use change makes it impossible to sustain the livestock industry. Research and extension efforts must be complemented by efforts to influence the course of land use change in the hardwood rangelands.

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Viewpoint: Are grazing rights on public lands a form of private property?

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Abstract

Some have argued that federal grazing preferences or permits are a form of private property and should be recognized as such by the federal government. This viewpoint studies the grazing controversy from 2 perspectives; legal and theoretical. A strict analysis of statutes and case law reveals some ambiguity in the law, but little that clearly supports the private property rights argument. A second analysis of several more theoretical approaches to the issue reveals a stronger case for private property based on the idea of customary use, as embodied in certain interpretations of the public trust doctrine and other alternative views. Because the non-legal argument is much more persuasive, it should be utilized more frequently by private property advocates. Opponents of the private property argument should consider that simple legal victory is often an inadequate solution to conflicts such as the grazing rights controversy. Advocates on both sides, as well as range managers and others simply wanting a better understanding of the issue, should make an effort to view the controversy from both of the perspectives presented here. Failure to do so will likely result in more lawsuits, more damaging controversy, and a continued lack of resolution to the conflict.

Key Words: customary use, grazing permits, planning, property rights, public land, public trust doctrine

"Seeing property is an act of imagination—and seeing property also reflects some of the cultural limitations on imagination. Different people see the signals of the surroundings through very different imaginative lenses, and they put those signals together in different property stories; they persuade themselves that the things they see can yield the security of entitlement, whatever that may entail, and then they act on the visible signals as if the signified entitlements were permanent, solid, objective. And to some degree they are—so long as everyone, or most everyone, is persuaded" (Rose 1994, p. 296).

In terms of the passage quoted above, there is no lack of imagination in the American West on the issue of grazing permits and property rights. Whether a grazing preference or permit (the 2 terms are different and will be distinguished shortly) is a form of protected private property is a strongly-contested issue in the courts and on the land itself with important consequences for land management. Most everyone, to paraphrase Rose, is *not* persuaded

at all about what a grazing permit signifies. This article will review the public lands grazing dispute using several theories of property to shed light on the subject. For while there has been a great deal of anger and rhetoric about the grazing permit issue, there has been relatively little quiet analysis and review. Land managers, ranchers, and others affected by the subject would do well to consider *all* sides of the issue in a more dispassionate manner. This paper hopes to be a small step in that process of better understanding.

Starting within the legal system, this essay will review the arguments of "private rights in public lands" advocates as represented by Nevada rancher Wayne Hage and attorneys Frank Falen and Karen Budd-Falen. Discussion of their arguments will entail an analysis of many of the federal statutes, state and federal court cases, IRS rulings, and Supreme Court decisions involved. When this legal review is complete, we will see that the grazing permit exists in a limbo of sorts, legally short of being a "vested right" of property, but a "thing of value" nonetheless. Ultimately, however, there is little in the current case law and statutes to support the legal property claims of the private rights advocates.

This legal analysis only paints half the picture. For a complete view, one needs to turn to other scholars and bring their "imaginative lenses" to bear on the subject. The theories of John Locke as expressed in the common law; of "new property" as described by Charles Reich and applied by Robert Nelson; of norms and customs as described by Robert Ellickson, and of the public trust doctrine as described by Rose and Joseph Sax all bring new insights to the dispute. More importantly, they illustrate the importance of custom as a persuasive, non-legal justification for private grazing rights. Finally, the essay discusses Rose's idea of "Property as Persuasion" as the unifying theme of the investigation. Rose's observations regarding the fragility of a system of property in general indicate how important it is to resolve the current disagreement in a manner that is persuasive to all.

"Private Rights in Public Lands"—The Legal Argument

Rancher and advocate Wayne Hage (1989, p. 4) asserts his case clearly: "The federal government owns the federal lands, but it does not own range rights to the federal lands. The private rancher owns the range rights to the federal lands." Hage bases his position on 2 primary lines of thought. The first is that specific ranchers earned a right to forage on public lands through the venerable western doctrine of "first in time, first in right." Initial settlers of the west staked a claim to a base property and to the associated rangelands surrounding it. The fee-simple claim on the base property was made under one of the various homesteading acts and is recognized by the government. The claim to the sur-

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rounding range forage is based upon a preference right to graze those lands that stems from prior appropriation of the water and forage therein combined with a "customary occupancy of the range" (Hage 1989, p. 11). These rights were recognized by the Supreme Court, according to Hage, in the 1890 decision *Buford v. Houtz* (133 U.S. 320). In *Buford*, Hage claims that the court declared a license created for graziers on the federal lands with the full endorsement and encouragement of the federal government. "Many," he argues, "viewed [this decision] as a federal endorsement of preemption as a means of recognizing private title to the range" (Hage 1989, p. 90). The subsequent development of permit systems by the Forest Service and later the Grazing Service were essentially codifications of these preference rights to graze. Thus, the grazing permit is different from and dependent upon the *pre-existing* right to graze. "The granting of a permit did not create any rights," Hage (1989, p. 187) argues, "it acknowledged pre-existing rights. . ." This distinction between a permit and an alleged underlying preference right is critical because of a long string of court cases that private rights advocates say find no property rights inherent in a grazing *permit* but remain silent on the issue of a preemptive or preference right to grazing (Falen and Budd-Falen 1993).

Hage (1989) cites 4 common transactions involving a grazing permit in support of his position. They are:

- (1) grazing rights to public lands are attached to base properties and transfer with them under private sales;
- (2) rights are therefore bought and sold from ranchers rather than the federal government;
- (3) the military pays compensation to ranchers when taking permit land formerly used for grazing; and,
- (4) the IRS includes the value of the grazing right in calculating estate and other taxes on ranch property.

These practices form a central part of many of the legal challenges to the "anti-property" views of government agencies. They will come up frequently in the legal cases discussed in this section.

Hage makes a second claim to grazing rights based on state and federal water law, and the doctrine of prior appropriation. Under this doctrine, water users in the arid west have a property right in the water they use (or "appropriate") from a local source. This right is based strictly on seniority of use, recognizing the first user as entitled to his or her full right before any other users may take their shares. Western water rights depend on a "beneficial use" of the water—one cannot simply divert water for no purpose to claim a water right. Grazing has been largely recognized as such a beneficial use and is therefore the key to retaining a rancher's water right. Loss of a beneficial use means loss of the appropriative right to those next in order of seniority. Thus, the belief in the west according to Hage (1989, p. 151) has been "he who owns the water owns the land." Furthermore, Hage (1989, p. 194) poses the following question: "If the stock water rights on the federal lands, established through livestock grazing as a proof of beneficial use are valid, how can the right to graze be invalid?" For Hage, the recognition of water rights as property under federal law *necessitates* a recognition of a property right in the accompanying beneficial use.

This is a basic outline of the argument for private property rights to graze on the public lands (henceforth referred to as simply the "private property" position or case). Further consideration of this argument requires a review of the actual legal history of the grazing permit question, to which this article will now turn.

Private Grazing Rights—A Legal Review

Any review of the grazing rights of ranchers must start (as Hage does) with the 1890 case *Buford v. Houtz*. In this case, a cattle rancher owning private land "checkerboarded" with public domain sections sued to prevent a nomadic sheep herder from grazing the rancher's private lands along with the public sections. The rancher was forced to seek legal remedy since he could not effectively fence his property without also enclosing the public domain, which would be illegal. The court showed the rancher little sympathy, finding that he was trying to monopolize the entire public-private tract through ownership of one-third the land. "The rights of all parties. . . is equal" to use the public domain (*Buford*, p. 326). Thus the court found against the plaintiff and for the shepherd.

This seems a strange case to claim victory for the rancher's right to graze public lands. But Hage (1989) cites a key passage from the decision. "We are of the opinion," the court declared, "that there is an *implied license*, growing out of the custom of nearly a hundred years, that the public lands of the United States. . . shall be free to the people who seek to use them where they are left open and unenclosed, and no act of government forbids this use. . . No doubt. . . this has been done with the consent of all branches of the government, . . . and with its direct encouragement" (*Buford*, p. 326). Hage (1989, p. 16) sees this finding and the term "implied license" as a recognition of the rancher's right to graze the range. Legally, of course, a license is essentially a permission to enter onto another's property without trespass—it is revocable without compensation and is not at all the same thing as a vested property right (Boyer et al., 1991, p. 317). Nevertheless, in Hage's view, the *Buford* decision left the rancher only a "step or two" away from fully private rights in public lands (Hage 1989, p. 16). Such a claim is hard to defend given the full facts of the case. The *Buford* court clearly concluded that the public lands are a type of open-access resource, free for all to use on an equal basis until otherwise announced by the government. By explicitly rejecting the argument for private ownership of public lands, the court anticipated and dismissed an argument for exclusive ownership similar to Hage's own position.

A trio of early twentieth century cases are key to further interpreting Hage's arguments. In 1911 the Supreme Court decided 2 cases back-to-back approving the right of the government to regulate or prohibit grazing on public lands—*Light v. United States* (220 U.S. 523) and *United States v. Grimaud* (220 U.S. 506). The *Grimaud* case ratified the authority of the fledgling U.S. Forest Service to promulgate regulations on its forest reserve lands. In *Light* (p. 535), the court tackled grazing rights head-on, reducing its tolerance of grazing on public lands by noting that the United States merely "suffered its public domain to be used for such purposes." This passive "failure to object" by the government did not give any "vested right" to the ranchers using the range, nor did it eliminate the federal power to "recall any implied license" for private use at any time. The third case provides an interesting twist on these themes. In *Omaechevarria v. State of Idaho* (246 U.S. 343 (1917)), the court ratified an Idaho statute excluding sheep from public rangelands traditionally grazed by cattle. By favoring the presence of cattle on the range, the decision could be seen as contrary to the reasoning in *Buford*. However, the court was careful to distinguish the two cases. The Idaho statute was enacted to "prevent breaches of the peace" between range users rather than provide any rights in public lands to specific citizens. The precedents of *Buford* and *Light* remained unchanged.

The next chapter in the story is the 1934 Taylor Grazing Act (TGA). This statute was the first formal attempt by the government to regulate grazing in the public domain rather than just on the forest reserves under the Forest Service. The TGA appears to be an amalgamation of compromise language, written under pressure from all sides on the range controversy. In the first sentence, for example, the act is described as being in effect over the public domain only "pending [the land's] final disposal" (48 Stat. 1269). The TGA set up the now familiar grazing districts and fee-and-permit system, with a new federal Division of Grazing served by livestock advisory boards to regulate the range. Preferences for grazing permits were given to landowners with a history of use (in the preceding 5 years) of the rangelands in question. The act gave permittees a first-right of renewal "in the discretion of the Secretary of the Interior," and entitled them to payment or compensation from new permittees for range improvements if the permit changes hands. More importantly for Hage, the act explicitly protected pre-existing rights "under existing law" unless otherwise provided in the act itself. The act also explicitly protected existing water rights, another important part of Hage's case.

The key phrase in the act, however, comes at the end of Section Three. "So far as is consistent with the purposes and provisions of this Act," the law reads, "grazing privileges recognized and acknowledged shall be adequately safeguarded, but the creation of a grazing district or the issuance of a permit pursuant to the provisions of this Act shall not create any right, title, interest, or estate in or to the land" (emphasis added). This statement has been an oft-cited reply against rancher claims of property rights ever since it was written into law 62 years ago. Hage has a response, however. His answer relies on the distinction between preference rights and grazing permits. As noted above, permits for Hage are merely a recognition of an already existing right of a rancher to graze these lands. Thus, the phrase in the TGA merely ratified that truth by declaring that no new rights in the range arise from mere grazing permits—in case some interloper gained such a permit and then thought he had an actual right to the range forage. "The [TGA] was specific," Hage (1989, p. 179) concludes, "in barring federal agents from creating their own clientele among graziers in the grazing districts by granting permits or including within a grazing district those stockmen without prior rights."

This is an interesting interpretation, and the statutory maintenance of prior claims by the act seems to add to the argument's credibility. A full reading of the act, however, as well as the cases reviewed above shows that Hage's view is ultimately hard to support. Buford and Light both indicate that the government recognized no special preference rights to grazing on public lands. The TGA itself is full of phrases declaring the ultimate authority of the government rather than the rancher to create, modify, or destroy these grazing rights. In Section 3, the Secretary is authorized to issue permits to "bona fide" settlers and ranchers "as under his rules and regulations are entitled to participate in the use of the range." In Section 7, the Secretary is authorized to "examine and classify" all grazing district lands and open them to other uses such as homesteading where he deems appropriate. In the U.S. Code referring to these issues, the Secretary is further authorized to lease additional land for grazing districts in order to "promote orderly use of the district and aid in conserving the forage resources of the public lands therein" (43 U.S.C. §315m-1). None of this language looks compatible with a recognition of

existing private rights to graze, and the subsequent case law bears this observation out.

Four years after the TGA passed, the ranchers gained a significant victory in the courts in Red Canyon Sheep Co. v. Ickes (98 F.2d 308 (1938)). The case arose over a plan by the government to trade lands currently grazed under permit for other lands in order to consolidate holdings. The permittee, Red Canyon Sheep Co., sued to stop the trade, arguing that its private landholdings and improvements would become "valueless" without the permit lands leaving the owners unable to run their business. The Red Canyon Court entered into a lengthy discussion of the preceding legal history of range rights, concluding importantly that TGA grazing rights are not "vested rights in property." But the court did not end its discussion on this point—"Yet, whether they [the permits] be called rights, privileges, or bare licenses, or by whatever name, while they exist they are something of real value to the possessors and something which have their source in an enactment of the Congress" (Red Canyon, p. 315). The court also made an interesting comparison to water rights relevant to Hage's argument. A water right is a "vested interest" but "something less than the full ownership of property" because it is a right only to use the water (sometimes called a "usufructuary right"). The court made another analogy between the right to hunt on public lands and the right to graze there—"both are subject to restriction or withdrawal. . .yet both are of value to the persons possessing them" (Red Canyon, p. 316).

The interest of "real value" to the permittee merits legal protection, said the court, and it invalidates the trade of land. The court indicated that legal protection for permittees is only against the illegal acts of the government, however, in ruling that the transfer in question is prohibited by law. The court refrained from ruling on whether any such transfer would be illegal under justifications other than those presented, such as Section 7 of the TGA (see discussion above). Thus, the Red Canyon decision establishes that the grazing permit has sufficient value to a permittee to merit protection against illegal and unauthorized actions by the government. Protection of the permit against legal government actions (such as federal regulation of grazing allotments or withdrawal of permit lands) was not addressed by the case.

In 1963, however, the Federal Courts decided another case similar to Red Canyon. In this instance (LaRue v. Udall, 324 F.2d 428), a Nevada grazing permittee was threatened with loss of his permit due to a government transfer of the permit lands to a private defense contractor. The permittee argued that the TGA does not authorize such transfers of land when they will destroy a ranch business. He also made the argument that he had pledged his permits as collateral on a loan, and therefore could not have them revoked per Section 3 of the TGA. The court did not agree with either of these arguments, stating that the transfer was within the Secretary's rights and that the right to renewal of a grazing permit pledged as a loan is only a right against other potential permittees, not a "vested interest" in the land preventing government action. In this case, the legal government action of a land transfer was permitted to occur without compensation to the permittee.

The final and most recent case to deal with the private property nature of grazing permits came before the Supreme Court in 1972. U.S. v. Fuller (409 U.S. 488) was a condemnation action by the government of 920 acres of a range permittee's base property owned in fee-simple. The legal question was whether the

access or right to the permitted lands should be included in calculating the value of the fee-simple lands condemned. The lower courts argued that the value of access to the permitted lands should be included, following the decision in a prior condemnation case involving access to grazing lands. The Supreme Court overturned this decision, ruling that the government should not compensate landowners for value "given" by virtue of ongoing government action. Citing several cases regarding condemnations along navigable waters, the court concluded that "If...the government need not pay for value that it could have acquired by exercise of a servitude arising under the commerce power, it would seem a fortiori that it need not compensate for value that it could remove by revocation of a permit for the use of lands that it owned outright" (p. 492). In this decision, the court formed a "working rule" that value-added by completed government works projects is not exempt from compensation, whereas value added by revocable benefits such as grazing permits is exempt. The court cited the TGA in noting that "no compensable property right [is] created in the permit lands themselves as a result of the issuance of the permit" (Fuller, p. 494).

The dissent in Fuller is worth reviewing both because it echoes some of the arguments of the pro-private rights advocates and because the case was decided on a 5-4 margin. Writing on behalf of the court's more liberal members, Justice Powell noted that grazing permits are of "considerable value" to ranchers. The dissenting Justices agreed with the actions of the lower court in considering the value of the permit in the condemnation action. If all the grazing land had been removed from grazing use at the same time as the condemnation, however, the dissenters would have agreed that compensation for the value of the permit would no longer be justified.

The cases noted above make it difficult to maintain the existence of private property rights in public lands on a legal basis. On numerous occasions, the courts have stated that grazing permits are not a "vested right" under the law and give no compensable interest in the land. Nevertheless, private-rights advocates such as Hage and Budd-Falen remain convinced of their legal arguments. In the wake of Fuller, for example, Falen and Budd-Falen make several points that must be considered. The first is the familiar argument that Fuller, like all cases cited here, dealt only with permit rights rather than the preference rights underlying them. The second is that the government only condemned part of Fuller's base property and that the plaintiff therefore never lost his grazing right and was due no compensation in any event. Third, Falen and Budd-Falen raise the taxability of grazing rights as firm evidence that a grazing preference is a property right. Finally, Hage's argument based upon western water law and grazing as a beneficial use remains to be considered.¹

A review of these private property rebuttals reveals a number of difficulties, some already touched upon in the preceding paragraphs. Taking the preference versus permit issue first, this article has already shown how Hage's view of the distinction is not supported by much of the language in the TGA or U.S. Code. Falen and Budd-Falen (1993, p. 510) cite several subsequent cases to

support the claim that "prior rights or uses in the federal lands have been [legally] recognized." The first is McNeil v. Seaton (281 F.2d 931 (1960)), in which a permittee (McNeil) sued to prevent loss of his grazing privileges due to changes in the rules of eligibility made by the Secretary of the Interior for his grazing district. Falen and Budd-Falen (1993, p. 510) claim that the decision acknowledged "once a preference right is established, the permittee is entitled to rely on it." The case does take a relatively pro-rancher stance, citing Red Canyon and the TGA to indicate that ranchers have some form of "rights" under the act and that the Secretary has an "affirmative obligation" to safeguard such grazing privileges. The preference right noted, however, is only against other potential competitors for the grazing permit (See also Coggins and Glicksman 1995, §19.02). It is not, and could not, be against the government itself—such a right to a permit does not legally exist. As the court itself noted—"It is clear...the Government for its own use may without payment of compensation withdraw the permit privilege (McNeil, p. 934, citing U.S. v. Cox, 190 F. 2d 293 (1951))." Thus, Falen and Budd-Falen's view is technically correct but obscures the more general point of the McNeil court—a rancher can rely on a preference right against other potential graziers only at the continued sufferance of the federal government.

A second case relied upon by Falen and Budd-Falen is Chournos v. United States (193 F.2d 321 (1951)). Another case from the Tenth Circuit Court of Appeals (whose judges are, according to McNeil, "thoroughly familiar with the problems of the range"), Chournos involved a complicated dispute between an owner of lands checkerboarded between public domain managed by the BLM. The rancher temporarily lost his grazing permit to the public domain interspersed within his lands, and sued for damages after the permits were finally issued. Falen and Budd-Falen cite the definition of the "purpose" of the TGA from the decision, that purpose being "to stabilize the livestock industry and to permit the use of the public range according to the needs and the qualifications of the livestock operators with base holdings" (Chournos, p. 323). Falen and Budd-Falen do not note that the court found for the government in this case, stating that the rejection of the rancher's application was within the "discretionary function" of the BLM and merited no damages.

Although these 2 cases (following Red Canyon) do recognize the value of a permit and a preference to permittees against other ranchers based on their prior use of the land, at no time does any court challenge the basic premise that these grazing rights are revocable at any time without compensation. Nor does the TGA provide any clear indication of making this distinction between permit rights and prior rights in the land. Indeed, in another federal decision on grazing rights the courts explicitly rejected the "preference right" line of argument. "It is safe to say," wrote the court in Osborne v. U.S. (145 F.2d 892 (1944)), "that it has always been the intention and policy of the government to regard the use of its public lands for stock grazing, either under the original tacit consent or...under regulation through the permit system, as a privilege which is withdrawable at any time for any use by the sovereign without the payment of compensation." As candidates for status as fully vested, compensable property rights, both grazing permits and preference rights come up short.

Leaving Falen and Budd-Falen's technical second point about the Fuller decision to a footnote, this review will next consider their observations regarding the IRS determination of grazing

¹Careful readers will note that the article has skipped Hage's argument about the Department of Defense recognizing grazing permits as a property right. This point turns out, however, to be an exception that proves the rule. In Osborne v. U.S., 145 F.2d 892 (1944), the court noted that the history of the TGA clearly indicates the World War II-era amendment regarding payment for DOD condemnations of grazing land is needed precisely because such actions are not normally compensable. If compensation were normally due, the specific TGA amendment for DOD actions would be redundant.

permits as a taxable form of property.² The property rights advocates offer a 1955 Tax Court decision (Shufflebarger v. Commissioner, 24 T.C. 980) as one of their strongest pieces of evidence. "Because the preference is not created by the federal government, but rather is bought and sold by private individuals, the Internal Revenue Service determined that the preference is, in fact, a property right" (Falen and Budd-Falen 1993, p. 511) A review of this case and supporting tax law and rulings is clearly required.

In Shufflebarger, the claimants argued that their preference right to grazing land has value only for the 8 years of the grazing permit and is therefore depreciable for tax purposes. The tax court found otherwise, observing that most permits are renewed indefinitely even while the government retains the formal option of canceling them at any time. In a footnote, the court made explicit its understanding of the difference between a permit and a preference. Permits are given to applicants who have "established preferences" which give the holder "special consideration over other applicants who have not (Shufflebarger, p. 981)." These preferences, the court noted, convey "no legal right to the use of [the] . . . range." A preference is a "thing of value," and therefore subject to taxation as "property" according to the IRS. A later IRS ruling #86-99 (as well as several intervening cases) affirmed this conclusion with respect to taxation of the value of a grazing permit for estate taxes, calling it "a valuable asset." Such a view does not disagree with the decisions reviewed in this essay—several of which note that a grazing preference right or permit is a thing of value. The IRS views such value as "property" for purposes of taxation. However, the IRS makes no stronger claim for the rights inherent in a grazing preference than the other courts noted herein. The Shufflebarger decision may encourage private-rights advocates by using the word "property" in conjunction with a grazing preference, but it is clearly a very different kind of property than the vested, compensable property rights Falen and Budd-Falen have in mind.

Finally, one must consider Hage's argument that grazing is a beneficial use appurtenant to an appropriative water right, and therefore a form of private property as well. In many respects, this argument may be the private-rights advocates' most successful foray into the legal arena. At least 1 previous case has held that "arbitrary and capricious" regulations by federal agencies on public lands may create a taking of private water rights (Fallini v. Hodel, 725 F. Supp. 1113 (1989)). More recently, the U.S. Court of Claims is hearing arguments in Hage's own lawsuit regarding an alleged taking of private water rights through reductions or cancellations of federal grazing permits (Hage v. U.S., 35 Fed.Cl. 147 (1996)). The argument in that case, as readers may recall, is that grazing federal lands is a "beneficial use" upon which the private water right depends. Remove the grazing permit, and one effectively removes the water right. Thus, the permit is not itself a form of private property (which argument has explicitly been rejected by the Hage v. U.S. court, following precedent cited in this essay), but its removal may lead to a compensable taking of private property in the form of an appropriative water right.

There are several possible counter-arguments to the water

rights claim. First of all, even an appropriative water right is a usufructuary one, providing the right to use the water but not to "own" the resource in the same manner as title in fee-simple.³ More importantly, it seems unclear that a beneficial use such as grazing is somehow a protected private property right because it happens to be part of the justification for a water right. At least 1 recent court decision has found "no support" for such an argument regarding grazing rights in the case law presented (Fulton v. U.S., 825 F.Supp 261 (1993)). Does a farmer have a "property right" to irrigate his land, one might ask, just because his appropriative water right depends on this activity? Furthermore, because federal law generally preempts state law on the public domain, and the federal legal right to withdraw a grazing permit is apparently undeniable, it is hard to see how a state water right could overrule this federal action on federal land. To argue otherwise is to claim, in effect, that the tail wags the dog.

In considering the water-rights argument, it is also important to remember that no court has yet found in favor of Hage's claim—the recent Hage v. U.S. ruling was only a denial of the government's motion for summary judgment on that point. Nevertheless, the water rights challenge may be the most likely to succeed in court exactly because it is furthest removed from a basic claim of private property in a grazing permit, preference, or permitted land itself. In the Fallini case, for example, the determination of a taking of private property was due to the diminution of value at a specific watering site following excessive BLM regulation for wild horse and burro access. There was no consideration of the rancher's grazing permit or preference right to graze the land. Similarly, the Hage v. U.S. case could eventually find a taking of Hage's water rights on public lands—but such a finding is significantly different than supporting a vested property interest in the grazing permit or the land itself. Under the water-rights argument, for example, any permit-losing rancher lacking a vested water right on public lands would still be out of luck.

Whether one sees a grazing right as a form of "property" depends ultimately on the view of property one has. Falen and Budd-Falen (1993, p. 505) cite a 19th Century Supreme Court decision in defining the contested term as embracing "all valuable interests which man may possess outside of . . . his life and liberty." Quoting from the dissent in that case, Falen and Budd-Falen do not entirely convey what the minority opinion in Campbell v. Holt (115 U.S. 620 (1885)) was trying to say. "The term 'property,'" said the dissent, ". . . is not confined to mere tangible property, but extends to every species of vested right" (Campbell, p. 630). But if property as relevant to the Fifth and Fourteenth Amendments covers all "vested rights," it does not cover grazing preferences or permits, both of which the courts have regularly declared not to be a kind of "vested right." The case law does, however, support a "thing of value" view of property for grazing permits as outlined by the Red Canyon court and the IRS in Shufflebarger and other rulings. Such a view acknowledges the clear financial advantages of a grazer's preference right against other ranchers, while stopping short of declaring that preference a vested right of private property, protected from uncompensated government action. But what does this legal hair-splitting mean

² The response to Falen and Budd-Falen's second point (that Fuller did not lose all his base property and therefore failed to lose his grazing right), is only that this may be true (the record is silent) but the distinction makes little difference to the general principle announced by the Supreme Court that such a loss would not be eligible for compensation in either case.

³ The Hage v. U.S. court rejected this argument, however, concluding that appropriative water rights are full property rights, "entitled to the full protection of the Constitution" (Hage v. U.S., p. 172). This view diverges from the opinion in Red Canyon cited earlier, which took a weaker stance on water rights as a form of protected private property (see discussion earlier in article).

for ranchers and federal land managers? Legal precedent aside, how might all sides better talk about the conflict? That is what the "imaginative lenses" of the next section of the article will attempt to reveal.

Seeing Property, Seeing Permits—Some Alternative Views

Following Rose (1994), this section will begin by looking at a couple of standard common law notions. It is an old principle of the law that first possession is the root of all title. This idea, of course, immediately raises the question of what counts for "first possession" (Rose 1994). The idea of first possession is an important part of Hage's argument for property rights in grazing preferences based on the maxim "first in time, first in right." But the common law doctrine cited by Rose actually exposes a basic practical problem within the rancher's case. First possession of 160 acres of farmland or a productive mining claim is relatively easy to establish. One can grow crops, build fences, install irrigation systems and generally occupy the land in an intensive manner. Possession of thousands of acres of grazing forage is more difficult to establish (stock ponds and salt licks to the contrary), especially when the government is unclear on the amount of acreage needed in the arid west to maintain a viable family ranch. In this respect, the law prohibiting fencing on the public domain in 1885 was a blow to ranchers hoping to support a claim to property rights through the first possession doctrine.

The nature of ranching in the arid west also resists the Lockean philosophy of ownership underlying the common law. For Locke (1690), the right to property arises from a "mixing" of one's labor with the items owned—what you work with is what becomes your property. This philosophy underwrites the ideal of the small farmer as propagated by the federal government through the Homestead Act and other efforts to support small private claims to land. It is harder to reconcile a Lockean notion of ownership with the grazing of hundreds of cattle on thousands of acres of open land, especially when those cattle are sometimes left untended for long periods. This is not to say that ranching is not as hard or harder work than farming—by all accounts such a claim would be absurd. The point is that the act of grazing in the arid west is more removed than crop farming from Locke's basic image of mixing one's personal sweat with each acre of the soil to make it one's own. Tangible evidence of labor on grazing lands (in the form of fencing, watering holes, or other improvements), is less obvious to the untrained eye than on a commercial farm with its large combines and orderly rows of crops. Furthermore, government policy towards homesteading and private land ownership consistently suffered from this "Lockean bias"—rejecting appeals (by John Wesley Powell and others) for a policy of larger homesteads on arid lands in favor of the traditional 160 acres plot and the travails of "dry farming." Ranchers in part have had a difficult time gaining ownership of grazing lands because of this Lockean bias.

A second common law doctrine relevant to grazing rights is that of "adverse possession." Rose (1994, p. 15) explains the idea as a "transfer" of property from "the title owner to another who is essentially a trespasser, if the trespasser's presence is open to everyone and lasts continuously for a given period of time, and so long as the title owner takes no action to get rid of him during that time." Ranchers such as Hage clearly use this type of reasoning in their property claims without specifying it by name. "[The continued inaction of Congress], Hage (1989, p. 151) writes, "[to disavow the rancher's grazing rights on public lands] was viewed

by westerners as a clear signal that the stockmen's land claims would eventually be... honored." While claims of adverse possession against government property are often restricted or prohibited by law (Powell, 1968, p. 1099), there is nevertheless some validity to this idea—the history of American settlement has often seen the recognition of previously illegal occupations of public land as later rights to title. Indeed, under the TGA, rights to grazing permits were established in part by existence of fencing and other improvements to the public domain prior to the act's passage. Nevertheless, in the ranching case the government did take some action against users of the public lands, noting in plain language on several occasions (Buford, Light, et al.) that use of the range was not a prelude to any sort of permanent property right. These decisions may not have physically removed ranchers from public lands, but they did clearly contest any claims of land ownership by parties other than the government.

Robert Nelson (1986) makes a different case for grazing permits as a form of private property. His view is that grazing permits are an example of Charles Reich's (1964) "new property" in government actions, following a pattern similar to the privatization of other formerly public efforts. Nelson (1986, p. 364) writes that "government has seldom succeeded when it has sought directly to 'privatize' a publicly owned or common property resource. By indirect routes, however... government has created many new private property rights in publicly owned resources." Nelson (1986) outlines 4 stages in the privatization process: (1) government grants new rights; (2) dominant users gain hegemony over how to administer those rights; (3) users become able to sell or otherwise "alienate" their rights; and finally, (4) government formally transfers the rights to the users and ceases regulation. Grazing permits are an example of a public action that has reached the third stage of "privatization"—transferability on the open market by users. They are, according to Nelson (1986, p. 369), "virtually a form of private property." Nelson (1986) notes the similarity between grazing permits and other forms of marketable "new property": broadcasting rights, rights to raft on public rivers, air pollution rights, and even in some cases zoning rights. It is important to keep in mind that in most of these examples, the government never intended for these rights to become private or quasi-private. And yet it keeps happening.

The idea of "new property" resonates with the "thing of value" view of grazing permits found in the courts. And Nelson's placement of the grazing permit in a more general category of similar "quasi-properties" adds depth to his argument. His view avoids the polar extremes of "private versus public" rights and in so doing brings a much-needed addition of complexity to the discussion. Rights are not simply public or private—they often take on aspects of both realms simultaneously. Of course, Nelson thinks that grazing permits have become almost entirely private rights at this point, which is overstating the case. Permits can be (and have been) revoked without compensation at the government's discretion—hardly an indication of a fully-private or even nearly-private right. Nevertheless, it is clear that any discussion of grazing rights must encompass a continuum of "privateness" rather than a binary "public or private" system in order to advance the issue.

Another provocative point raised by Nelson's piece is the experience of the Reagan administration in proposing to sell portions of the public domain in 1982. According to Nelson (1986, p. 373), "virtually every user of the public lands opposed this idea." The opposition included public lands ranchers. The reason for this, asserts Nelson (1986, p. 373), was that all of these users considered themselves as "holders of vested rights to continue exist-

ing land uses." This should come as a surprising statement to careful readers of the legal review in this article. Therein, it was noted that the courts repeatedly declared no "vested rights" to grazing or other uses of the public lands existed by law. Why, then, was the Reagan administration unable to sell the public lands even with the weight of the law behind them? In one sense, despite the legal precedent to the contrary, the government was unable to sell the lands because, as Nelson (1986, p. 373) says, "it did not really own them."

What is Nelson claiming here? To answer this fully, one needs to use another lens crafted by Robert Ellickson (1991) in his study of ranching in Shasta County, California. "Legal rules," writes Ellickson (1991, p. 40), "hardly ever influence the settlement of cattle-trespass disputes in Shasta County." This is true in the case of fencing disputes as well. What governs actions instead of written law are norms of behavior as worked out within the community—few residents even have any idea what the law says about the issue at hand. What is more interesting is that in cases where the law does have a significant role, local residents still misunderstand the rules. In vehicle-cattle collisions, for example, Ellickson's ranchers have a simple belief based on the difference between "open" (i.e. "fence out") and "closed" (i.e. "fence in") range: in an accident on open range, the "driver buys the cow"; on closed range, the situation is reversed and the "rancher buys the car." This belief is legally incorrect, at least in Shasta County. The law does not care whether an accident occurs on open or closed range—it only cares about the potential negligence of either party involved. Several high-profile cases have been decided within the county against the ranchers' idea of the open/closed range distinction. At least 1 case cost an under-insured rancher \$100,000 out-of-pocket in damages. And yet, local ranchers are more confident than ever that "the legal specialists, not they, are the ones ignorant of the governing legal rules" (Ellickson 1991, p. 103).

Nelson and Ellickson are describing a common phenomenon—one mirrored in the efforts of Hage and others like him. This phenomenon is the assertion of rights (property and otherwise) in the face of clear judicial and statutory evidence to the contrary. How can this happen? Part of the answer lies in the marginal value of law and the legal system to most of society. "Law is not central to the maintenance of social order" concludes Ellickson (1991, p. 280)—social norms and custom are. Therefore, the law often does best when it simply ratifies existing custom and social norms, rather than trying to go against the grain. This belief echoes Hage's comments quoted earlier about the value of custom and historical practice on the western range as the basis of property rights. What Ellickson and Nelson demonstrate with their examples is that norms and custom often win the battle with laws over the definition of ideas and beliefs. What the law says may be ignored as irrelevant by those relying on a different system of justice. Some ranchers believe they are not liable for accidents on the open range because they have always believed that. Similarly, traditional users of the public lands believe they have a "vested right" to those uses in spite of clear legal evidence to the contrary. The more the law tries to fight these deeply-held beliefs, the more unrest that occurs. As Ellickson (1986, p. 286) puts it, "lawmakers who are unappreciative of the social conditions that foster informal cooperation are likely to create a world in which there is both more law and less order."

What is most striking about this incongruity between law and custom is how often custom wins. The experience of the Reagan administration is a perfect example. Legally, no public lands user appears to have demonstrated in court the "vested rights" they claim. Despite this, the proposal to sell selected tracts of public land was sunk by the lobbying of groups who believed they had these rights by custom. And in winning this battle, the groups demonstrated that in one sense they do have these vested rights—if only in the political rather than the judicial arena. Similarly, the arguments of rancher-advocates such as Hage, Falen, and Budd-Falen generally fail in the judicial realm but have succeeded repeatedly in the political process, as demonstrated by their continuing victories over adversaries and would-be regulators. Nelson (1986) is absolutely right—in one important sense, users such as ranchers own the public range. The Reaganites tried to sell something that through custom was no longer theirs, even if they retained legal title.

The relevance of custom to property rights comes more sharply into view with consideration of the public trust doctrine. The idea of the public trust is one of inalienable rights of the public in certain common properties that the government cannot alienate or otherwise dispose. The doctrine focuses on a public trust in navigable waterways for commerce purposes, although lately that application has been broadened to include recreation and other rights in waterways and beaches (See Sax 1970 for an excellent review). According to legal theorists, the notion of the public trust stems from the authority given to customary uses of land or property in common law. "The medieval customary law," declares leading public trust scholar Joseph Sax (1980), "had the striking advantage of putting developed expectations, rather than formalities such as title ownership, at the center of attention." The same is true of the public trust—the clearest example from case law being Illinois Central Railroad v. Illinois (146 U.S. 387 (1892)) which found that just because the government nominally owned the Chicago waterfront did not mean they could sell the entire harbor to the local railroad. Customary use of this resource by the public trumped the legal powers of the legislature and prevented the sale.

In his public trust discussion, Sax (1980) particularly emphasizes the importance of expectations and custom in property law. "The central idea," he writes of the doctrine, "is preventing the destabilizing disappointment of expectations held in common but without formal recognition such as title" (Sax 1980, p. 188). His proposal is that expectations should carry more weight than "mere title" in many environmental and other natural resource disputes. Although Sax's agenda is clearly to expand control of the government over fee-simple property owners, his work has a surprising and important implication for the analysis herein. Certainly, Hage would argue that rangelands are a case where, to use Sax's (1980, p. 193) words, "title and expectations are not congruent." But in these cases, Sax (1980) urges his readers to give less consideration to title and favor expectation instead. Thus, the public trust doctrine (à la Sax) appears to support the private rights in public lands claim based on customary use.

There are clearly differences between the arguments based on custom made by Sax on the one hand and Hage on the other. Sax is lobbying on behalf of the customary public use of private lands, whereas Hage is arguing the opposite. Nevertheless, the value of the Sax article for our purposes is its ratification of the importance of custom in social order and property systems. We

hear the echoes of Ellickson when Sax (1980, p. 193) writes that the courts failure to recognize "expectations in ways that minimize destabilization of expectations could represent a failure to act for a public purpose." Hage can then reply to this by saying that one cannot have it both ways—if customary use of private lands confers property rights, then so should customary use of those properties owned in title by the government. To act otherwise *in either case* is to destabilize expectations at the expense of the public purpose.

Conclusion—A Threat to our Common Property

Rose (1994, p. 5) observes that private property regimes are themselves a sort of common property—one held together "only on the basis of common beliefs and understandings." To "own" something a person must provide "notice to the world" that it is her own in a manner that is understood by those around her. This communication must be ongoing to be effective—owners must speak and "keep on speaking" through whatever methods are culturally recognized in order to maintain their property rights. Sometimes these methods of communication will be through the law. Other times, as we have seen, they will not. In either case, the crucial aspect of ownership becomes convincing or persuading others that one has a property right under a mutually understood property regime. This is the basis of all property systems for Rose, and the idea behind the title of her book.

In the case of grazing rights, the dialogue of persuasion seems to be going on at 2 incompatible levels. Legally, as was shown in this review, the judiciary is telling ranchers in fairly certain terms that they own no vested or absolute private rights to or in the public lands. The graziers' claims also are challenged by public perceptions of the common law doctrine of first possession and the Lockean theories behind it. Culturally, on the range and in the legislature, the conversation is very different. Ranchers and other users of the public lands are telling themselves and anyone who will listen that they are the true owners of rights in the public domain. Basing their arguments on customary use, they follow their brethren in Shasta County by refusing to be persuaded by legal opinions to the contrary. The power of norms and custom over law in this dialogue should not be underestimated—even the common law idea of the public trust as promulgated by an environmentalist such as Joe Sax relies on the power of customary use over "mere title."

Rose (1994, p. 296) sounds a note of caution at the end of her book: "property regimes cannot bear very many or very frequent uses of force; force and violence are the nemesis of property, and their frequent use is a signal that a property regime is faltering." If the events of the last few years are any indication, the property regime of the western grazing lands is very much under attack. Public range managers and users are faced with 2 groups who are speaking without hearing, listening without understanding, and failing on both sides to be persuaded. The "cultural limitations" on imagination cited by Rose in the opening quotation are in full-force. What should be done?

A difficult but essential first step is to broaden the views of the parties involved. Jurists, administrators, and their supporters need to realize that court decisions and legal precedents sometimes carry much less strength than they might imagine. The persuasion process merely starts with a legal decision rather than ending with it. As many organizational theorists have noted, the authority of a rule lies in its acceptance by the subordinate rather than the rule-maker (Barnard, 1938). Similarly, ranchers and private-

rights advocates need to acknowledge the relative weakness of their legal case and move on, rather than continuing to press for victory in a battle that has already been mostly fought and lost. Their case is better made in the political and cultural realm, within the confines of current legal realities. At the risk of sounding naive, both sides need to see the world from another point of view. They need to use their "imagination," as Rose (1994, p. 297) urges, and realize that "what you see in property is what you and others have talked yourself into about those 'things'." What will happen if either side is able to see things from another point of view is beyond prediction, but that it would be an improvement on the current situation seems clear. To truly understand another's view requires a basic level of respect that brings with it a world of potential for resolution. As Rose (1994, p. 297) concludes, "given some imagination, you may always talk yourselves into seeing something else—with all the effects on understanding and action that a new 'envisioning' may bring." That is precisely the point of this essay—to bring a little imagination to the problem of property in grazing rights, so that at some point everyone might be speaking of the same thing.

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Technical note: Vegetation response to increasing stocking rate under rotational stocking

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Abstract

This 10-year study was designed to evaluate vegetation response to increasing stocking rates under rotational stocking (3 days graze, 51 days rest) and long-term rest. The 4 stocking rate treatments ranged from the recommended rate for moderate continuous grazing to 2.7 times the recommended rate. Common curly-mesquite [*Hilaria belangeri* (Steud.) Nash] increased ($P = 0.05$) in all grazed treatments and decreased in the livestock enclosure. Sideoats grama [*Bouteloua curtipendula* (Michx.) Torr.] along with other midgrasses decreased ($P = 0.07$) in all grazed treatments and increased in the livestock enclosure. Because the midgrasses were palatable species and not abundant, they were defoliated too intensively and too frequently. Rotational stocking was not able to sustain initial species composition at any of the stocking rates tested.

Key Words: botanical composition, native range, livestock grazing, grazing management, rotational grazing

Many different kinds of stocking methods have been examined on rangelands (Kothmann 1980, Heitschmidt and Taylor 1991, Holechek et al. 1989). During the past 2 decades, considerable attention has been given to rotational stocking methods that utilize recurring periods of stocking and rest among 2 or more paddocks in a grazing management unit. Rotational stocking methods have been recommended as a means to enhance vegetation, livestock, and wildlife production. Theoretically, benefits from rotational stocking result from control of selective grazing. Rotational stocking has been intensively studied on the Texas A&M University Research Station at Sonora, Tex., to determine its effects on rangeland hydrology (Thurow et al. 1987, 1988, and Warren et al. 1986a, 1986b), livestock production, and vegetation changes (Ralphs et al. 1990, Taylor et al. 1980, 1993a, 1993b, 1993c). The objective of this study was to determine the effects of stocking rate under rotational stocking on species composition and frequency of the primary herbaceous vegetation components.

Methods

A grazing study initiated in 1980 was continued until 1991. Ralphs et al. (1990) reported results from the first 5 years of this study. This paper analyzes the combined 10-year vegetation response data and compares it to vegetation changes in an adjacent ungrazed livestock enclosure.

The study was conducted on the Texas Agricultural Experiment Station located near Sonora, Tex. (31° N; 100° W). It lies in the Edwards Plateau region of Texas (Gould 1975) with an average elevation of 735 M. Precipitation is highly variable both between and within years. The average annual precipitation is 577 mm.

Soils were Tarrant stony clay, 8 to 15 cm deep, and Tarrant silty clay, 15 to 25 cm deep (members of the clayey-skeletal, montmorillonitic, thermic family of Lithic Haplustalls). Range site classification was Low Stony Hills (SCS 1972).

An 8.5-ha pasture was subdivided into 2 blocks of 4 pastures each for the grazed treatments (Table 1) with an additional pasture for a livestock enclosure. Four stocking rate treatments were randomly applied to the 4 pastures in each block. Stocking rates in block 2 were 20% greater than those in block 1 because there was a higher proportion of the deeper Tarrant silty clay soils which were more productive than the shallow Tarrant stony clay soil. Stocking rates were 1.38, 2.05, 2.64, and 3.46 AUM/ha for block 1, and 1.67, 2.52, 3.23, and 4.21 AUM/ha for block 2. These represented 1, 1.5, 2, and 2.5 times the recommended stocking rate for the respective sites (Merrill and Young 1954). Experimental procedures for livestock grazing and vegetation sampling followed those described by Ralphs et al. (1990). Herbaceous species from 50 quadrats were sampled in each pasture during September 1980, April 1985, and May 1991 using the two-step sampling technique described by Anderson and Kothmann (1982). Units of foliar cover were visually estimated using a 1 × 0.25-m frame sectioned with a 6.25-cm grid. Ten of the plots were clipped and species were separated and dried to determine weight per unit of cover, multiplied by the number of cover units of each plant species. Species composition by weight were calculated for the following 6 selected categories of herbaceous vegetation: (1) common curly-mesquite [*Hilaria belangeri* (Steud.) Nash], (2) other short grasses (red grama [*Bouteloua trifida* Thurb.], hairy grama [*B. hirsuta* Lag.], and hairy tridens

Table 1. Study design, area in pastures and stocking rate treatments.
Pasture sizes in Rep 2 were decreased 20% to increase stocking rates due to deeper, more productive soils.

Stocking rate treatment ¹	Rep 1		Rep 2	
	Stocking rates		Stocking rates	
	Area		Area	
	(ha)	(AUM/ha)	(ha)	(AUM/ha)
1.0x	1.68	1.19	1.0x	1.20
1.5x	0.98	2.05	1.5x	0.79
2.0x	0.75	2.64	2.0x	0.62
2.5x	0.58	3.46	2.5x	0.47

¹Increase in stocking rate compared to the recommended rate.

[*Erioneuron pilosum* (Buckl.) Nash], (3) threeawns (Wright threeawn [*Artisida wrightii* Nash] and purple threeawn [*A. purpurea* Nutt.]), (4) sideoats grama [*B. curtipendula* (Michx.) Torr.], (5) other midgrasses (fall witchgrass [*Digitaria cognata* (Schult.) Pilger], Merrill bluestem [*Bothriochloa edwardsiana* (Gould) L.R. Parodi], vine mesquite [*Panicum obtusum* Kunth in H.B.K.], and King Ranch bluestem [*B. ischaemum* (L.) Keng var. *songarica* (Fisch. & Mey.) Celarier & Harlan], and (6) cool-season grasses (Texas wintergrass [*Stipa leucotricha* Trin. & Rupr.], sedge [*Carex* spp.], and rescuegrass [*Bromus unioloides* Kunth in H.B.K.]).

Composition of species in the standing crop was calculated by dividing the standing crop of individual grass species by the total grass standing crop. A split-plot ANOVA was used to compare stocking rate treatments over time. Stocking rate was the whole plot, year was the split plot and pastures were experimental units. The enclosure data were not included in this analysis. Data from all stocking rate treatments were pooled and compared to the ungrazed treatment by a t-test. If the variance of the treatment means were found to be significantly different ($P < 0.05$), then an unpaired t-test for unequal variances was used, otherwise a test for equal variances was applied (SAS 1988).

Results and Discussion

Common Curly-mesquite

In 1980, common curly-mesquite averaged 26% of total grass standing crop by weight, ranging from 20% at the 2x stocking rate to 32% at the 1x stocking rate and 42% in the livestock enclosure (Table 2). In 1985, curly-mesquite averaged 35%, ranging from 33% at the 1x stocking rate to 37% at the 2.5x stocking rate. The livestock enclosure was not sampled in 1985. By 1991, curly-mesquite averaged 77% under grazing treatments, ranging from 70% at the 1x stocking rate to 79% at the 2x and 2.5x stocking rates but dropped to less than 1% of the grass standing crop in the livestock enclosure. The change in percent composition of curly-mesquite differed ($P < 0.05$) for the grazed treatments compared to the non-grazed treatments. Curly-mesquite increased more on the grazed pastures in the last 5 years (42%) than in the first 5 years (9%) ($P = 0.01$).

This non-linear increase of curly-mesquite from 1980 to 1991 is difficult to explain. Variable precipitation could be one factor that affected curly-mesquite. Precipitation was favorable for the first 5 years of the study (98% of average with 68% coming within the growing season). Precipitation was greater for the last 5-year period (101% of average with 76% coming during the growing season). An extremely cold period occurred during December

of 1983, which resulted in the die-off of large amounts of warm season grasses (mostly curly-mesquite; Fuhlendorf 1996). When curly-mesquite died in the enclosure, it opened a niche for the midgrasses to increase. However in the grazed treatments, midgrasses apparently were not able to exploit the reduced competition from curly-mesquite and it reestablished dominance. This could have been a greater factor influencing the response of curly-mesquite than precipitation.

An increase in curly-mesquite associated with increasing grazing pressure is a common vegetative response on central Texas rangelands (Merrill and Young 1959, Smeins and Merrill 1988). Curly-mesquite is a low, tufted, stoloniferous perennial with erect flowering culms which originate from small vegetative clumps. It has the ability to persist and even maintain dominance within grazed grassland communities because of its abilities to reproduce prolifically by seed and stolons (Smeins and Merrill 1988, Kinucan 1987). The response of curly-mesquite in this study is very similar to that under heavy continuous yearlong grazing. The authors predicted this response in their earlier conclusions (Ralphs et al. 1990).

The significant decrease in curly-mesquite in the enclosure is similar to the response of buffalograss [*Buchloe dactyloides* (Nutt.) Engelm.] in grazing exclosures in the Rolling Plains of

Table 2. Means and standard errors for species composition (percent based on grass standing crop) of major grasses for 1980, 1985, and 1991 in an enclosure and at 4 stocking rates (NS = not sampled).

Species	Stocking ¹ Rate	Year		
		1980	1985	1991
		----- (%) -----		
HIBE ²	1.0x	32 ± 2 ^a	33 ± 10 ^{ab}	70 ± 17 ^b
HIBE	1.5x	25 ± 5 ^a	40 ± 10 ^{ab}	79 ± 25 ^b
HIBE	2.0x	20 ± 2 ^a	32 ± 1 ^{ab}	78 ± 20 ^b
HIBE	2.5x	29 ± 12 ^a	37 ± 10 ^{ab}	79 ± 20 ^b
HIBE	0.0x	42 ± 23 ^a	NS	1 ± 1 ^b
SHGR ³	1.0x	32 ± 2 ^{ab}	36 ± 9 ^a	10 ± 7 ^b
SHGR	1.5x	25 ± 5 ^{ab}	43 ± 11 ^a	4 ± 2 ^b
SHGR	2.0x	25 ± 2 ^b	46 ± 3 ^a	8 ± 5 ^c
SHGR	2.5x	32 ± 8 ^{ab}	42 ± 6 ^a	11 ± 8 ^b
SHGR	0.0x	14 ± 10 ^a	NS	2 ± 1 ^a
ARS ⁴	1.0x	9 ± 1 ^a	8 ± 3 ^a	12 ± 8 ^a
ARS	1.5x	13 ± 6 ^a	3 ± 1 ^a	10 ± 9 ^a
ARS	2.0x	17 ± 4 ^a	4 ± 1 ^a	2 ± 1 ^a
ARS	2.5x	8 ± 3 ^a	4 ± 1 ^a	5 ± 3 ^a
ARS	0.0x	19 ± 4 ^a	NS	18 ± 8 ^a
BOCU ⁵	1.0x	5 ± 1 ^a	4 ± 1 ^a	1 ± 1 ^b
BOCU	1.5x	5 ± 1 ^a	2 ± 1 ^b	2 ± 1 ^b
BOCU	2.0x	9 ± 2 ^a	3 ± 2 ^{ab}	1 ± 1 ^b
BOCU	2.5x	4 ± 1 ^a	1 ± 1 ^b	1 ± 1 ^b
BOCU	0.0x	15 ± 7 ^a	NS	25 ± 1 ^b
MIDGR ⁶	1.0x	14 ± 1 ^a	14 ± 3 ^a	1 ± 1 ^b
MIDGR	1.5x	20 ± 5 ^a	7 ± 2 ^{ab}	1 ± 1 ^b
MIDGR	2.0x	15 ± 2 ^a	11 ± 3 ^a	9 ± 3 ^a
MIDGR	2.5x	16 ± 2 ^a	9 ± 4 ^{ab}	1 ± 1 ^b
MIDGR	0.0x	3 ± 2 ^a	NS	53 ± 10 ^b
CSGR ⁷	1.0x	8 ± 3 ^a	7 ± 1 ^a	14 ± 9 ^a
CSGR	1.5x	13 ± 2 ^a	6 ± 2 ^{ab}	1 ± 1 ^b
CSGR	2.0x	14 ± 1 ^a	5 ± 4 ^{ab}	2 ± 1 ^b
CSGR	2.5x	10 ± 2 ^a	8 ± 6 ^{ab}	3 ± 1 ^b
CSGR	0.0x	8 ± 4 ^a	NS	2 ± 2 ^a

¹Increase in stocking rate compared to the recommended rate.

²HIBE = Common curly-mesquite.

³SHGR = Short grasses.

⁴ARS = Threeawn.

⁵BOCU = Sideoats grama.

⁶MIDGR = Midgrasses.

⁷CSGR = Cool season grasses.

^{abc}Means within rows with different letter differed significantly ($P < 0.05$).

Texas (Kothmann et al. 1978). Apparently the characteristics that serve curly-mesquite so well under intensive grazing are ineffective when grazing is removed.

Other Shortgrasses

Average shortgrass composition for all grazed treatments ranged from 28.5% in 1980 to 42% in 1985 and dropped to 8% in 1991. The trend was similar for all treatments. Change in shortgrass composition for the grazed treatments was not different from the ungrazed treatment ($P = 0.15$). Shortgrasses are probably less competitive for sunlight and nutrients than either curly-mesquite or midgrasses and appear to respond to the combined increase or decrease of these other categories of grasses.

Threeawn Species

In 1980, threeawn species averaged 12% of the grass composition, ranging from 8% in the 2.5x treatment to 17% in the 2.0x treatment. The livestock enclosure was 19%. In 1985, threeawn species had decreased to an average of 5% for all stocking rate treatments. In 1991, threeawn species averaged 9%, ranging from 18% of the grass composition in the enclosure to 2% for the 2.0x treatment. Threeawn species composition was stable for the enclosure and the 2 lighter stocked grazing treatments (1.0x and 1.5x) but decreased under the heavier stocked treatments. However, the percent change in threeawn composition for the grazed treatments compared to the ungrazed treatment was not different ($P = 0.20$). Threeawns generally are considered to have a low preference value (Taylor 1973). Forage demand exceeded forage production at the heavier stocking rates. Even marginally preferred plants were negatively impacted as the grazing intensity and frequency increased. The response of threeawns in the current study was as an increaser (Dyksterhuis 1949).

Sideoats Grama

Sideoats grama with a mean composition of 6% in 1980, ranged from 4% to 9% for the grazing treatments and totaled 15% for the enclosure. By 1985, sideoats had decreased in all grazing treatments to a mean of 1%.

Sideoats grama is a high seral grass in the western part of the Edwards Plateau and is considered a preferred forage for cattle, sheep, and goats (Ralphs et al. 1990, Taylor 1973, Robinson 1990). Sideoats grama is also considered a key management species and a good indicator of rangeland health. If management reduces sideoats and other midgrasses, infiltration rate decreases, erosion rate increases, and water storage capacity of the soil decreases (Thurow 1990). Erosion not only exports nutrients needed for forage production but also reduces the depth of the soil.

These results raise concern because sideoats is an important grass in this region. It does not appear to be possible to sustain sideoats grama with the frequency and the intensity of defoliation used in this grazing study ($P = 0.01$; grazed compared to ungrazed). The significant increase of sideoats in the enclosure indicates that conditions were favorable for sideoats grama during the study period.

Other Midgrasses

Midgrasses responded to the treatments in a manner similar as sideoats grama. Initial midgrass composition ranged from 14%

for the 1.0x treatment to 20% for the 1.5x treatment with a mean of 16% (Table 2). Midgrasses represented 3% of the grass composition for the enclosure. Midgrass composition for the stocking treatments decreased to 10% in 1985 and then decreased to 3% in 1991. Midgrass composition increased to 53% for the enclosure in 1991 and was greater ($P = 0.01$) than in the grazed treatments.

Cool-season Grasses

Cool-season grasses were represented mostly by Texas wintergrass. This was the only category which had a significant interaction ($P = 0.06$) between year and stocking rate. Percent composition of cool-season grasses decreased from 1981 to 1991 in all grazed treatments except the 1.0x stocking rate (Table 2). Cool-season grasses also declined in the enclosure, 8% in 1981 to 2% in 1991. There was no difference ($P = 0.35$) in the percent change of cool-season grass composition between the grazed and ungrazed treatments. Distribution of precipitation may have had a greater influence on cool-season grasses than the experimental treatments. Most of the precipitation for the 10-year study occurred during the warm season.

Conclusions

Rotational stocking with 3-day graze periods and 51-day rest periods was not able to sustain initial species composition at any stocking rate tested. Curly-mesquite increased in all stocked treatments, while midgrasses and sideoats grama decreased. These results were predicted in 1985 and confirmed as the study was conducted for another 5 years. Because the midgrasses were palatable species and not abundant, they were defoliated too intensively and too frequently to remain in the community at previous levels. From this study, stocking rates at or above moderate stocking could not be recommended for rotational stocking with short periods of rest. However, previous research on the Sonora Research Station demonstrated that rotational stocking with longer rest periods (> 80 days) during the growing season did allow midgrasses to increase (Taylor et al. 1993a). Exclusion of livestock grazing resulted in midgrasses dominating the site.

Management Implications

Even though rotational stocking methods have been claimed to improve or maintain range condition, range managers must be alert when implementing rotational stocking on semi-arid rangelands. Increasing the density and production of preferred plants is a difficult and slow process. The presence of competing vegetation and the influence of precipitation, soil type, and intensity and frequency of grazing results in variable responses to stocking methods.

For rotational stocking to be successful, we recommend monitoring of grazing use on preferred plants. Range managers must then adjust both grazing methods and animal numbers to maintain proper use on key forage species. We also want to emphasize that these results may not apply to all locations; i.e., these management implications should be limited to locations with vegetation, soils, and environment that are similar to those represented in this study.

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Technical Comment

Comment: Plant, small mammal, and avian diversity following control of honey mesquite, *J. Range Manage.* 50:205–212 by Roger Peterson, 1750 Camino Corrales, Santa Fe, N.M. 87505

Chances are 9 to 1 that your roof will collapse. Should you do something about it? No! according to Nolte and Fulbright (1997: *Journal of Range Management* 50:205–212). They reason that 9 to 1 odds are not at the level of scientific proof (usually taken to be 19 to 1 or, for some purposes, 99 to 1), therefore “it does not appear that your roof will fall.” Or rather, in their terms, herbicide treatment “does not appear to negatively impact plant and vertebrate species richness and diversity. . .”

Nolte and Fulbright set out to test the hypothesis that herbicide application to kill honey mesquite would reduce plant and vertebrate species richness and diversity. They found that for plants and birds, species richness and Shannon’s diversity index increased or stayed constant on untreated plots but decreased (usually decisively) or stayed constant (when the control figure was more than doubling) after treatment. By their analysis these decreases (or in one case, relative decrease) in diversity due to treatment did not attain to the 19 to 1 confidence level, even though they were all in the same, negative direction. They concluded that there appeared to be no negative affect of herbicide treatment. The correct conclusion (if their analysis were correct) would be that they had not proved that there was an effect; that is, they had not proved the roof would fall. That’s different from proving it won’t.

I and most reasonable people will act on 9 to 1 probabilities. Treatment mesquite under conditions of Nolte and Fulbright’s experiment probably causes decreased diversity.

Response to Comment: Plant, small mammal, and avian diversity following control of honey mesquite by Tim Fulbright and Kenneth Nolte, Texas A&M University Kingsville, Campus Box 218, Kingsville, Tex. 78363.

We wish to respond to Mr. Rober Peterson’s critique of our article *Plant, small mammal, and avian diversity following control of honey mesquite*. Mr. Peterson stated “they reason that 9 to 1 odds are not at the level of scientific proof.” We assume he is referring to our use of a significance level of 0.05 rather than 0.10. Selection of a significance level is an arbitrary decision. We chose $\alpha = 0.05$ to be conservative, i.e. to avoid type I errors. Most of the differences in our study were not large enough to be declared statistically significant at a significance level of 0.05. We could have chosen $\alpha = 0.10$. In 2 cases, post-treatment differences between controls and treatments could have been declared significant at the 0.10 level. But in other cases the *P* values were larger.

Mr. Peterson stated that “decreases in diversity due to treatment did not attain to the 19 to 1 confidence level, even though they were all in the same negative direction.” We reported 5 post-treatment species richness and Shannon’s index comparisons in the paper. In 3 cases, species richness values were lower in the herbicide treatments (plants in 1992 and 1993 and birds) and in 2 cases species richness values were the same or greater in the herbicide treatments (small mammals in 1992 and 1993). Shannon’s index was higher in the herbicide treatment in 1 of 5 cases. Beta

diversity (vegetation patchiness) values were greater in herbicide treatments in 1992 and 1993. Thus, not all values in the herbicide treatments were in the “same negative direction.”

We clearly pointed out the weakness of our study. Replication was limited, rainfall was above average during both years, and the study only lasted two years. Based on the results of our study, we believe one should be cautious in concluding that treating shrublands with herbicide does or does not reduce species diversity. Rather, our study was one case, with well above average rainfall and a fairly selective herbicide treatment in which statistically significant ($P < 0.05$) differences were not observed. Clearly, additional research in other ecosystems and climatic regimes is warranted and needed. Then we can collate the body of information available and search for patterns.

Book Reviews

The Lochsa Story—Land Ethics in the Bitterroot Mountains. By Bud Moore. 1996. Mountain Press, Missoula, Montana. US\$20.00 paper. ISBN 0-87842-341-9.

Bud Moore's history of the Lochsa region is a personalized account, combining his experiences as a native of the area with broader themes of the development and use of this portion of North Idaho. The book opens in 1930 with his first unaccompanied exploration into the area at age 12, where he encountered a grizzly bear at dusk while approaching his camp site. In later years he spent 2 solitary winters trapping in the Lochsa wilderness, worked seasonally for the US Forest Service, and eventually served as District Ranger at Powell from 1949 to 1956. His perspective is that of a life-long land user and land manager. His deep attachment to the Lochsa and concern for its resources are evident.

Early chapters cover use and travel in the area by Indians, the Expedition of Lewis and Clark, mining exploration and the ensuing Nez Perce War, and abortive attempts of railroad interests for disposal of land grants. Chapters on fur trapping, the Great Burn of 1910, the reoccurrence of massive wildfires in 1934, US Forest Service enforcement of state game preserve regulations, and other introductory events in Forest Service management include interviews by the author of original participants or their descendants. Combined with Moore's knowledge of trapping and logging, these chapters include details which add to the book's depth. Chapters on the extinction of the Lochsa's grizzlies, and lost gold treasures combine lore and historical details.

Opening of the Lochsa after World War II was dramatically influenced by insects and other disturbances. Moore relates in four chapters the acceleration of road building and logging to harvest timber infested with spruce bark beetles, and spruce budworm control in 1956 with widespread aerial spraying of DDT. He feels that while these actions were supported by contemporary professional opinion, they exemplify the preoccupation of land managers with development of the timber resource at the expense of watershed and wildlife protection.

Consequences of these decisions lead to Moore's concluding theme: the need for national forest policy based on limits of the resource, sustainable management only where sustainable, and detailed on-site evaluation of interdependent resources. Moore builds to this ideal through discussion of conflicts between wilderness and multiple-use philosophies, public and professional criticism of clearcutting, and enactment of forest management legislation in the 1970's. An entire chapter is devoted to the 1987 forest plan for the Lochsa.

From a vantage point overlooking the Selway Wilderness to the south and logged forest land to the north, Moore concludes that forest management on the Lochsa, as in the northern Rockies as a whole, has permitted more aggressive development than can be sustained and too little consideration for environmental protection. While critical of some Forest Service practices, he remains supportive of the agency's attempts for resource protection and management using an ecosystem-based philosophy.

As a regional history, *The Lochsa Story* balances national trends with the stories, lives, and places which color how these ideas unfolded. Local detail is more anecdotal than analytical. Allowable timber harvest figures for the Lochsa are mentioned, but discussion of environmental effects of logging practices, acreage and extent of fires or other land treatments, or wildlife population data are not included to support his views.

The author's experiences, lyrical descriptions, over 250 photos, and 13 maps convey the area's vastness and beauty. The book is recommended to those who have interest in this region, the outdoors in general, or US Forest Service policy and history. Moore's call to stewardship is appropriate as well for users and managers of other natural resources.—*Courtney B. Smith*, Clarkston, Washington.

Barns of the West. A Vanishing Legacy. By Arthur A. Hart. 1996. Historic Idaho, Inc., Boise. 112 p. US\$29.95 cloth. ISBN 0-9631258-9-3.

When I arrived at Washington State University in 1981, the building on campus that most impressed me was the old beef barn near my office. The immense wooden hulk was unoccupied except for a graduate student caretaker, and its acreages of white paint and cedar shingles were in some disrepair, recently abandoned by the university in favor of new livestock facilities of steel and concrete. Even in its supposed obsolescence, I could see in its massive, well-preserved frame the kind of publicly-funded overbuilding that would, now 60 years later, be no doubt classified as condemnably unsafe. The iron-hard first-growth Douglas-fir beams, stalls and feed bunks had physically outlasted the function and fashion of the modern, efficient university. It exemplified the agri-architectural relics that are the subject of *Barns of the West*, a new book surveying the old and vanishing barns of that region, focusing especially on the Northwest.

As a survey of barns of the West, the book is more pictorial than literary. Dispersed throughout all of the photo captions and the brief sections of text are sufficient details of barn structure and function to more than satisfy the reader at a coffee table, maybe fewer than would satisfy a student of the subject. The book might best be characterized as a photographic history of barns for the intellectually curious traveler or casual historian, who will likely find it fully satisfying.

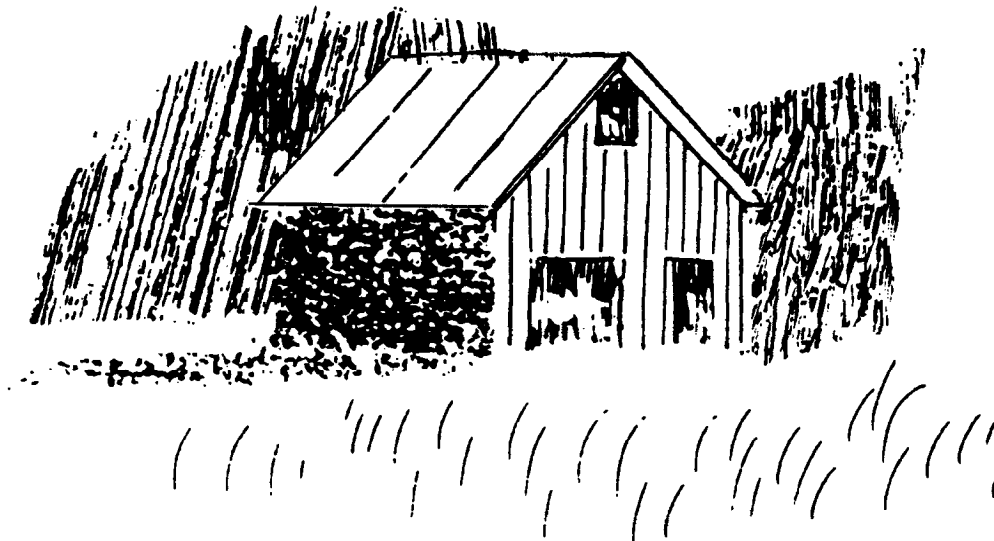
It is organized, more or less, into 15 short chapters, the first 7 with headings related to barn structure like *roof styles*, *windows*, and *silos*. Following them are a chapter on round barns, one on log barns, and a seemingly out-of-place chapter on barn surfaces and sidings. Additional chapters deal with barn landscapes, barns of Alaska, and hop barns. A personal epilogue by the author follows in which he reminisces about the barn and its many uses on the family farm of his early years in western Oregon. Not just farm animals, but barn swallows, flickers, and some of the best cats I know were born in barns like that one, and reading the author's reminiscences reminded me that an old barn, like an old tree, is never really dead. Included in *Barns of the West* are a

modest bibliography of books on barns, and a thorough index to allow the reader or peruser to find any photograph or topic in the brief text.

And there isn't much actual text at that, with the photographs and captions constituting most of the book. The photographs, most in black and white, some in color, are more realistic, less cosmetically touched up than the kind found on most calendars. The color photographs are important in showing painted sidings, but the black-and-white photographs showcase the gothic shapes and silhouettes of the old barns.

Even though they are often uneconomical relics, it seems many of these barns should be saved, and used, *as barns* just because they are aesthetically, historically and functionally worth saving. Hart's book shows many styles of western barns in all states of use and disuse, and some photographs are of barns that are no longer standing. If the photographs of dilapidated barns don't speak loudly enough, the text is interwoven with realistic reminders that "viable adaptive reuses" of such barns must be found if most of them are to survive and avoid the subtitle of a *vanished legacy*.

The old beef barn on campus near my office hasn't exactly vanished, but it isn't exactly *there* either. Targeted for "adaptive viable reuse" about 10 years ago, its voluminous frame was gutted and it was converted into the University Alumni Centre (sic), as its visitor brochure reads, "the most beautiful and architecturally significant university alumni centre in the country." The Northwest Douglas-fir interior in 1920's *feed bunk moderne* was replaced by trim and furnishings of recent tropical mahogany (and other select, tropical hardwoods) from Latin American rainforests. Sections of floor tiles and fine paneling are inscribed with the names of thousands of financial contributors. Ten years later, it is still the most opulent building on campus, a fine example of how a visionary architect and a few million dollars can convert a structure of great style and function into a structure of great style and function. It is a peerless place for university fundraisers to court potential university benefactors. So bovine moos have been replaced by financial schmoose, and even though it doesn't look much like a barn any more, you can be sure the old place stills needs shoveled out now and then.—*David L. Scarnecchia*, Washington State University, Pullman, Washington.



Erratum

In the May issue of *JRM* 50:226–230 Figure 1, which appeared on page 227, was difficult to read due to a printing error. The article was entitled *Aspects of coyote predation on Angora goats* by Lamar A. Windberg, Frederick F. Knowlton, Steven M. Ebbert, and Brian T. Kelly. The following is a corrected copy of the figure.

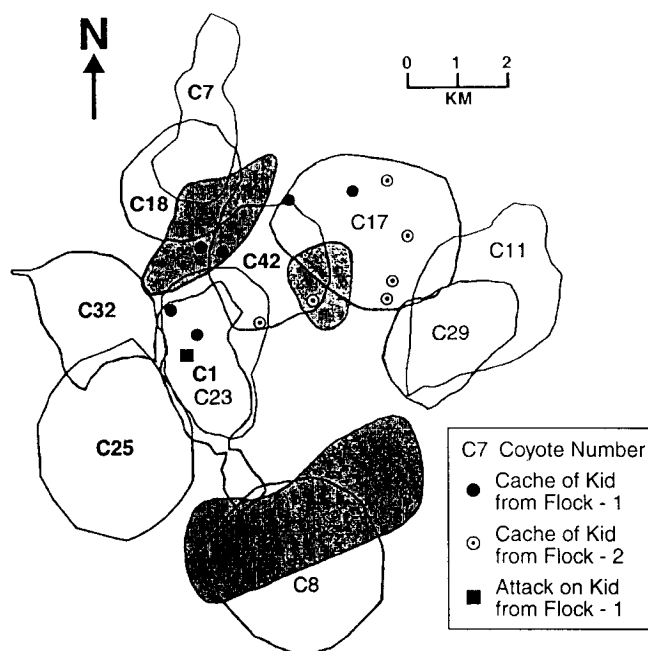


Fig. 1. Distribution of 12 food caches of Angora kids, and 1 site of attack, by coyotes in relation to core areas of coyote territorial ranges. Shaded areas represent minimum observed ranges of 3 flocks of goats (Flock-1 = upper, Flock-2 = middle, Flock-3 = lower). Coyote identification numbers in boldface print indicate individuals that consumed goat.

Associate Editor Nominations *Journal of Range Management*

Replacements are needed for Associate Editors of the *Journal of Range Management* retiring from the Editorial Board in February 1998. We are seeking nominees with expertise in the following general areas:

plant physiology,
plant ecology
economics,
improvements
reclamation, and
soils.

Associate Editors serve for 2 years with an optional 2 additional years with the concurrence of the Editor, *JRM*. To nominate a candidate for this important and demanding position, ascertain that the individual is available and willing to serve and then send a letter of nomination to the Editor describing the nominee's qualifications. Interested individuals may nominate themselves. The candidate will be asked to supply a list of publications and an account of experience in reviewing manuscripts.

Send nominations by **1 Aug. 1997** to: Gary Frasier, Editor, *Journal of Range Management*, 7280 Stag Hollow Road, Loveland, Colorado 80538.