

# Journal of Range Management

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- 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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# Application of non-equilibrium ecology to rangeland riparian zones

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## Abstract

Traditional theories of plant succession leading to a single equilibrium community are being re-evaluated. Alternative theories involving multiple steady states, and state-and-transition processes have been postulated to more adequately reflect the dynamics of rangeland ecosystems. The ecological literature provides examples of apparent thresholds in arid and semi-arid plant communities, however the literature is void of discussion of the applicability of non-equilibrium ecological theory to riparian areas contained within the rangelands of the world.

In arid and semi-arid environments the availability of soil water is critical in the determination of the composition of the plant community. In this study we hypothesized that the relationship between soil moisture and depth to groundwater within the riparian zone controlled the composition of the associated plant communities. These soil water, groundwater, plant community composition relationships were used to test the applicability of state and transition models to riparian zones.

Water table levels within an irrigated eastern Oregon riparian valley were monitored for 2 consecutive summers. The study area was mapped into 4 distinct plant community types on the basis of dominant graminoids. We measured depth to the water table, soil moisture content, relative species composition, litter, percent bareground and percent relative basal cover of key plant species and life forms. Relationships between water table levels, soil moisture content and plant communities were analyzed. Results indicated the 4 plant communities contained within this study area can be segregated on the basis of soil moisture content and/or depth to groundwater during the growing season. Ecological states and transition zones based on soil moisture content and/or water table depth were determined.

**Key Words:** riparian plant communities, groundwater, soil moisture, state and transition model

An important criterion of the applicability of a model or theory is its ability to predict the consequences of humans' activities with acceptable precision over timescales relevant to manage-

## Resumen

Las teorías tradicionales de sucesión vegetal que conducen a una sola comunidad en equilibrio están siendo revaluadas. Para reflejar mas adecuadamente las dinámicas de los ecosistemas de pastizal se han postulado teorías alternativas que involucran estados estables múltiples y procesos de estado y transición. La literatura ecológica provee ejemplos de umbrales aparentes en comunidades vegetales áridas y semiáridas; sin embargo, esta literatura esta carente de discusión respecto a la aplicabilidad de la teoría ecológica de no-equilibrio en áreas ribereñas de los pastizales del mundo. En los ambientes áridos y semiáridos la disponibilidad de agua en el suelo es crítica en la determinación de la composición de la comunidad vegetal. En este estudio nosotros hipotetizamos que la relación entre la humedad del suelo y la profundidad del agua subterránea dentro de las zonas ribereñas controló la composición de las comunidades vegetales asociadas. Estas relaciones entre el agua del suelo, el agua subterránea y la composición de la comunidad vegetal se utilizaron para probar la aplicabilidad de los modelos de estado y transición en las zonas ribereñas. Durante 2 veranos consecutivos se monitorearon los niveles del agua freática dentro de un valle ribereño irrigado del este de Oregon. El área de estudio se mapeó dentro de 4 tipos distintos de comunidades vegetales que se distinguieron entre ellos por las gramíneas dominantes. Medimos la profundidad del manto freático, el contenido de humedad del suelo, la composición relativa de especies vegetales, el mantillo, el porcentaje de suelo desnudo y el porcentaje relativo de cobertura basal de las especies clave y formas de vida. Se analizaron las relaciones entre los niveles del agua freática, contenido de humedad del suelo y la comunidad vegetal. Los resultados indicaron que las 4 comunidades vegetales incluidas en el área de estudio pueden ser segregadas en base del contenido de humedad del suelo y/o la profundidad del agua subterránea durante la estación de crecimiento. Se determinaron zonas estados ecológicas y transición basadas en la humedad del suelo y/o profundidad del manto freático.

ment. After 40 years of applying the quantitative climax model of Dyksterhuis (1949) to rangeland management, its predictive capabilities have come under scrutiny in disturbance based ecosystems. The inability of the model to handle multiple vectors of change (climatic variation, fire, plant introduction, grazing) have led some ecologists to abandon the model completely (Wilson 1984, Smith 1988). Traditional theories of plant succession leading to a single equilibrium community have been found to be inadequate for understanding the complex successional

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pathways of semi-arid and arid rangeland ecosystems (Westoby 1980, Anderson 1986, Foran et al. 1986, Laycock 1991, Tausch et al. 1993). The recognition of this inadequacy has generated a search for an alternative theory that more adequately reflects the dynamics of rangeland ecosystems. Theories involving multiple successional pathways, multiple steady states, and state-and-transition processes are gaining in acceptance.

Westoby et al. (1989) proposed the use of a state-and-transition model as the basis for describing rangeland dynamics. A state is defined as an alternative, persistent vegetation community which is not simply reversible in the linear successional framework. Transitions between states are triggered by natural events (e.g., weather or fire) or by management actions. Transitions may occur very quickly, as in the case of fire, or slowly over an extended period of time as in the case of a shift in weather patterns. Regardless of the rate of change, the system does not come to rest halfway through a transition (Westoby et al. 1989). Transitions are also referred to as thresholds (Friedel 1991). Friedel suggested that environmental change can be discontinuous, with thresholds between alternative new states of species assemblages. Thresholds have 2 important characteristics: first they are the boundary in space and time between 2 states; and second, the initial shift across the boundary is not reversible on a practical time scale without significant inputs of energy and time.

Examples of thresholds in arid and semi-arid plant communities are recorded in the ecological literature (Archer and Smeins 1991, Friedel 1991, Laycock 1991), however, the discussion of the applicability of non-equilibrium based models for riparian areas within the arid and semi-arid rangelands of the world is just emerging. Weixelman et al. (1997) developed a state-and-transition model for a dry graminoid meadow located in central Nevada, however, the dominant species along with the meadow soil type does not classify the site as riparian. While riparian zones constitute only a small fraction (2–3%) of the areal extent of rangelands in the 11 western United States, they provide a disproportionate amount of the forage consumed by livestock and are vital for the support of fish and wildlife (Kauffman and Krueger 1984). Given the importance of riparian zones to livestock production as well as fish and wildlife habitat it is critical that proposed successional models be tested for accuracy in the prediction of riparian vegetation response to management.

## Methods

### Study Area

The study was conducted in Bear Valley in south central Grant County, Ore. Grant County, situated in the Central Blue Mountains of east-central Oregon, lies between 44° and 45° north latitude and 118° and 120° west longitude. Valley floor elevation ranges from 1,387 to 1,440 m. Climate is characterized by cold winters, moderate summers, and low precipitation. The 30-year average summer temperature in Bear Valley is 13.8°C and mean maximum temperature of 26.7°C occurs during July and August. Average winter temperature is –4.87°C with the mean minimum of –13.1°C occurring in January. Temperature extremes range from 37.8 to –44.4°C. Mean annual precipitation is 33.2 cm and occurs primarily from November through June with the majority of it coming in the form of snow. Mean annual snowfall is 162 cm.

Bear Valley is divided by Scotty Creek, a second-order stream, flowing from the west and Bear Creek, a third-order stream, flowing from the east. Both these streams join the Silvies River near the south central portion of Bear Valley. The valley floor is wide and unconstrained with slopes of less than 2%. The valley soil was classified at the series level as Damon silty clay loam. The soil is poorly drained, formed in mixed alluvium with a restrictive layer at 100 to 130 cm. Permeability is moderately slow, estimated at 1.5 to 5.0

cm hr<sup>-1</sup>. Available water holding capacity is 18 to 25 cm and effective rooting depths are 75 to 100 cm (Stringham 1996).

A mosaic of private family-owned livestock ranches cover the valley floor within Bear and Silvies valleys, bordered by the surrounding Malheur National Forest. Cattle production is the primary economic enterprise. Subterranean irrigation, where water is diverted from the stream, carried by a ditch along the flood plain edge and allowed to return to the stream via subsurface interflow is applied to the privately owned riparian pastures to increase production of native and seeded grasses. Many meadows are hayed in late July for supplemental winter livestock feed.

### Plant Community Designation

Initial reconnaissance of the study area indicated that 4 distinct plant community types representing a mesic to hydric moisture regime could be identified on the basis of dominant graminoids. Community types were identified by ocular assessment (Table 1). The number of plots of each type of community included in the study is noted.

Eleven, 1 ha plots were randomly located within the irrigated meadows straddling the associated stream channel. Seven of the plots were located along Bear Creek and 4 along Scotty Creek. All 4 Scotty Creek plots and 4 of the Bear Creek plots included areas on the uphill side of the irrigation ditch providing 8 replications of the dry bluegrass (DB) community type.

Table 1. Plant communities as defined by dominant graminoids.

Plant Communities	
<b>Wet Meadow (WM)</b> <b>community</b> replication = 7	<i>Carex nebrascensis</i> Dewey (Nebraska sedge) <i>Carex rostrata</i> Stokes (beaked sedge) <i>Deschampsia cespitosa</i> (L.) Beauv. (tufted hairgrass) <i>Beckmannia syzigachne</i> (Steud.) Fern. (slough grass) <i>Agrostis alba</i> L. (redtop)
<b>Moist Meadow (MM)</b> <b>community</b> replication = 8	<i>Alopecurus pratensis</i> L. (meadow foxtail) <i>Carex nebrascensis</i> Dewey (Nebraska sedge) <i>Juncus balticus</i> Willd. (baltic rush) and other grasses, rushes, and forbs
<b>Moist Bluegrass (MB)</b> <b>community</b> replication = 11	<i>Poa pratensis</i> L. (Kentucky bluegrass) <i>Phleum pratense</i> L. (timothy) <i>Bromus inermis</i> Leys. (smooth brome) <i>Alopecurus pratensis</i> L. (meadow foxtail) and annual and perennial forbs
<b>Dry Bluegrass (DB)</b> <b>community</b> replication = 8	<i>Poa pratensis</i> L. (Kentucky bluegrass) <i>Bromus inermis</i> Leys. (smooth brome) <i>Koeleria cristata</i> Pers. (junegrass) <i>Poa sandbergii</i> Vasey (Sandbergs bluegrass) <i>Festuca idahoensis</i> Elmer (Idaho fescue) <i>Sitanion hystrix</i> (Nutt.) Smith (Squirreltail) <i>Chrysothamnus viscidiflorus</i> (Hook.) Nutt. (green rabbitbrush) <i>Artemisia tridentata</i> ssp. <i>vaseyana</i> Nutt. (mountain big sagebrush) and annual and perennial forbs and other grasses

Replication of the wet meadow (WM), moist meadow foxtail (MM), and moist bluegrass (MB) plant communities within the 11 plots was unbalanced with a total of 7, 8, and 11 replications, respectively.

### Cover and Species Composition

Point sampling using the point intercept method as described by Pieper (1973) was used to estimate basal cover, species composition, litter, and bare ground. Five, 15 m transects, with points every 15 cm, were randomly located in each plant community within each plot. Determinations were made in mid-June 1994 and mid-June 1995.

### Soil Classification

Fifteen soil pits were excavated with a backhoe in October 1995. Seven pits were located in the moist bluegrass community type, 3 each in the dry and meadow foxtail communities and 2 in the wet meadow type. At least 1 soil pit was located in each of the 11 plots. Horizons were described to a depth of 150 cm and the permeability estimated for each horizon.

### Soil Moisture

Soil moisture was measured at 2 week intervals in each community type within each plot from late May through September. Gravimetric soil moisture content was determined using the method described by Gardner (1986). One sample from both the 30 cm and 45 cm depths were collected from each plant community within each plot. No soil moisture samples were collected from flooded communities, however, ponded conditions were noted.

### Water Table Depth

Water table depth was measured on 10 day intervals from late May through September in each plant community within each plot. Five transects each consisting of 4 shallow groundwater access tubes were placed perpendicular to the creek in each of the plots for a total of 220 access tubes. The transects were located on both sides of the creek in an alternate fashion beginning at a randomly selected point. Within a transect, the first access tube was located within 1 m of the stream channel. The placement of the remaining 3 tubes was determined by plant community change and/or distance from the previous tube being greater than 8 m and less than 25 m. This resulted in transect length varying from 45 to 60 m.

Access tubes were chosen over piezometers to allow for measurement of the actual depth to groundwater instead of

head pressure which may give a false indication of groundwater depth (Jury et al. 1991). Access tubes were constructed of 19 mm PVC pipe with 3 mm diameter holes drilled from the bottom of the tube to within 15 cm of the top. The access tube at creekside was placed at a depth of 120 cm or base flow level of the creek, which ever was greater. Differences in ground surface elevation from the creek-side tube to the 3 additional tubes within the transect was determined using standard survey methods. Access tube depth for the remaining tubes within a transect was calculated based on the creek-side tube depth plus or minus the change in ground surface elevation.

### Statistical Analysis

Indicator species analysis was used to indicate the concentration of species abundance and faithfulness of occurrence of identified species within the specified plant communities (Dufrene and Legendre 1997). The method produces indicator values for each species in each group and tests the values for statistical significance using a Monte Carlo technique. Plant community designations on the basis of dominant graminoid were confirmed.

Soil moisture and percent basal cover by dominant plant species and life forms were analyzed between plant communities within years and across years. Eleven locations (1 ha plots) were included in the analysis. The design was blocked by location and a mixed model ANOVA was used to determine within year differences (SAS 1994). A nested ANOVA, with year nested within plant community was used to identify between year differences when no significant year interaction occurred.

All plant species with sparse distributions were not analyzed statistically (< 5% basal cover). However, the relative percent basal cover of the life form groups of forbs, other grasses, mosses, rushes/sedges, and shrubs were analyzed.

The pair-wise mean comparison method was applied to basal cover and soil moisture means when F-tests were significant at ( $P \leq 0.10$ ). This allowed identification of plant community attributes that were significantly different across plant communities. Between year comparisons were made when F-tests of the year nested within plant community component of the model was significant at ( $P \leq 0.10$ ). Simple linear regression was used to determine the relationship between soil moisture and depth to water table.

## Results and Discussion

Climate data from the Oregon Climate Service weather station located in the south central portion of Bear Valley at Seneca, Ore. was used for this study. Annual precipitation for 1994 was 21.2 cm, 11.9 cm below the 30 year average and the mean maximum temperature was 1°C warmer. Annual precipitation for 1995 was 45.7 cm, 12.5 cm above the 30 year average (Oregon Climate Service 1995). Both years are representative of the extreme ends of the precipitation history for Bear Valley. This large variance in precipitation over the 2 years of the project provided an opportunity to study the response of the vegetative communities to different environmental conditions.

### Indicator Species Analysis

Relative abundance and frequency by plant community type were utilized to calculate indicator values using the Dufrene and Legendre (1997) method. Indicator values range from 0 (no indication) to 100 (perfect indication). Perfect indication implies that the presence of a species points to a particular group without error given the current data set. Table 2 presents the indicator values for the combined 1994 and 1995 species data. Indicator values for the dry bluegrass community (Table 1)

**Table 2. Indicator values for selected species by plant community. Values were determined using both 1994 and 1995 frequency data.**

Species	Indicator Values			
	DB	MB	MM	WM
<i>Alopecurus pratensis</i>	1	5	80	1
<i>Poa pratensis</i>	31	47	3	5
<i>Deschampsia cespitosa</i>	0	0	2	65
<i>Carex/Juncus</i> spp.	3	12	18	59
<i>Bromus pratense</i>	7	18	0	0
<i>Phleum pratense</i>	1	51	3	6
other grass	48	6	1	8
<i>Artemisia tridentata</i> ssp. <i>vaseyana</i>	40	0	0	0

were highest for the mountain big sagebrush (*Artemisia tridentata* ssp. *Vaseyana* Nutt.), Kentucky bluegrass (*Poa pratensis* L.) and the other grass category which included species such as Idaho fescue (*Festuca idahoensis* Elmer), junegrass (*Koeleria cristata* Pers.), and sandbergs bluegrass (*Poa sandbergii* Vasey). The moist bluegrass community (Table 1) indicator values showed a dominance of Kentucky bluegrass and non-native timothy (*Phleum pratense* L.) whereas the moist meadow foxtail (*Alopecurus pratensis* L.) community (Table 1) indicator values were highest for non-native meadow foxtail. Tufted hairgrass (*Deschampsia cespitosa* (L.) and the sedge/rush category showed the highest indicator values for the wet meadow community (Table 1). The indicator values for each species in each group were tested for statistical significance using a Monte Carlo technique with 1,000 permutations. All indicator values were found to be significant at the 95% level ( $p < 0.05$ ).

## Basal Cover

Comparisons of the basal cover of individual key plant species and life forms by year are presented in Table 3. The wet meadow community had a significantly greater amount of tufted hairgrass and the combined sedge/rush category than the other 3 communities in both years. Meadow foxtail was found in significantly

**Table 4. Seasonal trends in average soil moisture content at 30 and 45 cm depth for 1994 within different plant communities. DB = dry bluegrass; MB = moist bluegrass; MM = moist meadow foxtail; WM = wet meadow. Comparisons are by date and depth across plant communities. Lower case superscripts are for 30 cm depths and upper case superscripts are for 45 cm depth.**

	DB		MB		MM		WM*	
	30 cm	45 cm	30 cm	45 cm	30 cm	45 cm	30 cm	45 cm
	----- (%) -----							
16 Jun	25 <sup>a</sup>	28 <sup>A</sup>	42 <sup>b</sup>	48 <sup>B</sup>	51 <sup>c</sup>	58 <sup>C</sup>	62 <sup>c</sup>	72 <sup>C</sup>
26 Jun	27 <sup>a</sup>	31 <sup>A</sup>	34 <sup>b</sup>	38 <sup>B</sup>	45 <sup>c</sup>	49 <sup>C</sup>	46 <sup>c</sup>	64 <sup>C</sup>
7 Jul	22 <sup>a</sup>	27 <sup>A</sup>	31 <sup>b</sup>	35 <sup>B</sup>	34 <sup>c</sup>	46 <sup>C</sup>	48 <sup>c</sup>	56 <sup>C</sup>
16 Jul	18 <sup>a</sup>	21 <sup>A</sup>	25 <sup>b</sup>	31 <sup>B</sup>	28 <sup>c</sup>	37 <sup>C</sup>	39 <sup>c</sup>	41 <sup>C</sup>

\*Sites with standing water were assumed to have 85% soil moisture.

**Table 5. Seasonal trends in average soil moisture content at 30 and 45 cm depth for 1995 within different plant communities. DB = dry bluegrass; MB = moist bluegrass; MM = moist meadow foxtail; WM = wet meadow. Comparisons are by date and depth across plant communities. Lower case superscripts are for 30 cm depths and upper case superscripts are for 45 cm depth.**

	DB		MB		MM		WM*	
	30 cm	45 cm	30 cm	45 cm	30 cm	45 cm	30 cm	45 cm
	----- (%) -----							
13 Jun	34 <sup>a</sup>	36 <sup>A</sup>	52 <sup>b</sup>	58 <sup>B</sup>	66 <sup>c</sup>	81 <sup>C</sup>	85 <sup>d</sup>	85 <sup>C</sup>
29 Jun	30 <sup>a</sup>	32 <sup>A</sup>	53 <sup>b</sup>	62 <sup>B</sup>	63 <sup>c</sup>	69 <sup>C</sup>	85 <sup>d</sup>	85 <sup>C</sup>
13 Jul	25 <sup>a</sup>	30 <sup>A</sup>	39 <sup>a</sup>	46 <sup>B</sup>	60 <sup>c</sup>	70 <sup>C</sup>	76 <sup>c</sup>	77 <sup>C</sup>
25 Jul	22 <sup>a</sup>	27 <sup>A</sup>	34 <sup>a</sup>	41 <sup>A</sup>	51 <sup>b</sup>	56 <sup>B</sup>	60 <sup>b</sup>	62 <sup>B</sup>

\*Soil moisture content was not analyzed statistically due to a large number of sites with free standing water.

greater amounts in the moist meadow foxtail community for both years when compared to all other communities studied. The moist bluegrass community exhibited significantly more Kentucky bluegrass than the other 3 plant communities in 1994 and 1995. Although the dry bluegrass type

had significantly less Kentucky bluegrass than the moist bluegrass type it had significantly more than the wet community and moist meadow foxtail community in 1994. In 1995, the same results occurred for the moist meadow foxtail community. Delineation of the 4 communities on the basis of dominant graminoid proved efficient and statistically significant.

**Table 3. Mean percent basal cover of individual key species and life forms within the dry bluegrass (DB), moist bluegrass (MB), moist meadow foxtail (MM), and wet meadow (WM) communities. Standard error is in parentheses.**

	DB		MB		MM		WM	
	1994	1995	1994	1995	1994	1995	1994	1995
	----- (%) -----							
Kentucky bluegrass	14.4 (±5.5)	5.4 (±3.1)	17.9 (±9.1)	10.4 (±3.4)				
Meadow foxtail			4.5 (±5.1)	.75 (±1.1)	27.1 (±10.8)	16.6 (±4.5)	1.2 (±1.5)	.43 (±.48)
Timothy			6.3 (±5.4)	4.6 (±2.9)				
Tufted hairgrass							10.3 (±13.0)	8.0 (±9.4)
Sedge/Rush			4.8 (±3.6)	1.9 (±1.9)	7.6 (±4.0)	3.2 (±1.5)	20.0 (±8.2)	13.7 (±3.8)
Moss					10.0 (±8.6)	14.1 (±15.2)	17.2 (±8.7)	30.1 (±10.1)
Forbs	10.3 (±3.3)	6.6 (±2.7)	9.6 (±5.6)	8.3 (±3.5)	7.0 (±4.1)	2.1 (±2.6)	6.3 (±3.3)	2.3 (±1.8)
Shrubs	1.1 (±.5)	.31 (±.31)						
Total Grass	21.2 (±2.0)	11.6 (±2.8)	32.6 (±5.6)	17.8 (±3.7)	32.2 (±9.3)	19.2 (±3.0)	19.6 (±8.6)	13.0 (±7.3)
Total Basal Cover	34.2 (±8.8)	20.2 (±4.0)	47.1 (±7.5)	28.2 (±4.8)	46.8 (±9.3)	24.6 (±3.8)	34.2 (±8.8)	29.2 (±6.1)

## Soil Moisture

Seasonal trends in soil moisture content for 1994 and 1995 at the 30 and 45 cm depth for the 4 plant community types are presented in Tables 4 and 5. Korpela (1992) measured soil moisture content in similar plant communities in a non-irrigated riparian area in northeastern Oregon. Results for the moist bluegrass and dry bluegrass communities were quite similar to the current study with the moist bluegrass community averaging at least 10% greater soil moisture content throughout the growing season. Pairwise comparisons of soil moisture averages within years across plant communities by date and depth showed significant differences in moisture content existed between the dry bluegrass and all other communities and moist bluegrass and all other communities. These results were consistent for both years. The soil moisture content within the moist meadow foxtail community was not significantly different than the wet meadow soil moisture early in the season, how-

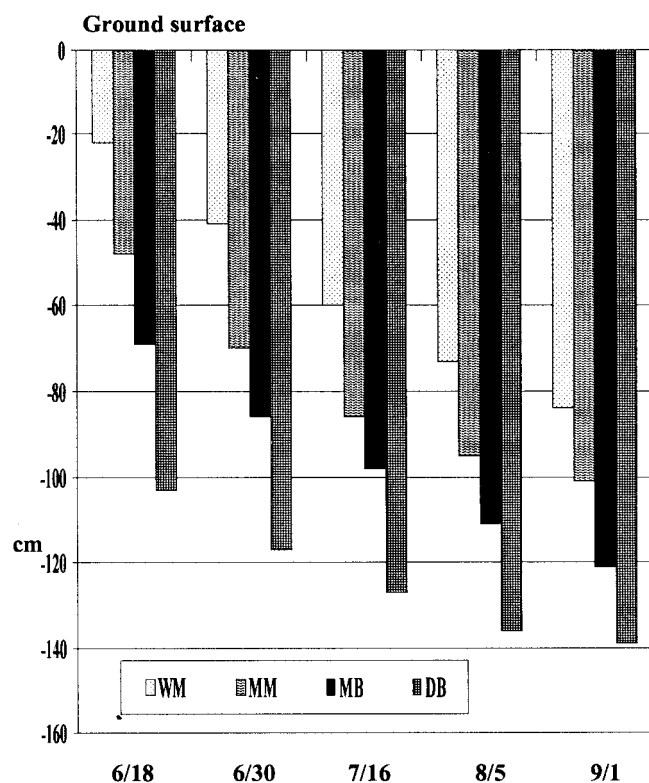


Fig. 1. Seasonal trends in average depth to the water table for 1994 within different plant communities designated as follows: MB = moist bluegrass, DB = dry bluegrass, MM = moist meadow foxtail, and WM = wet meadow.

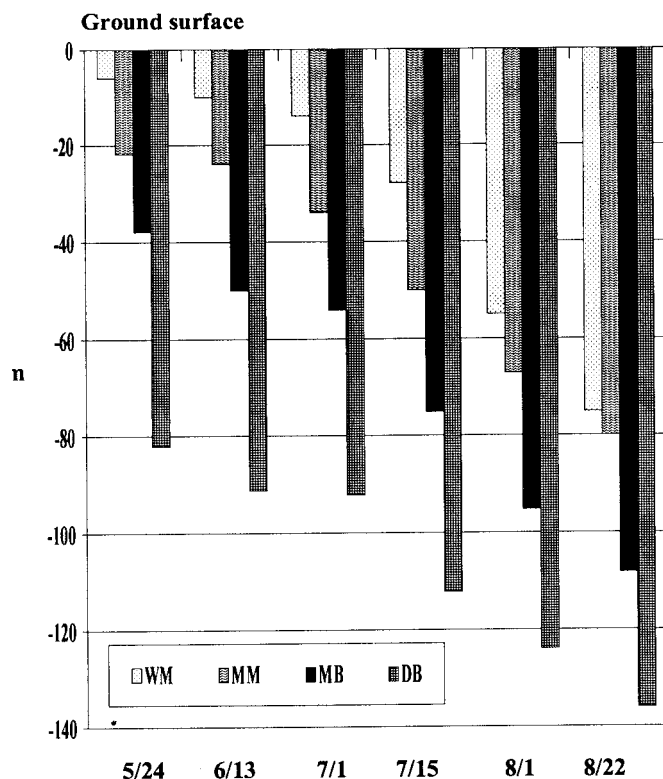


Fig. 2. Seasonal trends in average depth to the water table for 1995 within different plant communities designated as follows: MB = moist bluegrass, DB = dry bluegrass, MM = moist meadow foxtail, and WM = wet meadow.

ever a difference did exist at the 30 cm depth by mid-June in 1995. Sampling began in mid-June 1994 and we assume that due to extremely dry conditions this relationship was not observed but may have existed earlier in the season.

### Water Table Depth

Trends in depth to the water table for the 4 plant communities are illustrated in Figures 1 and 2. Padgett (1982) monitored water table levels in several plant community types in central Oregon and found that the water table level in Kentucky bluegrass communities was generally 50 cm or more below the surface. Korpela (1992) studied water table trends in a dry bluegrass, moist bluegrass and wet meadow communities in northeastern Oregon. He reported water table depths of 50 cm or more for the moist bluegrass community and 100 cm or more for the dry bluegrass during the growing season. Water table depths for these communities within this study area were similar to Korpela's during the 1994 growing season but were generally 20 cm closer to the surface during the 1995 growing season. This result can be attributed to the increased water

available for irrigation during 1995. Padgett (1982) found that the water table in wet meadows dominated by beaked sedge (*Carex rostrata* Stokes) or water sedge (*C. aquatilis* Wahl) was at or near the ground surface until mid-summer, similar to trends for wet meadow communities within this study.

Ponded conditions occurred at 26% of the 46 wet community sampling sites in mid-June 1994 and 67% had a water table  $\leq 30$  cm below the soil surface. The moist meadow foxtail community had a water table within 30 cm of the surface at 17% of the sampling sites in mid-June 1994. In 1995, ponding occurred at 50% of the wet meadow and 6% of the moist meadow foxtail sites in late May. By mid-June ponding had ceased in the moist meadow foxtail community while 41% of the wet meadow sites remained ponded. Ponding continued through mid-July at 10% of the wet community sites. The water table was within 30 cm of the ground surface during mid-June 1995 for 91% of the wet meadow sites and 63% of the moist meadow foxtail sites. By mid-July only 8% of the moist meadow foxtail sites had a water table  $\leq 30$  cm below the surface while the wet community had 63%.

### State and Transition Determination

Depth to groundwater during the growing season was pivotal in the definition of states for 3 of the plant communities at the peak of the growing season. Due to the differences in precipitation amounts between the 2 years of the study, mid-June 1994 average depth to groundwater was compared with late-June 1995 data. The average depth to groundwater by plant community is presented in Table 6. Significant differences in depth to the water table during the growing season were found between all the plant communities for both 1994 and 1995. Although there exists a significant difference in depth to the water table between the moist bluegrass and dry bluegrass community this environmental variable was not utilized to determine the states and transitional zone between these 2 communities. Soil moisture content within the top 45 cm of the soil profile was considered to have a greater influence on species composition for the dry bluegrass community than depth to groundwater.



**Table 6. Average water table depth for the wet meadow, moist meadow foxtail, moist bluegrass, and dry bluegrass communities at the peak of the growing season (cm). Comparisons are within year across plant communities. Standard errors in parentheses.**

	Wet Meadow	Moist Meadow Foxtail	Moist Bluegrass	Dry Bluegrass
	----- (cm) -----			
16 Jun 94	23 <sup>a</sup> (.28)	49 <sup>b</sup> (1.9)	70 <sup>c</sup> (2.0)	104 <sup>d</sup> (3.0)
28 Jun 95	14 <sup>a</sup> (2.1)	34 <sup>b</sup> (2.4)	59 <sup>c</sup> (1.7)	98 <sup>d</sup> (3.0)

**Table 7. Average soil moisture content in percent for the moist meadow foxtail, moist bluegrass, and dry bluegrass communities at 30 and 45 cm depth at the peak of the growing season. Comparisons are within a year and depth across plant communities. Standard errors in parentheses.**

	Moist Meadow Foxtail	Moist Bluegrass	Dry Bluegrass
	----- (%) -----		
16 Jun 94 30 cm	51 <sup>a</sup> (2.8)	42 <sup>b</sup> (2.8)	25 <sup>c</sup> (3.3)
28 Jun 95 30 cm	63 <sup>a</sup> (5.8)	46 <sup>b</sup> (2.3)	30 <sup>c</sup> (3.1)
16 Jun 94 45 cm	58*	45 <sup>b</sup> (2.6)	28 <sup>c</sup> (2.8)
28 Jun 95 45 cm	69*	62*	32 <sup>c</sup> (4.7)

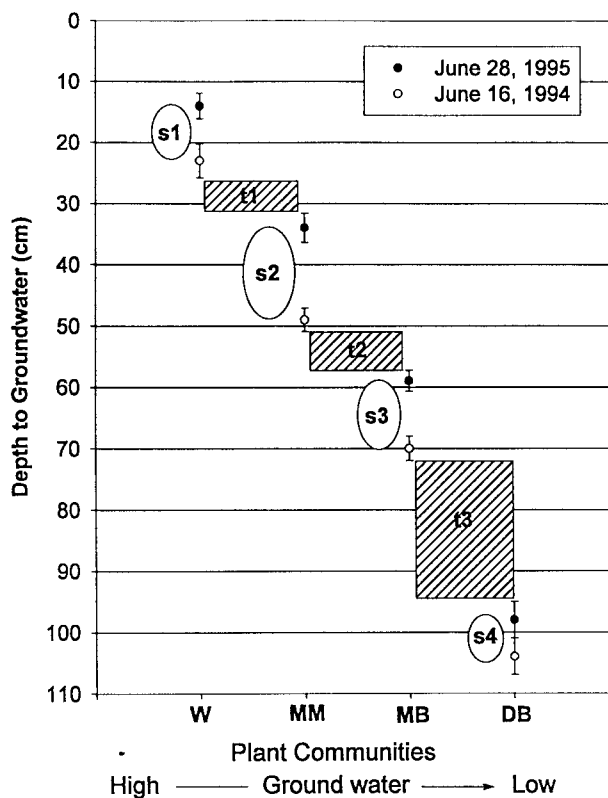
Average soil moisture content in mid-June 1994 and late-June 1995 for the dry bluegrass, moist bluegrass, and meadow foxtail communities contained within this study area are presented in Table 7. Significant differences in soil moisture content during the growing season were found between the dry bluegrass and moist bluegrass communities at the 30 cm and 45 cm depth for 1994 and the 30 cm depth for 1995. Greater than 30% of the soil moisture measurement sites within the moist bluegrass community in 1995 at the 45 cm depth exhibited free standing water, therefore, soil moisture comparisons were not made. Due to the difficulty with accurately measuring soil moisture content in saturated soils additional comparisons between plant communities were not made.

The extreme differences in precipitation during the 2 years of the study was expressed in the soil moisture content and water table depth within plant communities across years (Tables 6 and 7). This range in soil water components provided critical information in the determination of plant community ecological thresholds. States were conservatively estimated by the difference between the wet (1995) and dry (1994) year average soil water component for the specified plant community. Transitions between states were determined by the difference in the average soil water component plus or minus the standard error between the two specified plant communities.

The threshold between the moist bluegrass community and the dry bluegrass community was distinct. The ranges in

average soil moisture for these 2 plant communities did not overlap. The average soil moisture content in the moist bluegrass community during the dry year was 12% greater than the average soil moisture content in the dry bluegrass community during the wet year (Table 7). The dry bluegrass state occurs within the 25 to 30% soil moisture range at 30 cm depth at the peak of the growing season, whereas, the moist bluegrass state occurs within the 42 to 46% soil moisture range at 30 cm depth. Thus, the transition zone between the dry bluegrass community and the moist bluegrass community lies between 33.1 and 39.2% soil moisture at the 30 cm depth.

The states and transition zones for the other 3 community types were determined using the depth to groundwater data for June. The transition zone between the moist meadow foxtail and moist bluegrass community as determined by depth to groundwater was distinct. The average



**Fig. 3. Conceptual model of changes in plant community as a function of changing water table level. Plant community states are indicated by "s" and transitions between states by "t". The apparent ecological amplitude of a community is portrayed by the vertical height of the ellipse. The time or energy required to move from 1 plant community state to the next is illustrated by the vertical height of the transition box. Average mid-June depth to groundwater by plant community for 1994 and 1995 is presented. States were determined by the average plus or minus the standard error. Transitions between states were determined by difference in ground water depth between the driest (1994) and the wettest (1995) years data for s1 and s2, s2 and s3, s3 and s4. W = wet, MM = meadow foxtail, MB = meadow K. bluegrass, DB = upland K. bluegrass.**

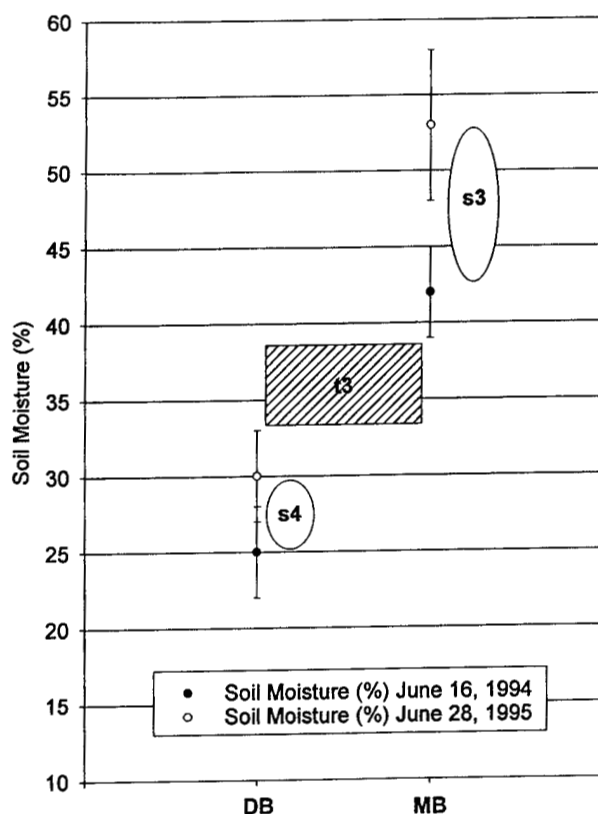


Fig. 4. Conceptual model of changes in plant community as a function of growing season soil moisture. Plant community states are indicated by "s" and transitions between states by "t". The apparent ecological amplitude of a community is portrayed by the vertical height of the ellipse. The time or energy required to move from 1 plant community state to the next is illustrated by the vertical height of the transition box. Average mid-June soil moisture for the dry bluegrass (DB) and moist bluegrass (MB) communities for 1994 and 1995 is presented. States were determined by the average plus or minus the standard error. Transitions between states were determined by the difference in soil moisture between the driest (1994) and wettest (1995) years data for s3 and s4.

depth to groundwater within the moist bluegrass community for the wet year was 59 cm whereas the average depth to groundwater for the moist meadow foxtail community during the dry year was 49 cm (Table 6). Thus, the transition zone was estimated to lie between 50.1 cm and 57.3 cm in depth to groundwater in mid to late June. The moist bluegrass state exists between a depth to groundwater of 59 to 70 cm whereas the moist meadow foxtail state lies between a water table depth of 34 to 49 cm. During the dry year the depth to groundwater within the wet meadow community averaged 23 cm and during the wet year 14 cm. The transition zone between the wet meadow and the moist meadow foxtail communities was estimated to occur between water table depths of 25.8 and 31.6 cm.

## Conclusions

Our results suggest that models of vegetation dynamics based on the concepts of non-equilibrium ecology are appropriate tools for predicting change within the riparian zone. State-and-transition models specify a "state" as an alternative, persistent vegetation community which is not simply reversible in the linear successional framework. In addition, transitions are defined as the boundary in space and time between 2 states with the initial shift across the boundary permanent, on a practical time scale, without significant inputs of time and energy. Two conceptual models using the results of this research are presented in Figures 3 and 4. Plant community states are indicated by "s" and transitions between states by "t". The apparent ecological amplitude of a community is portrayed by the vertical height of the ellipse. The time or energy required

to move from one plant community state to the next is illustrated by the vertical height of the transition box. The vertical height of the transition between the dry bluegrass and moist bluegrass communities based on depth to water table is relatively large (Fig. 3). Since this exceeds the potential rooting depth of the herbaceous component of the dry bluegrass community it was not considered a correct threshold. The appropriate model for the relationship between these 2 communities was based on soil moisture content and is presented in Figure 4.

The process of plant community change with respect to soil water components appears to be step-wise rather than linear. This implies a community may be stable and resistant to change up to a critical threshold. Once this threshold is crossed, changes can be dramatic and potentially irreversible over a time frame relevant to management. The semi-arid West contains examples of riparian zones which have been dewatered through the gullyng of the associated alluvial stream channel. However, these models suggest that minor changes of 10 to 20 cm in the depth to groundwater can produce profound change in the associated riparian plant community. Further testing of these concepts across a variety of soils and climates is needed for verification and refinement of the proposed model.

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# Activity budgets and foraging behavior of bison on seeded pastures

BRUCE D. RUTLEY AND ROBERT J. HUDSON

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## Abstract

Activity budgets and foraging behavior of yearling bison (*Bison bison* L.) on pasture were studied during quarterly trials between June 1994 and December 1995. Daily activity patterns were polyphasic with alternating bouts of foraging and resting activity. During winter, bison displayed 2 main daytime foraging bouts and significant nighttime foraging. During summer, phasic activity was poorly expressed due to the increased number of cycles. Total foraging time declined from summer to winter ( $763 \pm 62$  to  $470 \pm 32$  min day<sup>-1</sup>) while bedding bout length increased ( $121 \pm 13$  to  $276 \pm 26$  min day<sup>-1</sup>). Bison selected forage higher in crude protein ( $12.9 \pm 0.8$  vs  $10.0 \pm 0.8\%$ ), higher in predicted digestible energy ( $2.70 \pm 0.09$  vs  $2.17 \pm 0.09$  Mcal kg<sup>-1</sup>), lower in acid detergent fiber ( $31.9 \pm 0.9$  vs  $38.8 \pm 0.9\%$ ), and lower in lignin ( $4.8 \pm 0.3$  vs  $6.8 \pm 0.3\%$ , respectively) than forage available within grazed patches.

**Key Words:** nutritional ecology, forage intake, annual grazing, forage selection

Ruminants exhibit regular polyphasic activity patterns, alternating between foraging and resting/ruminating activity (Gates and Hudson 1983, Hudson and Watkins 1986). This basic pattern is pre-empted by walking between bedding and feeding sites, moving to alternate feeding sites, social interactions, and predator avoidance (Renecker and Hudson 1993). Wild ruminants alter their daily activity pattern in response to seasonal fluctuations in forage biomass and environmental temperature (Trudel and White 1981, Hudson and Frank 1987).

Foraging behavior of bison (*Bison bison* L.) (Peden et al. 1974, Hudson and Frank 1987, Plumb and Dodd 1993) and partial activity budgets (Belovsky and Slade 1986) have been described. However, there is little published information on foraging behavior and activity budgets of farmed bison annual grazing seeded pasture. Under these conditions, full expression of activity rhythms and the rumen repletion-depletion cycle is expected. This study was conducted to provide this information and to determine the response of bison to seasonal variations in forage

## Resumen

El patrón de actividades y el comportamiento de forrajeo de bisontes (*Bison bison* L.) apacentando praderas se estudiaron en ensayos cuatrimestrales conducidos entre junio de 1994 y diciembre de 1995. Los patrones de actividad diaria fueron polifásicos con ratos alternantes de actividades de descanso y apacentamiento. Durante el invierno, los bisontes mostraron 2 ratos principales de apacentamiento diurno y apacentamiento nocturno significativo. En verano, la actividad fásica fue pobremente expresada debido al incremento del número de ciclos. El tiempo total de forrajeo disminuyó del verano al invierno (de  $763 \pm 62$  a  $470 \pm 32$  min día<sup>-1</sup>) mientras que la longitud de los períodos de descanso aumentó (de  $121 \pm 13$  a  $276 \pm 26$  min día<sup>-1</sup>). El forraje seleccionado por el bisonte, comparado con el disponible dentro de los parches apacentados por ellos, fue más alto en proteína cruda ( $12.9 \pm 0.8$  vs  $10.0 \pm 0.8\%$ ) y energía digestible predicha ( $2.70 \pm 0.09$  vs  $2.17 \pm 0.09$  Mcal kg<sup>-1</sup>) y más bajo en fibra ácido detergente ( $31.9 \pm 0.9$  vs  $38.8 \pm 0.9\%$ ) y lignina ( $4.8 \pm 0.3$  vs  $6.8 \pm 0.3\%$ ).

quality. We document the response specific to changes in activity budgets (foraging, resting and minor activity time), and length of foraging and resting bouts. We also tested the hypothesis that bison would select forage of a higher quality than that available to them from within grazed patches or the sward.

## Materials and Methods

### Location and Climate

The study was conducted at the Center for Agricultural Diversification, Dawson Creek, British Columbia ( $55^{\circ} 44' 30''$  N,  $120^{\circ} 30' 00''$  W; elevation 670 m) located 600 km northwest of Edmonton, Alberta. The area is located entirely within the Alberta Plateau—an extension of the Great Plains. The area is in the aspen grove (wooded bluffs interspersed with open grasslands) and mixed-wood trembling aspen (*Populus tremuloides* L.), balsam poplar (*Populus balsamifera* L.), white spruce (*Picea glauca* L.), black spruce (*Picea miriana* L.), and willow (*Salix* spp. L.) sections of the boreal forest (Department of Energy, Mines and Resources 1974). Annual average rainfall is 430 mm with 330 mm falling during the growing season (April to September). Annual snow accumulations of 40 cm are common but are reduced due to recurring chinook winds. Mean January,

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July, and annual temperatures at Dawson Creek, British Columbia are -15, 15, and 1 C, respectively, whereas daily temperatures of 32 (August) and -44 C (January) are extremes.

### Vegetation and Phenology

The study pasture was 5.4 ha in size, was fenced for bison, and had a southern aspect. It was established over 10 years earlier to introduced grasses and forbs, had not been fertilized for 5 years, yet remained productive. Grasses predominated and included smooth brome (*Bromus inermis* Leyss.), timothy (*Phleum pratense* L.), quackgrass (*Elytrigia repens* (L.) Nerski), and Kentucky bluegrass (*Poa pratensis* L.). Predominant cultivated forbs were alfalfa (*Medicago sativa* L.) and red clover (*Trifolium pratense* L.). Dandelion (*Taraxacum officinale* Weber.) was the predominate weedy forb. Although, forages began growth in late April, they were unable to sustain grazing until late May. Dandelions emerged in mid-May and were the most visible dicot in early June. Inflorescence of grasses appeared by mid-June and alfalfa was in full bloom by 1 July. First frost occurred in mid-September and grasses senesced by late September.

### Study Animals

Three male and 3 female bison yearlings were selected from a local commercial herd and transported to the study location in late May each year. Animals were selected from the 1993 calf crop for Year 1 trials (June 1994 to March 1995) and from the 1994 calf crop for Year 2 (June 1995 to December 1995). Selected bison ( $228 \pm 17$  kg Year 1;  $213 \pm 15$  kg Year 2) were representative of commercial bison ( $209 \pm 1$  kg; Rutley et al. 1997). Colored ear tags were attached in both ears prior to release into study pasture. Study animals were used in conjunction with another experiment (Rutley and Hudson 2000).

### Activity Budgets

Bison were observed for activity during 7 trial periods conducted at each equinox and solstice between June 1994 and December 1995. The 7 trial periods included June 1994, September 1994, December 1994, March 1995, June 1995, September 1995, and December 1995. Two consecutive 24-hour observation sessions began 6 days (Day-6) prior to the handling of the study animals (designated as Day 0). Three days after the study animals were handled, and in conjunction

with the collection of fecal samples, a subsequent 24-hour observation session occurred (Day 3). Disturbance attributed to the presence of the observers was considered minimal. Full moon corresponded with at least a portion of the first 5 trial periods.

Animals were observed from a truck with binoculars. Activities of individual animals were recorded at 5-minute intervals using the instantaneous scan method (Altmann 1974). Activity categories were: 1) foraging-actively engaged, 2) foraging-moderately engaged, 3) foraging-consuming hay, 4) ruminating, 5) resting-standing, 6) resting-lying (bedding), 7) resting-sleep (laying flat out), 8) minor-water, 9) minor-walking, 10) minor-play, after Gates and Hudson (1983). Bison did not have access to browse. Interacting with other bison, grooming and 'milling' were included in the minor activity category. Location within the field by grid and weather were simultaneously recorded.

The analysis was based on 38,880 individual records, recorded at 5-minute intervals, obtained during 6,048 scans within twenty-one, 24-hour observation sessions. Because it was not always possible to identify individuals during night hours, only the number of animals participating in an activity were recorded and used for analyses. To accommodate occasional unequal group sizes and different starting times, the following method of summing was used. The total number of animals observed and the number of animals participating in a designated activity during each 5-minute interval was recorded. The number of animals participating in each category for each 5-minute interval over the next 24 hours was summed to become the category 24-hour total (CT24). The CT24 for each category was then expressed as a ratio of the total number of possible animal observations (CT24%). The CT24% data from the two, 24-hour observation sessions at Day -6, combined with the Day 3 observation session CT24% data, became the data set for the trial period. For the final analyses of activity budgets, the subcategories within foraging, resting and minor activity were collapsed (Gates and Hudson 1983).

Length of foraging bout was calculated as the interval between the time when the majority (> 50%) of the group began foraging until the majority stopped foraging. Bedding bouts were defined as the interval between when the majority of the herd was laying down until the majority was standing up and moving away from the bedding site. Time foraging or bedded was

calculated as the sum of 5-minute intervals associated with that activity.

### Forage Biomass and Quality

To estimate available forage within the study pasture (sward), ten, 0.5-m<sup>2</sup> quadrats were assigned in a completely random design in Year 1 and a stratified random design in Year 2. In Year 2, the study pasture was divided, by grid, into 10 equal areas. A location within the grid was selected at random and the corresponding site within the field was staked (station). In conjunction with each trial period, a site immediately adjacent to the station was sampled in a manner that prevented re-sampling.

Bison were tracked during each trial period to determine if they grazed areas within the sward that were different from the sward in general. Once defoliation was confirmed, bison were gently disturbed and the grazed area flagged (grazed patch). Ten sites were identified during each trial period. Within each grazed patch, the site of defoliation was identified. Adjacent forage that was similar to the defoliation site, yet had escaped immediate grazing, was sampled (feeding station). The composition of consumed forage was determined from 20 emulated bites collected from each feeding station (Hudson and Frank 1987).

Plant height for both the sward and grazed patches was estimated as the average of 12 measures of plant height, selected at random within a 1/12 area by grid within the 0.5-m<sup>2</sup> quadrat. An ocular estimate, taken from 1.2 m above the quadrat, was used to estimate the percentage of bare ground:grasses:weedy forbs:cultivated forbs:litter:feces for each sward site and grazed patch. Both sward sites and grazed patches were harvested with hand shears and hand raked to simulate close grazing. Harvested forage was separated as grasses, forbs and litter, dried at 60 C, and stored until forwarded for composition analyses for crude protein (CP), calcium (Ca), phosphorus (P), potassium (K), magnesium (Mg), sodium (Na), acid detergent fibre (ADF), digestible energy (DE), and acid detergent lignin (ADL) (Norwest Labs, Lethbridge, AB).

Growing conditions for 1994 and 1995 were typical for the Peace Country. Because the stocking rate within the trial pasture was so low, following the June 1994 trial the study animals were removed to an adjacent pasture and 22, two-year-old bison bulls were grazed for 12 days to emulate moderately intense grazing. Trial bison were not returned until 21 days

before trial 2 (September 1995). In Year 2, no additional grazing occurred and the study animals remained within the pasture for the duration of the year. During the growing season, forage biomass within the sward ranged from 288 g m<sup>-2</sup> to 196 g m<sup>-2</sup> (Table 1).

**Table 1. Biomass within sward sites and grazed patches.**

Trial Period	Sward site (g m <sup>-2</sup> )	Grazed patch (g m <sup>-2</sup> )
Jun. 1994	275	263
Sept. 1994	288	311
Dec. 1994	253	na
Mar. 1995 <sup>1</sup>	8	16
Jun. 1995	281	297
Sept. 1995	196	231

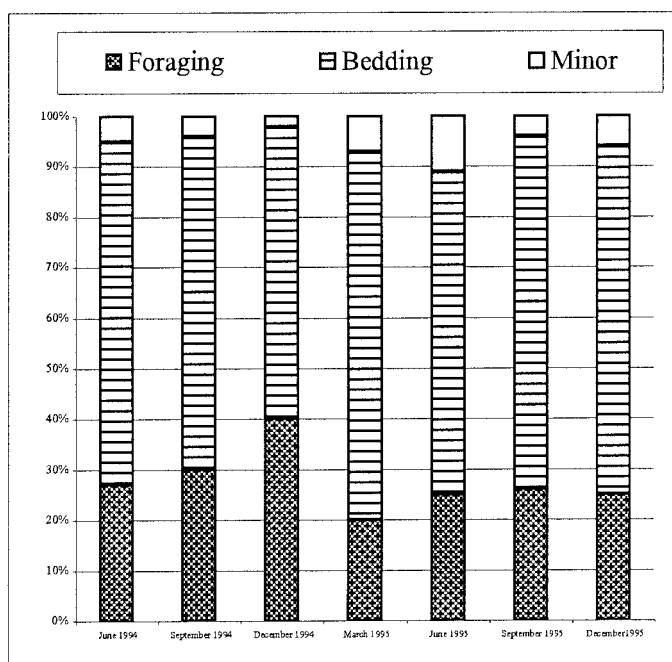
<sup>1</sup>Only forage above the snowpack was considered available.

In March 1995 and December 1995 bison did not graze due to severe icing of pasture and heavy snow cover, respectively. As they did not venture far from the plowed roadway required for vehicle access, and in the interests of their welfare, supplemental hay was provided (supplementation; March 1995, 9.9% CP mixed grass/legume hay; December 1995, 8.3% CP oat hay). In March 1995, after a series of snow, chinook and re-freezing cycles, available forage was restricted to 8 g m<sup>-2</sup> within the sward. When bison attempted to graze in March 1995, they sought out sites where forage was above the snowline. However, only a very limited amount of forage was available (16 g m<sup>-2</sup>).

### Statistical Analyses

Gender was not evaluated as a source of variation. A one-way analysis of variance (ANOVA, MS Excel ver 5.0) tested seasonal differences in foraging, resting and minor activity, and plant height for each trial period.

Seasonal differences in the activity budget, foraging and bedding bouts, foraging and bedding bout length, and total foraging and bedding time were determined using the PROC MIXED procedure (SAS 1996). Three season-feed groups were created. The summer grazing group consisted of the June 1994, September 1994, June 1995 and September 1995 trials. The December 1994 trial was the winter grazing group. The March 1995 and December 1995 trial periods were included in the supplementation group. Season-feed group was included in the model as a fixed effect. Trial within season-feed group (error term) was included as a ran-



**Fig. 1. Percentages of the 24 hour activity budget for yearling bison during indicated trial period.**

dom effect. Tukey's test was used for multiple comparisons.

As the dependent variables associated with quadrat structure and forage composition were correlated with each other, analyses were conducted using GLM-MANOVA (SAS 1996). Univariate ANOVA was reported for individual dependant variables. Due to the limited number of independent observations, multivariate analyses were performed on only crude protein and acid detergent fiber in the PROC GLM-MANOVA procedure (SAS 1996).

Mean composition of seasonal forage within feeding stations, grazed patches and sward sites were determined using the PROC MEANS procedure (SAS 1996). Due to the limited number of independent observations, multivariate analyses were performed including only crude protein and acid detergent fiber in the PROC

GLM-MANOVA procedure (SAS 1996). This procedure was repeated including crude protein and acid detergent lignin in the model.

All differences discussed in the Results and Discussion were statistically significant at the 5% level of probability.

## Results

### Seasonal Activity Budgets

Resting and foraging were the most time consuming activities of yearling bison (Fig. 1). Time foraging was always less than time resting and ranged from 40 ± 2% while grazing in December 1994 to 20 ± 2% during supplementation in March 1995. Bison allocated more time to foraging during winter grazing (39.6%) than for summer grazing (26.6%) or during supplementation (22.0%) (Table 2). Time resting

**Table 2. Percentages (± SE) of the 24 hour activity budget for yearling bison by season-feed group<sup>1</sup>.**

Season-feed group	Activity		
	Foraging	Resting	Minor
	----- (%) -----		
Summer grazing <sup>2</sup>	26.6 <sup>b</sup> ± 1.2	67.2 <sup>ab</sup> ± 1.3	6.2 <sup>a</sup> ± 1.5
Winter grazing <sup>3</sup>	39.6 <sup>a</sup> ± 2.4	58.5 <sup>b</sup> ± 2.6	1.8 <sup>a</sup> ± 3.1
Supplementation <sup>4</sup>	22.0 <sup>b</sup> ± 1.7	71.1 <sup>a</sup> ± 1.9	6.9 <sup>a</sup> ± 2.2

<sup>1</sup>Means (± SE) within columns with different letters are significantly different at P < 0.05.

<sup>2</sup>Summer grazing = Jun. 1994, Sept. 1994, Jun. 1995, and Sept. 1995 grazing periods.

<sup>3</sup>Winter grazing = Dec. 1994 grazing period.

<sup>4</sup>Supplementation = Mar. 1995 and Dec. 1995 grazing periods.

**Table 3. Foraging and bedding activities of yearling bison summarized by season-feed group<sup>1</sup>.**

Season-feed group	Foraging			Bedding		
	Number of foraging bouts	Foraging bout length	Total foraging time	Number of bedding bouts	Bedding bout length	Total bedding time
	(bouts day <sup>-1</sup> )	(minutes)	(min. day <sup>-1</sup> )	(bouts day <sup>-1</sup> )	(minutes)	(min day <sup>-1</sup> )
Summer grazing <sup>2</sup>	8.0 <sup>a</sup> ± 1.0	69 <sup>a</sup> ± 9	470 <sup>b</sup> ± 32	6.6 <sup>a</sup> ± 0.5	121 <sup>b</sup> ± 13	793 <sup>a</sup> ± 31
Winter grazing <sup>3</sup>	6.7 <sup>a</sup> ± 2.0	123 <sup>a</sup> ± 17	763 <sup>a</sup> ± 62	3.0 <sup>a</sup> ± 1.0	276 <sup>a</sup> ± 26	698 <sup>a</sup> ± 61
Supplementation <sup>4</sup>	5.5 <sup>a</sup> ± 1.4	77 <sup>a</sup> ± 12	418 <sup>b</sup> ± 44	5.8 <sup>a</sup> ± 0.8	142 <sup>b</sup> ± 18	795 <sup>a</sup> ± 43

<sup>1</sup>Means (± SE) within columns with different letters are significantly different at  $P < 0.05$ .

<sup>2</sup>Summer grazing = Jun. 1994, Sept. 1994, Jun. 1995, and Sept. 1995

<sup>3</sup>Winter Grazing = Dec. 1994.

<sup>4</sup>Supplementation = Mar. 1995 and Dec. 1995.

during winter grazing (58.5%) was shorter than during supplementation (71.1%). Time resting during summer grazing was not different from time resting during supplementation. Minor activities ranged from 2 ± 1% of the activity budget during

December 1994 to 12 ± 1% during June 1995 (Fig. 1), however seasonal differences were not significant (Table 2).

During winter grazing, bison foraged 763 min day<sup>-1</sup> compared with 470 and 418 min day<sup>-1</sup> during summer grazing and supplementation, respectively (Table 3).

Bedding bouts were longest during winter grazing (276 min day<sup>-1</sup>) compared with 121 and 142 min day<sup>-1</sup> for summer grazing and supplementation, respectively (Table 3).

### Daily Activity

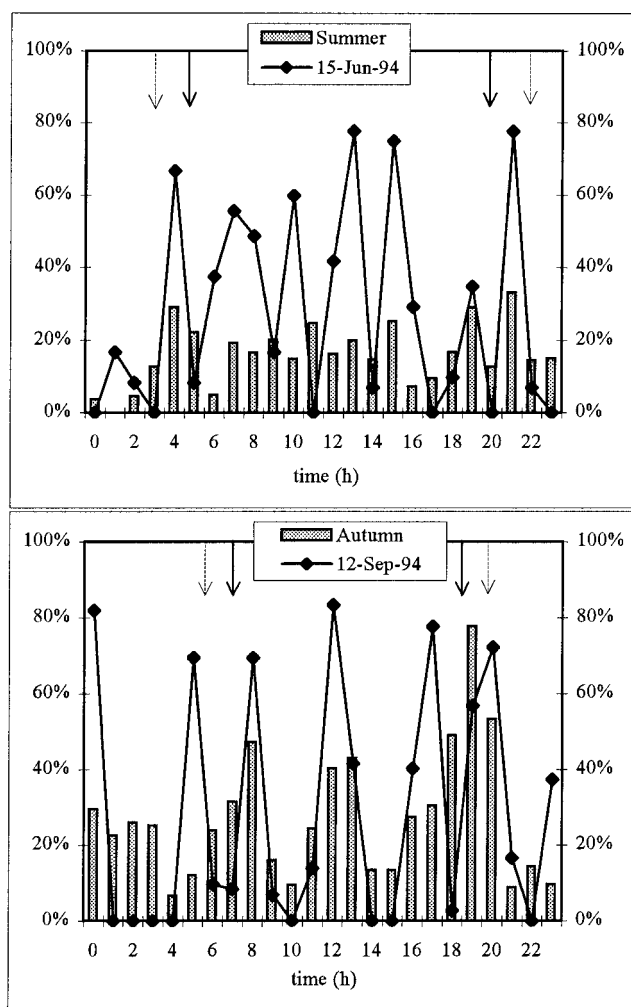
Bison alternated foraging and resting bouts over the 24-hour activity cycle. Phasic activity was poorly expressed in the June grazing period due to the increased number of cycles (Fig. 2). In June, bison tended to bed immediately following a foraging bout with rumination occurring half the time. Bedding was soon followed with another foraging period. Near sundown bison tended to become quite active and milled for some time prior to an intense foraging bout as darkness fell.

During September grazing, a prolonged foraging bout began prior to sunrise (Fig. 2). A mid-morning rest, mid-day foraging period, and late afternoon rest followed, with foraging activity increasing in frequency in late afternoon, peaking between sundown and dusk. Following dusk, bison tended to bed for a few hours, then graze during the early morning hours before bedding until near dawn.

Winter grazing patterns were similar to September patterns except that there were only 2 main grazing bouts during the day, following sunrise and prior to sunset (Fig. 3). Midnight grazing activity occurred regularly and rivaled early morning grazing. Minor activities were minimal during this period.

Severe snow conditions limited grazing in March 1995 and December 1995. An extended bedding period prior to sunrise, more limited nighttime foraging, and less defined foraging-resting cycles during the day (supplementation, Fig. 3), resulted. Activity declined sharply following sundown.

In comparison to winter grazing (December 1994), supplemented bison (December 1995) exhibited a foraging-feeding pattern with 1) less pronounced foraging peaks following sunrise and near



**Fig. 2. Averaged seasonal daily foraging patterns (solid bars) and the foraging pattern for a single day (line) expressed as a percentage of time bison were active within each 1-hour interval. Top: summer grazing. Bottom: autumn grazing. Sunrise-sunset indicated by solid arrow. Daylight-dark indicated by broken arrow.**

**Table 4. Quadrat composition within grazed patches and sward sites—June and September trial periods data pooled<sup>1</sup>.**

Type	Quadrat Composition						
	Plant height	Bare ground	Graminoids	Weedy forbs	Cultivated forbs	Litter	Feces
	(cm)	(%)	(%)	(%)	(%)	(%)	(%)
Grazed patches	24.7 <sup>a</sup> ± 1.9	3.8 <sup>a</sup> ± 2.2	49.8 <sup>a</sup> ± 4.2	14.6 <sup>a</sup> ± 2.4	23.4 <sup>a</sup> ± 3.4	7.6 <sup>b</sup> ± 1.3	0.8 <sup>a</sup> ± 0.4
Sward sites	26.1 <sup>a</sup> ± 1.7	5.9 <sup>a</sup> ± 2.2	47.0 <sup>a</sup> ± 3.3	13.6 <sup>a</sup> ± 2.3	18.5 <sup>a</sup> ± 3.0	14.5 <sup>a</sup> ± 2.5	0.5 <sup>a</sup> ± 0.3

<sup>1</sup>Plant height was analyzed as a one-way ANOVA quadrat composition was analyzed using the GLM-Multivariate procedure. Means (± SE) within columns with different letters are significantly different at  $P < 0.05$ .

sunset, 2) more pronounced resting activity following sundown, and 3) more frequent nighttime foraging cycles during supplementation (Fig. 4).

### Sward Structure, Forage Quality and Diet Selection

There was no difference in plant height,

between grazed patches and sward sites, however, bison selected and grazed patches that were of equivalent plant height but were lower in litter (7.6 vs 14.5%) (Table 4).

Chemical composition of forage within feeding stations (emulated bites) was higher in CP (12.9 vs 10.0%), and predicted DE (2.70 vs 2.17 Mcal kg<sup>-1</sup>), but lower in

ADF (31.9 vs 38.8%) and ADL (4.8 vs 6.8%) than forage within grazed patches (Table 5). Sward sites contained 8.7% CP, 2.21 Mcal kg<sup>-1</sup> DE, 39.0% ADF, and 6.1% ADL. Bison consistently grazed both graminoids and forbs within the same feeding station, however, they would frequently graze exclusively on forbs (primarily *Medicago* spp.) or graminoids.

Chemical composition of consumed forage varied with grazing period. Crude protein was lower in March (6.6 ± 4.4%) than in June (15.9 ± 3.1%) or September (11 ± 3.1%). Acid detergent fiber was lower in June (27.2 ± 2.9%) and September (29.8 ± 2.9%) than March (44.7 ± 4.0%). Acid detergent lignin was lower in June (3.5 ± 0.2%) and September (4.4 ± 0.2%) than March (8.3 ± 0.3%).

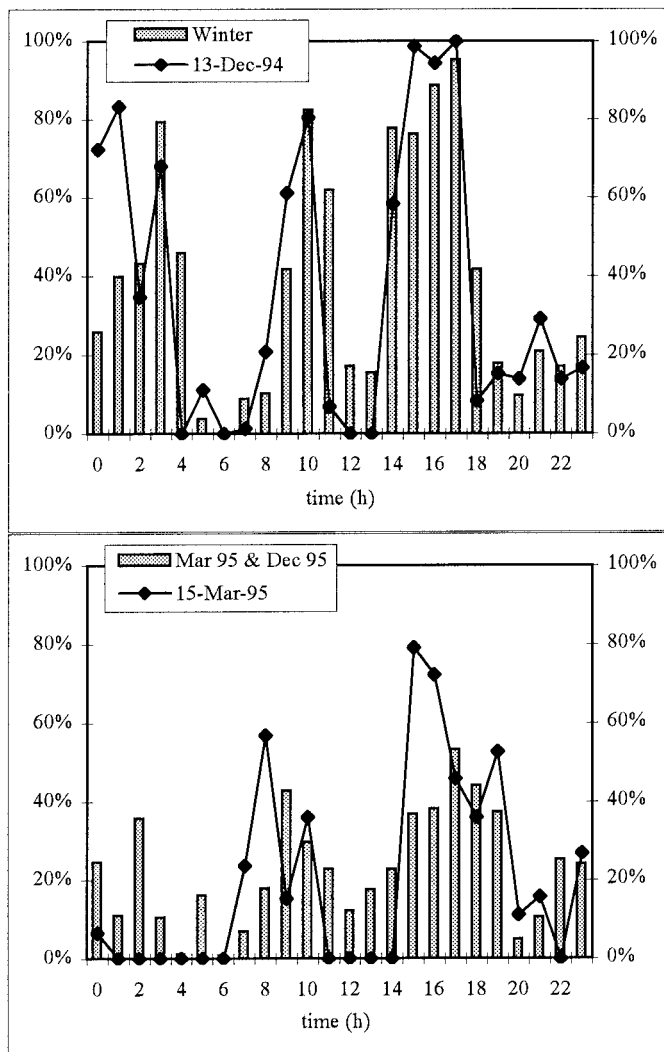
Yearling bison obtained all their forage while grazing during December 1994 when snow depth was between 39 and 23 cm (Table 6). By the beginning of the March 1995 trial, a series of chinooks and refreezing created an impenetrable 28 ± 4 cm snow pack. Therefore, bison consumed supplemented hay. After a chinook, 21 March, 1995, significantly reduced the snow pack to 17 cm, bison resumed grazing on a limited basis. They grazed patches that had significantly less snow cover than the sward and they grazed patches that contained significantly greater accessible forage biomass than was contained within sward sites.

### Discussion

Bison adjusted grazing behavior in relation to their seasonal nutritional requirements and pasture conditions. This was evident both in activity budgets and selectivity in foraging.

### Activity Patterns

Activity patterns for free-grazing bison were distinctly polyphasic in most seasons, a pattern common among wild and domestic ruminants (Eriksson et al. 1981). Activity patterns were generally consistent day to day, however they would shift an



**Fig. 3. Averaged seasonal daily foraging patterns (solid bars) and the foraging pattern of a single day (line) expressed as a percentage of time bison were active within each 1-hour interval. Top: winter grazing. Bottom: supplemented. Winter sunrise 0930 sunset 1550. Winter daylight 0820 dark 1700.**



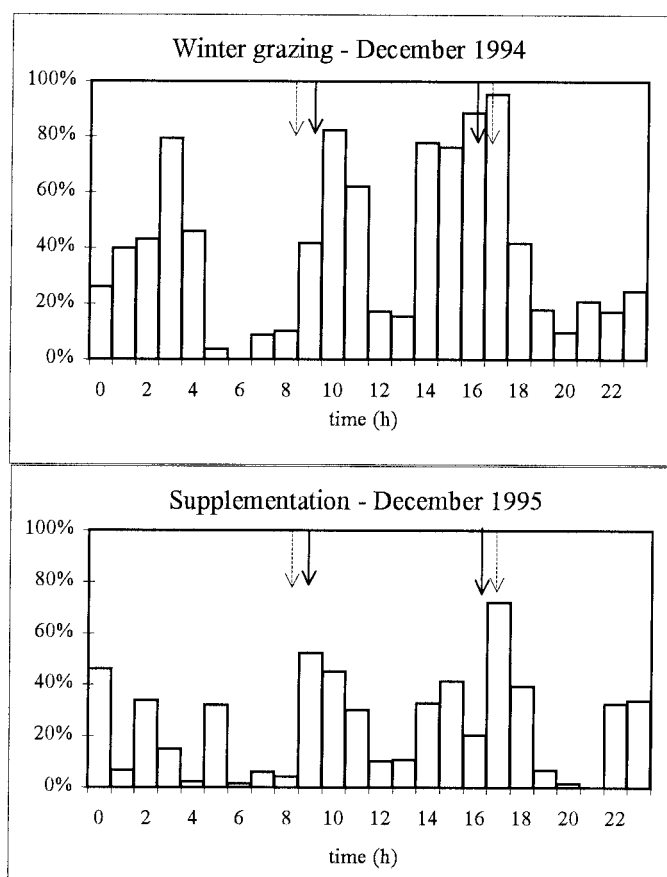


Fig. 4. Daily activity pattern of yearling bison during winter grazing (top) and during supplementation (bottom). Sunrise-sunset indicated by solid arrows. Daylight-dark indicated by broken arrows.

hour or 2 causing bedding activities to be averaged with foraging activity. While the number of foraging and bedding cycles is adequately displayed the amplitude is more accurately reflected by the single day pattern.

The number of summer foraging bouts in the current study ( $8.0 \pm 1.0$  bouts day<sup>-1</sup>) are intermediate to bison on northern mixed prairie ( $10.5 \pm 0.7$  feeding bouts day<sup>-1</sup>; Plumb and Dodd 1993) and bison in boreal mixed-wood forest (4–5 feeding bouts day<sup>-1</sup>; Hudson and Frank 1987). Winter grazing activity patterns in the current study were similar to autumn activity patterns observed by Hudson and Frank (1987).

Seasonal changes in foraging activity for bison appear related to more than just biomass as sward biomass varied little throughout the year, but foraging bout length and total foraging time increased from summer to winter. The role of snow cover and photoperiod as it affects annual requirements remain to be determined for bison (Rutley 1998).

As expected, foraging time increased

and resting time decreased from summer to winter. Unexpectedly, time in minor activities remained constant. Current data do not support the hypotheses that foraging bouts would be longer and less frequent in winter versus summer.

Provision of supplemental feed altered foraging behavior. Foraging and resting cycles of bison (this study) and reindeer

(Eriksson et al. 1981) became less distinct. Bison allocated less time to grazing while supplemented which is consistent with cattle (Krysl and Hess 1993). For bison, time allocated to minor activities was similar to time allocated during summer grazing, even though daytime temperatures ranged between  $-12$  and  $-22^{\circ}\text{C}$  during supplementation. DelGiudice et al. (1994) found supplemented bison to exhibit more favorable urea nitrogen to creatinine (U:C) and potassium to creatinine (K:C) ratios than free-grazing Yellowstone bison indicative of less nutritional stress.

## Foraging Activity

Time allocated to summer grazing (470 min day<sup>-1</sup>, 45% of daylight hours) was considerably greater than that of bison on the National Bison Range in Montana (178 min day<sup>-1</sup>, daylight hours, Belovsky and Slade 1986), but less than bison grazing boreal pastures in central Alberta (8.7 hours day<sup>-1</sup>, Hudson and Frank 1987). Despite differences in latitude, ecotype and nighttime foraging activity, time foraging (expressed as a percentage of daylight; 45% in current study) is equivalent to the 44% reported by Plumb and Dodd (1993) for bison grazing northern mixed prairie in South Dakota.

## Winter Grazing

In the current study, yearling bison grazed when snow depth was 39 cm (December 1994) but not when snow depth was 47 cm (December 1995). Under the deeper snow conditions, yearling bison consistently utilized the plowed roadway for “relatively easy and energy-efficient travel” as do Yellowstone bison (Meagher 1989). Reynolds and Peden (1987) reported little differences in feeding and non-feeding sites for snow depth and density; however, in March 1995 following a chi-

Table 5. Chemical composition of forage within feeding station (emulated bites), grazed patches and sward sites for yearling bison grazing seasonal pasture.

	Feeding station	Grazed patches	Sward sites	SEM
Crude Protein (%) <sup>1,2</sup>	12.9	10.0	8.7	0.8
Calcium (%)	0.65	0.67	0.54	0.05
Phosphorus (%)	0.22	0.20	0.19	0.01
Potassium (%)	1.8	1.5	1.3	0.1
Magnesium (%)	0.26	0.27	0.26	0.02
Sodium (%)	0.03	0.03	0.03	0.01
Acid Detergent Fibre (%) <sup>1</sup>	31.9	38.8	39.0	0.9
Digestible Energy (Mcal kg <sup>-1</sup> )	2.70	2.17	2.21	0.09
Acid Detergent Lignin (%) <sup>2</sup>	4.8	6.8	6.1	0.3

<sup>1</sup>Crude protein and acid detergent fibre significantly different at  $P < 0.05$  under GLM-Multivariate analysis.

<sup>2</sup>Crude protein and acid detergent lignin significantly different at  $P < 0.05$  under GLM-Multivariate analysis.

**Table 6. Influence of snow depth and condition on grazing behaviour of yearling bison.**

Date	Site <sup>1</sup>	Depth	Snow Condition <sup>2</sup>	Behavior <sup>3</sup>
12 & 13 Dec. 1994	Snow station	39 ± 1.3	Powder	Graze
21 Dec. 1994	Snow station	22 ± 0.4	Powder	Graze
22 Dec. 1994	Sward Site	23 ± 0.7	Powder	Graze
23 Dec. 1994	Grazed Patch	23 ± 1.7	Powder	Graze
14 & 15 Mar. 1995	Snow Station	28 ± 3.8	Hard Pack	No Graze
20 & 21 Mar. 1995	Snow Station	26 ± 0.8	New over pack	No Graze
22 Mar. 1995	Snow Station	17 ± 1.3	New over pack	No Graze
23 Mar. 1995	Sward Site	23 ± 2.4	New over pack	No Graze
24 Mar. 1995	Grazed Patch	13 ± 0.8	New over pack	Supple. Graze <sup>4</sup>
Dec. 1995	Snow station	47 ± 0.2	Powder	No Graze

<sup>1</sup>Combined measurements from a snow station and within sward sites and grazed patches.

<sup>2</sup>Powder = crystallized powder snow easily moved by grazing bison. Hard Pack = packed snow that yearling bison were unable to penetrate. New over pack = fresh powder over existing Hard Pack.

<sup>3</sup>Graze = forage intake exclusively from grazing; No Graze = refused to graze - forage intake from supplemented hay.

<sup>4</sup>Bison voluntarily grazed exposed forage, therefore forage intake 24 Mar., 1995 was from both grazing and supplemented hay.

nook, bison grazed patches with a more limited snow cover (13 cm) than the sward (23 cm). Deeper snow (43 cm) associated with higher elevations "had a more compromising effect on the nutritional status" of Yellowstone bison than the lower snow depths (8 cm) of the lower ranges (DelGiudice et al. 1994).

Condition of snow pack affected grazing behavior (Reynolds and Peden 1987, Meagher 1989). Telfer and Kelsall (1984) rated bison as having little adaptive ability for feeding above the snow. McHugh (1953) observed that bison do not paw to expose snow covered forage. Consistently, yearling bison had difficulty foraging when the sward was covered with a hard snow pack (March 1995) because they rarely clipped off exposed forage and pawed infrequently.

Group size and experience contribute to bison's ability to winter graze. In December 1995, 42, two-year old bison in an adjacent field, and herds within the Peace Country, continued to graze in the presence of 47 cm of snow. Prior experience and acquired knowledge enable mixed bison herds in Yellowstone National Park to forage regularly in snows 60 cm deep (Meagher 1989).

### Grazing Behavior and Diet Selection

Although bison are roughage grazers adapted to low quality forage, they are selective when conditions allow (Peden et al. 1974, Belovsky 1986, Plumb and Dodd 1993, Coppedge et al. 1998). Bison (this study) consistently consumed the upper portion of the plant. This enabled them to consume a diet that was higher in CP and DE, and lower in ADF and ADL, compared to forage available to them from within grazed patches and the sward.

In cattle and sheep, rumination and eating time are shorter when neutral detergent fibre (NDF) of consumed forage is lower (Welsh and Smith 1969, 1970). In elk and mule deer, mean retention time increases as lignin content increases; mean cell wall thickness increases linearly as NDF increases; and mean cell wall thickness is related to mean particle breakdown time (Spalinger et al. 1986). Therefore, selection of a diet low in fiber and lignin would ultimately decrease rumination, handling and mean retention time, thus enabling bison to consume greater quantities of high quality forage. Although bison are known for their ability to utilize poor quality forages, it is clear that when high quality forage is available, they will actively select it. In addition, when forage within the sward is of poorer quality, as it is in winter, bison continue to be selective by continuing to graze the upper portions of the plant.

### Scanning Frequency and 24-hour Observation Scans

Boertje (1985) hypothesized that one could base 24-hour activity patterns as an extrapolation of a single active-rest cycle, thus reducing the need for nighttime observations. Collins and Smith (1989) observed free-grazing reindeer (24-hour observations) on the Seward Peninsula, Alaska and observed that daytime-only observations overestimated feeding by 37%. Plumb and Dodd (1993) discontinued nighttime observations of bison because they observed very little grazing activity during preliminary observations. Current observations with free-grazing bison would, however, support the conclusion of Collins and Smith (1989) that "behavior budgets based on daytime observations [only] may be significantly

biased and of questionable value".

Frequency of activity scans was evaluated during this study. Compared to 5-minute scans (benchmark), scans at 10 and 15-minute intervals provided records of foraging activity that varied from the bench mark by -55 to 35% and -10 to 30%, respectively. Minor activities occurred infrequently and in one, 2-hour segment, 10-minute scan overestimated minor activity by 200% and 15-minute scans missed the activity completely, with a concurrent 30% overestimation of grazing activity. Therefore, 5-minute activity scans are considered necessary to adequately categorize activity in small group free-grazing bison.

## Conclusions and Management Implications

Bison altered their activity budget from summer to winter by increasing foraging time and decreasing bedding time. Total time foraging and bedding bout length were greatest during winter grazing. Activity budget is best described as polyphasic, alternating between bouts of foraging and resting activity. Activity was distinctly triphasic during winter grazing bouts when bison displayed 2 main daytime foraging bouts and significant nighttime foraging activity. Phasic activity was poorly expressed during June and September grazing periods primarily due to the increase in the number of foraging bouts.

Seasonal changes in foraging activity for bison appear more related to forage quality than biomass. Bison graze selectively throughout the year by consistently consuming the upper portion of the plant which was lower in acid detergent fiber and lignin, thus higher in crude protein and digestible energy than that available from within grazed patches and the sward.

Yearling bison are able to winter graze under adequate sward cover and in acceptable snow conditions. Under more severe snow conditions, yearling bison maintained separate from the main herd, require supplementation. Provision of supplemental feed, however, alters foraging behavior, therefore managers must select a winter feeding program that is consistent with their overall management goals.

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# Breeding bird responses to juniper woodland expansion

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## Abstract

In recent times, pinyon (*Pinus* spp.)-juniper (*Juniperus* spp.) woodlands have expanded into large portions of the Southwest historically occupied by grassland vegetation. From 1997–1998, we studied responses of breeding birds to one-seed juniper (*J. monosperma*) woodland expansion at 2 grassland study areas in northern Arizona. We sampled breeding birds in 3 successional stages along a grassland-woodland gradient: un-invaded grassland, grassland undergoing early stages of juniper establishment, and developing woodland. Species composition varied greatly among successional stages and was most different between end-points of the gradient. Ground-nesting grassland species predominated in uninvaded grassland but declined dramatically as tree density increased. Tree- and cavity-nesting species increased with tree density and were most abundant in developing woodland. Restoration of juniper-invaded grasslands will benefit grassland-obligate birds and other wildlife.

**Key Words:** *Juniperus monosperma*, grassland, pinyon-juniper, Arizona, southwestern U.S., avian communities, succession

Since European settlement, pinyon (*Pinus* spp.)-juniper (*Juniperus* spp.) woodlands have expanded into large portions of the southwestern U.S. historically occupied by grassland (Miller 1921, Leopold 1951, Johnsen 1962, Rogers et al. 1984, Cinnamon 1988). Livestock grazing and fire suppression commonly are cited as causes of woodland expansion (Johnsen 1962, West 1984). Other factors linked to woodland expansion include climate change, long-term biogeographic patterns, and tree reestablishment following harvest by aboriginal Americans (Samuels and Betancourt 1982, Betancourt 1987, Jameson 1987).

The effects of juniper woodland expansion on wildlife have received little study and are not well understood. Because grassland birds are closely tied to habitat structure (Rotenberry and Wiens 1980, Wiens and Rotenberry 1981, Cody 1985), invasion of woody vegetation has serious implications for grassland avifauna (Knopf 1994). A better understanding of wildlife responses to woodland expansion will help resource managers design effective

## Resumen

En tiempos recientes, bosques de piñón (*Pinus* spp.) y enebro (*Juniperus* spp.) han invadido porciones grandes del Suroeste históricamente ocupadas por vegetación de prado. De 1997–1998, estudiamos el efecto de la expansión de bosque de enebro (*J. monosperma*) sobre una comunidad reproductiva de aves en 2 áreas de estudio en el norte de Arizona. Examinamos la comunidad de aves en 3 etapas de sucesión a lo largo de una gradiente de pradera-bosque: pradera no-invasada, pradera sujeta a etapas iniciales de establecimiento por enebro, y bosque en desarrollo. La composición de especies varió bastante entre etapas de sucesión pero la mayor variación ocurrió entre extremos del gradiente. Especies que anidan en el suelo de praderas predominaron en praderas no-invasadas, pero disminuyeron dramáticamente al aumentar la densidad de árboles. Especies que anidan en árboles y en cavidades aumentaron con mayor densidad de árboles y ocurrieron en mayor abundancia en bosque en desarrollo. La restauración de praderas invadidas por enebros será de beneficio para las aves, y otra vida silvestre, que dependen de praderas.

tive treatments and restoration programs for grassland and woodland habitats (Loftin et al. 1995).

Our objective in this study was to quantify effects of juniper woodland expansion on breeding bird communities in cold-temperate grasslands of northern Arizona. We predicted that development of woodland vegetation in grassland habitats would alter the breeding avifauna, with effects at both the community and species levels.

## Materials and Methods

### Study Areas

The study was conducted at 2 areas in northern Arizona, representing the transition zone between Plains and Great Basin grasslands (Brown 1982). Grasslands at both areas were undergoing succession to one-seed juniper (*Juniperus monosperma* (Engelm.) Sarg.) woodland and had not received treatments intended to control woody vegetation (e.g., herbicide application, prescribed fire, tree cutting, or mechanical control).

The Chevelon study area is located 38 km southeast of Winslow, Arizona (Lat 35° 40' N, Long 110° 45' W). Elevations range from 1,834–1,901 m, with annual precipitation averaging 20.4 cm. Soils are derived from limestone and sandstone parent

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materials. Dominant grass species include blue grama (*Bouteloua gracilis* (H.B.K.) Lag.), ring muhly (*Muhlenbergia torreyana* (Kunth) Hitchc.), and bottlebrush squirreltail (*Sitanion hystrix* (Nutt.) J.G. Smith). Scattered shrubs were present, primarily four-wing saltbush (*Atriplex canescens* (Pursh) Nutt.), Bigelow sagebrush (*Artemisia bigelovii* Gray), and Fremont barberry (*Berberis fremontii* Torr.). Colorado pinyon (*Pinus edulis* Engelm.) was present on widely scattered microsites with shallow, rocky soils. The area was grazed each year by cattle and horses, primarily during winter and spring.

The Wupatki study area is located in the north-central portion of Wupatki National Monument, 48 km northeast of Flagstaff, Ariz. (Lat 35° 35' N, Long 111° 28' W). Elevations range from 1,591–1,645 m, with annual precipitation averaging 20.0 cm. Soils are derived from limestone and sandstone parent materials, overlain by a layer of volcanic cinders. Dominant grass species include needle-and-thread (*Stipa comata* Trin. and Rupr.), blue grama, galleta (*Hilaria jamesii* (Torr.) Benth.), black grama (*B. eriopoda* Torr.), and alkali sacaton (*Sporobolus airoides* Torr.). Shrubs were relatively sparse, consisting largely of rubber rabbitbrush (*Chrysothamnus nauseosus* (Pall.) Britton). Livestock have been excluded from Wupatki for ca. 20 years.

### Sampling Design

We used aerial photos and ground surveys to identify and map grassland-woodland successional stages present on both study areas. Because juniper reproduction tends to occur as discrete, episodic events (Arnold et al. 1964), we delineated successional stages based upon overall physiognomy of the existing plant community, i.e., grass cover, tree size, and tree density. To minimize effects of environmental heterogeneity, we only mapped uniform vegetation types that were >100 ha in size, avoiding transition zones between successional stages.

Three successional stages were present on the study areas: (1) un-invaded grassland without juniper; (2) grassland undergoing early stages of juniper establishment, with scattered small junipers; and (3) developing woodland with abundant larger trees (Table 1). At both study areas, we randomly selected 4 replicate stands within each successional stage for bird and habitat sampling.

### Bird Sampling

We used distance sampling (Buckland et al. 1993) to estimate breeding bird abun-

**Table 1. Density and height of one-seed juniper (*Juniperus monosperma*) along a grassland-juniper woodland successional gradient at 2 northern Arizona study areas, 1997–1998. Values are means  $\pm$  1 SE.**

Study area Successional stage	Tree density (trees ha <sup>-1</sup> )	Tree height (m)
<b>(Chevelon)</b>		
Uninvaded grassland	0	—
Early establishment	10.0 $\pm$ 2.5	2.0 $\pm$ 0.2
Developing woodland	92.3 $\pm$ 8.8	2.7 $\pm$ 0.1
<b>(Wupatki)</b>		
Uninvaded grassland	0	—
Early establishment	10.6 $\pm$ 2.9	2.3 $\pm$ 0.2
Developing woodland	41.9 $\pm$ 6.2	3.4 $\pm$ 0.1

dance. Within each stand, we randomly located a 1-km transect containing 5 sampling points spaced 250 m apart. Each point was sampled 3 times during June 1997 and June 1998, once by each of 3 observers. Count duration was 5-min per point. Sampling visits occurred 7–9 days apart, during a 2-hour period beginning at sunrise. Counts were not done during periods of rain or strong wind. Observers received extensive training in bird identification and distance estimation prior to field work (Kepler and Scott 1981). We collected distance measurements as grouped data (Buckland et al. 1993:110), where each bird detection was placed into 1 of 6 distance intervals (0–5 m, 6–10m, 11–25 m, 26–50 m, 51–125 m, and >125 m). Observers used laser rangefinders and marker flags placed at known distances to assist in accurate distance estimation.

### Habitat Sampling

Cover of herbaceous and shrub vegetation was measured on twenty, 50-m point-intercept transects, randomly located along each transect. Tree density and tree height were measured in a 4 X 50 m plot centered on the long axis of the intercept transect. Herbaceous vegetation was sampled each year. Trees and shrubs were sampled once during 1997.

### Data Analysis

We used program DISTANCE (Thomas et al. 1999) to estimate bird density. Analyses were done only for species with  $\geq$ 50 detections. Because sample sizes were small, we pooled all detections to fit a common detection function, then used this function to derive density estimates for individual transects within years (Buckland et al. 1993:74). Candidate models were evaluated using Akaike's Information Criterion (AIC),  $\chi^2$  goodness of fit statistics, and visual inspection of probability density functions fitted by DISTANCE.

We used Jaccard's index (*J*) (Ludwig and Reynolds 1988) to assess similarity in bird species composition among stands representing different stages of woodland expansion. We also tallied proportions of species that belonged to each of 4 nesting guilds (ground, shrub, tree, or tree cavity). Guild classifications were based upon Ehrlich et al. (1988) and observational data collected during this study.

Species richness was estimated using a jackknife estimator (Burnham and Overton 1978), as implemented in program COMDYN (Nichols et al. 1996). This estimator is an extension of mark-recapture theory and incorporates heterogeneity in species' detectability across multiple sampling events (Nichols et al. 1998).

We used Repeated Measures Analysis of Variance (Neter et al. 1990:1035) to test for overall differences in bird response variables among successional stages. If stage effects were significant ( $P \leq 0.05$ ), and stage X year interactions were not present ( $P \geq 0.05$ ), we used Scheffe's post-hoc test to compare mean values among individual stages (Zar 1984:196). Differences among stages were considered significant at  $P \leq 0.05$ . Data from the 2 study areas were analyzed separately, because of substantial edaphic differences affecting understory vegetation, woodland succession and potentially, breeding birds. Habitat characteristics among successional stages were summarized as means and associated standard errors; hypothesis tests on these data would have little value, as null hypotheses were known to be false *a-priori* (Johnson 1999).

## Results

### Habitat Characteristics

Habitat characteristics differed among successional stages at both sites. Habitat differences were most prevalent in the tree component, with one-seed juniper absent

**Table 2. Cover and height of grasses and shrubs along a grassland-juniper woodland successional gradient at 2 northern Arizona study areas, 1997–1998. Values are means  $\pm$  1 SE.**

Study area Successional stage	Grasses		Shrubs	
	Cover	Height	Cover	Height
	(%)	(cm)	(%)	(cm)
<b>(Chevelon)</b>				
Un-invaded grassland	28.8 $\pm$ 2.9	8.5 $\pm$ 0.4	5.2 $\pm$ 0.4	25.7 $\pm$ 1.5
Early establishment	29.5 $\pm$ 1.8	10.1 $\pm$ 0.3	3.0 $\pm$ 0.3	35.5 $\pm$ 1.1
Developing woodland	30.3 $\pm$ 1.1	7.6 $\pm$ 0.4	2.3 $\pm$ 0.3	49.3 $\pm$ 10.3
<b>(Wupatki)</b>				
Un-invaded grassland	57.1 $\pm$ 1.8	35.4 $\pm$ 1.2	0.3 $\pm$ 0.1	60.2 $\pm$ 6.5
Early establishment	54.4 $\pm$ 1.6	37.2 $\pm$ 0.6	1.8 $\pm$ 0.3	53.6 $\pm$ 1.9
Developing woodland	38.9 $\pm$ 2.0	25.8 $\pm$ 0.7	2.1 $\pm$ 0.5	44.5 $\pm$ 1.7

in un-invaded grassland, but increasingly abundant in early establishment and developing woodland conditions (Table 1). Tree density was highest in developing woodland, with mean values of 92 and 42 trees/ha at Chevelon and Wupatki, respectively. Tree size also increased along the grassland-woodland gradient. The largest trees were present in developing woodland, averaging 2.7 and 3.4 m in height at Chevelon and Wupatki, respectively. Fewer differences were apparent in the grass and shrub components. Grass cover and height were greater at Wupatki than at Chevelon, but values were similar among stages within sites (Table 2). At Chevelon, shrub cover decreased along the grassland-woodland gradient, but shrubs (primarily Fremont barberry) were much taller in the developing woodland stage. At Wupatki, shrub cover increased and shrub height decreased with woodland succession.

### Breeding Bird Community Attributes

A total of 22 bird species was detected, 21 at Chevelon and 17 at Wupatki (Table 3). Most species occurred in 1 or 2 of the 3 successional stages present at each area. Composition of the breeding avifauna changed dramatically with woodland expansion. Values of  $J$  ranged from 0.11–0.40 and 0.13–0.52 at Chevelon and Wupatki, respectively (Table 4). At both sites, endpoints of the successional gradient (un-invaded grassland versus developing woodland) had the fewest species in common. The greatest degree of overlap was found between un-invaded grassland and developing woodland at the Chevelon area, and between early establishment and developing woodland at Wupatki.

Species richness increased with woodland expansion, ranging from 4.4–19.5 and 3.0–10.5, at Chevelon and Wupatki, respectively (Fig. 1). Richness differed among stages at both sites (Chevelon:  $F_{2,9} = 493.79$ ,  $P < 0.0001$ ; Wupatki:  $F_{2,9} = 30.37$ ,  $P \leq 0.0001$ ), and was lowest in un-

invaded grassland and highest in developing woodland. Species richness was significantly different between un-invaded grassland and developing woodland at both sites. Species richness was not significantly different in un-invaded grassland and early establishment woodland at Chevelon, but did differ at the Wupatki area. Richness differed in early establishment and developing woodland at Chevelon but did not differ at Wupatki.

Bird community composition changed dramatically along the grassland-woodland gradient. The proportion of ground-nesting species differed among all stages at both sites (Chevelon:  $F_{2,9} = 43.1$ ,  $P \leq$

0.0001; Wupatki:  $F_{2,9} = 99.61$ ,  $P \leq 0.0001$ ). Ground-nesters predominated in un-invaded grassland, but decreased sharply with increasing tree density (Fig. 2). The proportion of tree-nesting species also differed among all stages at both sites (Chevelon:  $F_{2,9} = 60.27$ ,  $P \leq 0.0001$ ; Wupatki:  $F_{2,9} = 126.59$ ,  $P \leq 0.0001$ ). Tree-nesters represented the bulk of the avifauna in developing woodland, but still were well-represented in early establishment woodland at both sites. Cavity-nesting species were relatively uncommon at Wupatki and did not differ among stages ( $F_{2,9} = 2.38$ ,  $P = 0.15$ ). Cavity-nesters made up a greater proportion of the avifauna at Chevelon and varied among stages ( $F_{2,9} = 46.20$ ,  $P \leq 0.0001$ ). Like tree nesters, cavity-nesting species were most common in developing woodland and rare or absent in earlier successional stages. Proportions of shrub-nesting species did not vary significantly among stages at either area (Chevelon:  $F_{2,9} = 4.13$ ,  $P = 0.053$ ; Wupatki:  $F_{2,9} = 4.07$ ,  $P = 0.054$ ).

### Bird Abundance

The majority of bird species occurred in relatively low numbers; only 12 species were detected often enough for density

**Table 3. Occurrence of 22 breeding bird species along a grassland-juniper woodland successional gradient at 2 northern Arizona study areas, 1997–1998. Stages were: 1 = un-invaded grassland, 2 = early woodland establishment, 3 = developing woodland.**

Species	Chevelon			Wupatki		
	1	2	3	1	2	3
Mourning dove ( <i>Zenaida macroura</i> L.)		√	√		√	√
Ash-throated flycatcher ( <i>Myiarchus cinerascens</i> Lawrence)			√			√
Cassin's kingbird ( <i>Tyrannus vociferans</i> Swainson)			√			√
Horned lark ( <i>Eremophila alpestris</i> L.)	√	√	√	√	√	√
Scrub jay ( <i>Aphelocoma coerulescens</i> Bosc)			√			√
Pinyon jay ( <i>Gymnorhinus cyanocephalus</i> Wied)			√		√	√
Plain titmouse ( <i>Parus inornatus</i> Gambel)			√			√
Common bushtit ( <i>Psaltiriparus minimus</i> Townsend)			√			√
Bewick's wren ( <i>Thyromanes bewickii</i> Audubon)		√	√			
Townsend's solitaire ( <i>Myadestes townsendi</i> Audubon)					√	
Mountain bluebird ( <i>Sialia currucoides</i> Bechstein)		√	√			
Western bluebird ( <i>Sialia mexicana</i> Swainson)			√			
Northern mockingbird ( <i>Mimus polyglottos</i> L.)	√	√	√		√	√
Loggerhead shrike ( <i>Lanius ludovicianus</i> L.)	√	√	√		√	√
Black-throated sparrow ( <i>Amphispiza bilineata</i> Cassin)		√	√			
Lark sparrow ( <i>Chondestes grammacus</i> Say)	√	√	√		√	√
Spotted towhee ( <i>Pipilo erythrophthalmus</i> L.)			√			
Chipping sparrow ( <i>Spizella passerina</i> Bechstein)			√			√
Scott's oriole ( <i>Icterus parisorum</i> Bonaparte)		√	√		√	√
Brown-headed cowbird ( <i>Molothrus ater</i> Boddaert)			√			√
Eastern meadowlark ( <i>Sturnella magna</i> L.)	√	√		√	√	√
Western meadowlark ( <i>Sturnella neglecta</i> Audubon)	√	√		√	√	√

**Table 4. Similarity of breeding bird species composition along a grassland-juniper woodland successional gradient at 2 northern Arizona study areas, 1997–1998. Values are mean Jaccard index (J) values across years  $\pm$  1 SE. Potential index values range from 0–1, representing no species in common and total overlap, respectively.**

Study area		
Successional stage	Uninvaded grassland	Early establishment
<b>(Chevelon)</b>		
Early establishment	0.40 $\pm$ .04	
Developing woodland	0.11 $\pm$ .01	0.25 $\pm$ .01
<b>(Wupatki)</b>		
Early establishment	0.26 $\pm$ .02	
Developing woodland	0.13 $\pm$ .01	0.52 $\pm$ .02

estimation. Three ground-nesting grassland species were most strongly associated with un-invaded grassland and early establishment stages (Tables 5 and 6). Eastern and western meadowlarks were found in un-invaded grassland and early establishment woodland at Chevelon, and in all 3 successional stages at Wupatki. At both sites, meadowlarks were most abundant in early establishment woodlands. Horned larks were present in all successional stages at both sites, but were most abundant in un-invaded grassland. One ground-nesting species (spotted towhee) was present only in developing woodland at Chevelon.

We obtained density estimates for 1 shrub-nesting species present in early establishment and developing woodlands. At Chevelon, lark sparrows were present in all stages and were most abundant in developing woodland. At Wupatki, lark sparrows were found in early establishment and developing woodland, and were most abundant in the latter.

Six tree-nesting species had adequate sample sizes to estimate density. These species were largely restricted to developing woodland at Chevelon, but did occur in early establishment woodland at Wupatki. Common bushtits were present only in developing woodland at both sites. Chipping sparrows were found only in developing woodland at Chevelon. Northern mockingbirds were present in all successional stages at Chevelon, but only in early establishment and developing woodland at Wupatki. At both sites, mockingbirds were most abundant in developing woodland. At Wupatki, mourning doves were similarly abundant in early establishment and developing woodland. Pinyon jays were found only in developing woodland at Chevelon and were equally abundant in early establishment and developing woodland at Wupatki. Scott's orioles were found in early establishment and developing woodland at both sites, but were most abundant in the latter. Cavity-nesting species were largely restricted to developing woodland.

Ash-throated flycatchers were present in developing woodland at both sites. Bewick's wren occurred in early establishment and developing woodland at the

**Table 5. Density estimates of 11 breeding bird species from 4 nesting guilds along a grassland-juniper woodland successional gradient at Chevelon study area, northern Arizona, 1997–1998. Values are means across years  $\pm$  1 SE.**

Guild Species	Un-invaded grassland	Early establishment	Developing woodland
<hr/> (birds ha <sup>-1</sup> ) <hr/>			
<b>(Ground-nester)</b>			
Meadowlark <sup>1</sup>	0.02 $\pm$ 0.01	0.05 $\pm$ 0.02	a <sup>2</sup>
Horned lark	0.43 $\pm$ 0.03	0.37 $\pm$ 0.03	0.04 $\pm$ 0.02
Spotted towhee	a	a	0.08 $\pm$ 0.02
<b>(Shrub-nester)</b>			
Lark sparrow	p <sup>3</sup>	0.04 $\pm$ 0.01	0.21 $\pm$ 0.03
<b>(Tree-nester)</b>			
Pinyon jay	a	a	0.03 $\pm$ 0.01
Common bushtit	a	a	0.19 $\pm$ 0.07
Northern mockingbird	p	0.12 $\pm$ 0.02	0.25 $\pm$ 0.05
Chipping sparrow	a	a	0.23 $\pm$ 0.03
Scott's oriole	a	p	0.06 $\pm$ 0.01
<b>(Cavity-nester)</b>			
Ash-throated flycatcher	a	a	0.10 $\pm$ 0.02
Bewick's wren	a	p	0.07 $\pm$ 0.02

<sup>1</sup>Includes eastern and western species, which often could not be distinguished.

<sup>2</sup>a = absent from all transects.

<sup>3</sup>p = present on 1 or more transects, but not detected during sampling visits.

**Table 6. Density estimates of 9 breeding bird species from 4 nesting guilds along a grassland-juniper woodland successional gradient at Wupatki study area, northern Arizona, 1997–1998. Values are means across years  $\pm$  1 SE.**

Guild Species	Uninvaded grassland	Early establishment	Developing woodland
<hr/> (birds ha <sup>-1</sup> ) <hr/>			
<b>(Ground-nester)</b>			
Meadowlark <sup>1</sup>	0.06 $\pm$ 0.02	0.25 $\pm$ 0.05	0.10 $\pm$ 0.03
Horned lark	0.33 $\pm$ 0.02	0.29 $\pm$ 0.02	0.08 $\pm$ 0.01
<b>(Shrub-nester)</b>			
Lark sparrow	a <sup>2</sup>	p <sup>3</sup>	0.21 $\pm$ 0.02
<b>(Tree-nester)</b>			
Mourning dove	a	0.16 $\pm$ 0.06	0.13 $\pm$ 0.04
Pinyon jay	a	0.06 $\pm$ 0.04	0.06 $\pm$ 0.02
Common bushtit	a	a	0.04 $\pm$ 0.04
Northern mockingbird	a	0.06 $\pm$ 0.01	0.23 $\pm$ 0.03
Scott's oriole	a	0.02 $\pm$ 0.01	0.07 $\pm$ 0.02
<b>(Cavity-nester)</b>			
Ash-throated flycatcher	a	a	0.03 $\pm$ 0.01

<sup>1</sup>Includes eastern and western species, which often could not be distinguished.

<sup>2</sup>a = absent from all transects.

<sup>3</sup>p = present on 1 or more transects, but not detected during sampling visits.

Chevelon area, being most abundant in the latter successional stage.

## Discussion

Woodland expansion had a strong and consistent influence on grassland avifauna. Ground-nesting grassland species predominated in un-invaded grassland, but declined as tree density increased. The proportion of tree- and cavity-nesting species increased with woodland succession and was highest in developing woodland. Shrub-nesters did not respond to woodland expansion, probably because shrubs were relatively sparse on our study

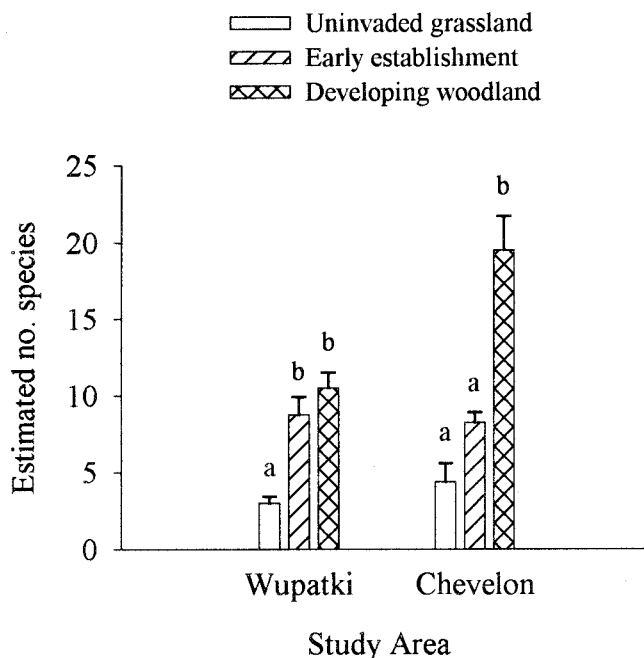


Fig. 1. Breeding bird species richness (mean  $\pm$  1 SE) along a grassland-juniper woodland successional gradient at 2 northern Arizona study sites, 1997–1998. Significant differences within sites (repeated measures ANOVA followed by Scheffe's post-hoc means test,  $P \leq 0.05$ ) are indicated by lowercase letters above histogram bars.

areas, and shrub density and shrub size were similar among successional stages. The breeding avifauna changed dramatically with woodland succession; differences were most pronounced between endpoints of our gradient (un-invaded grassland versus developing woodland). Differences in species composition within successional woodlands appeared proportional to the magnitude of change in the tree component. For example, at the Chevelon area, tree density increased by nearly an order of magnitude between early establishment and developing woodland, and species overlap was low ( $J = 0.25$ ). In contrast, there was only a 4-fold difference in tree density between these stages at Wupatki, and species overlap was much higher ( $J = 0.52$ ). Studies in other North American grasslands also have reported substantial avifaunal changes in response to woodland expansion. In southern Arizona, invasion of mesquite (*Prosopis* spp.) increased breeding bird species richness, but decreased habitat suitability for several grassland species (Lloyd et al. 1998). Shelterbelt plantings in the Great Plains and midwestern U.S. have been colonized by bird species historically associated with savanna and deciduous forests (Martin 1981, Yahner 1983, Knopf 1994).

The avian community changes that we observed were consistent with results of

previous studies in northern Arizona. LaRue (1994) reported that horned larks and meadowlarks were the dominant breeding species on mined areas revegetated to grassland, whereas juniper-invaded grasslands supported tree-nesting species including northern mockingbirds, loggerhead shrikes, chipping sparrows, and Scott's orioles. Prior breeding bird surveys at Wupatki found 17 species (primarily tree-nesters) at a juniper savannah area, compared to 8 species at a grassland area (Beatty 1978). Within Southwestern pinyon-juniper woodlands, breeding bird diversity and abundance have been positively correlated with tree density and tree size (Masters 1979, Sedgwick 1987, LaRue 1994).

The inverse of the woodland expansion pattern has been found in studies of breeding birds in treated pinyon-juniper woodlands; where fire, herbicides, and mechanical treatments have been used to create openings dominated by herbaceous and shrub vegetation. Treated areas were dominated by ground-nesting and grassland bird species (Grue 1977, Kruse et al. 1979, LaRue 1994). Diversity was highest in undisturbed woodlands and at woodland edges adjacent to treated areas (O'Meara et al. 1981, Sedgwick and Ryder 1987). Foliage and cavity nesting species were more abundant in or restricted to untreated or lightly treated woodlands (Sedgwick

and Ryder 1987, La Rue 1994).

Responses of breeding birds to woodland expansion likely are driven by linkages between individual species and floristic and physiognomic habitat features (Rotenberry and Wiens 1980, Wiens and Rotenberry 1981, Cody 1985). The addition of a tree component provides nesting and foraging opportunities for woodland species, but reduces habitat suitability for grassland-obligate birds. The presence of woody vegetation may further influence community structure by altering predation risk for "cover-dependent" versus "cover-independent" bird species (Lima and Valone 1991).

## Conclusions and Management Recommendations

Woodland expansion is an important issue in Southwestern grasslands, particularly on public lands (Loftin et al. 1995). While the grassland bird species that we studied are not currently listed as threatened, endangered, or "species of concern," continued expansion of juniper in northern Arizona grasslands will result in additional, substantial habitat change over the long-term and reductions in the numbers of grassland-obligate birds.

Our results suggest that removal or reduction of invasive juniper will improve breeding habitat for horned larks, meadowlarks, and other grassland-obligate birds in northern Arizona. Grassland restoration would likely benefit other wildlife species. Juniper woodland expansion has been found to decrease habitat quality for pronghorn (*Antilocapra americana* Ord) and increase susceptibility to predation (Alexander and Ockenfels 1994, R. Ockenfels, Arizona Game and Fish Dept., pers. comm.). Anecdotal observations made during this study also suggest that woodland expansion is detrimental to Gunnison's prairie dogs (*Cynomys gunnisoni* Baird). Active prairie dog towns were present on or near all transects in uninvaded grassland, but were absent in successional woodlands.

Several factors should be considered by resource managers planning grassland restoration projects. True "restoration" is likely possible only in areas along the grassland-woodland interface that historically were occupied by grassland vegetation. Type conversions in higher elevation "true" pinyon-juniper woodlands are expensive and generally have short-lived effects. A density of  $\geq 10$  juniper trees  $\text{ha}^{-1}$  is an approximate threshold at which habi-

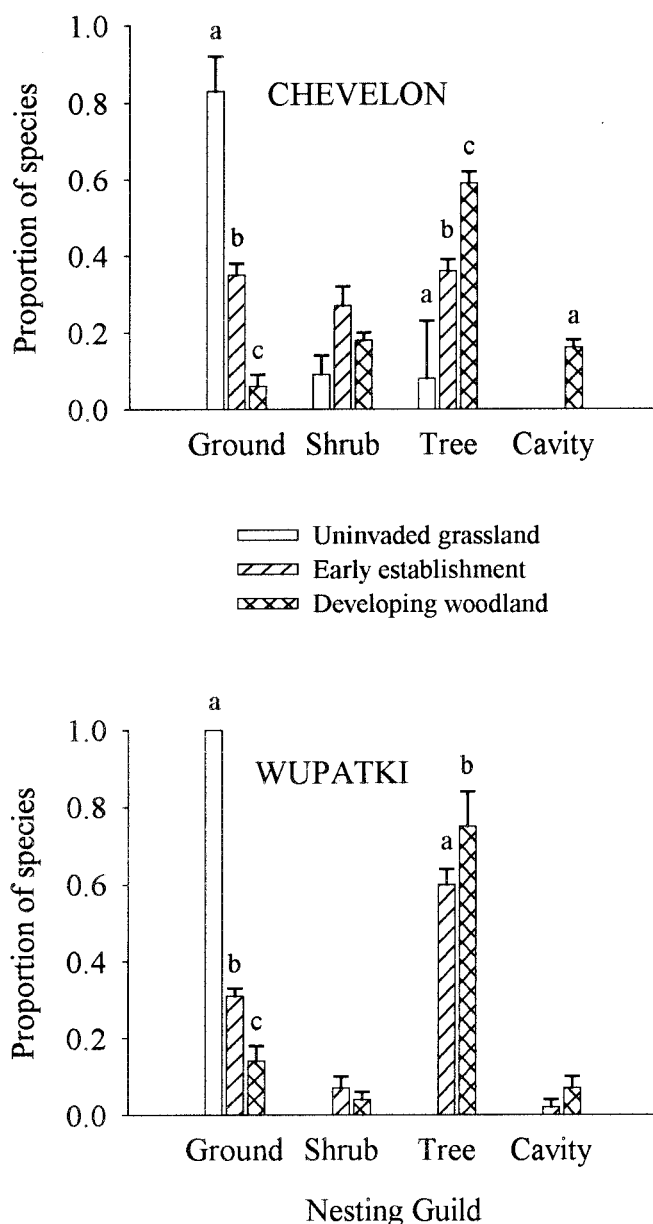


Fig. 2. Breeding bird nesting guild composition along a grassland-juniper woodland successional gradient at 2 northern Arizona study sites, 1997-1998. Values are mean proportion of species belonging to each guild  $\pm$  1 SE. Missing bars reflect zero values for particular successional stages. Significant differences among successional stages within sites (repeated measures ANOVA followed by Scheffe's post-hoc means test,  $P \leq 0.05$ ) are indicated by lowercase letters above histogram bars.

tat suitability for grassland species declines and at which restoration treatments should be considered. Priority should be given to sites that have a well-established perennial grass component, as artificial seeding and surface treatments needed to establish grasses will greatly inflate project cost. Artificial seeding may be difficult or impractical where upper soil horizons have been lost to erosion. Shrubs that provide nesting cover and song perches for breeding birds (e.g., four-wing saltbush and

Fremont barberry) should be retained; however, where shrubs are rare or absent, a low density (2-4 trees/ha) of small (< 1.5 m tall) junipers may be left on the site.

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# Escape protein and weaning effects on calves grazing meadow regrowth

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## Abstract

Forty spring-born calves grazing subirrigated meadow regrowth after haying in July were assigned to 2 weaning and 2 supplementation treatments in fall of 1995 and 1996. Weaning treatments were weaning on 1 September or nursing during the duration of the trial. Supplementation treatments were no supplement or supplemental undegraded intake protein (UIP). An 80:20 (dry matter basis) blend of sulfite liquor treated soybean meal and feather meal was the source of undegraded intake protein (undegraded intake protein = 45% of supplement dry matter). Supplemented nursing calves received 0.50 kg of supplement daily whereas supplemented weaned calves received 0.91 kg of supplement daily. Weaned and nursing calves grazed subirrigated meadow regrowth throughout the trial. The trials were conducted from 17 October to 18 November 1995 and 5 September to 4 November 1996. Milk intake was measured by the weigh-suckle-weigh technique. Diet samples collected from ruminally cannulated calves after rumen evacuation averaged 12.5% crude protein and 54.8% in vitro organic matter digestibility. No supplementation x weaning management interactions were detected ( $P > 0.18$ ). Nursing calves had greater weight gains (0.95 vs. 0.59 kg day<sup>-1</sup>;  $P = 0.001$ ) and lower forage intakes (2.36 vs. 2.96 kg day<sup>-1</sup>;  $P = 0.009$ ) than weaned calves. Supplementation with undegraded intake protein increased ( $P = 0.03$ ) daily gains of calves compared to nonsupplemented calves 0.88 vs 0.66 kg day<sup>-1</sup>, respectively. Forage intake as a percentage of body weight tended to be higher in non-supplemented calves ( $P = 0.09$ ). However, total intake (forage plus supplement) as a percentage of body weight tended to be higher in supplemented calves ( $P = 0.14$ ). Total intake (kg day<sup>-1</sup>) was greater ( $P = 0.01$ ) for calves supplemented with undegraded intake protein. Milk intake did not differ between supplemented and unsupplemented calves ( $P > 0.52$ ). We concluded that subirrigated meadow regrowth forage was limiting in metabolizable protein and that milk represents an important source of metabolizable protein for grazing calves.

**Key Words:** undegraded intake protein, beef calves, forage intake, forage digestibility

## Resumen

40 becerros nacidos en primavera, que apacentaban el rebrote de praderas subirrigadas después de segadas para heno en julio, se asignaron a 2 tratamientos de destete y 2 tratamientos de suplementación en otoño de 1995 y 1996. Los tratamientos de destete fueron: destetarlos el 1 de septiembre o amamentarlos durante la duración del experimento. Los tratamientos de suplementación fueron: no suplementación y suplementación de proteína no-degradada (PND). La fuente de proteína no-degradada fue una mezcla (80:20% en base seca) de pasta de soya tratada con licor de sulfito y harina de pluma (Proteína no-degradada = 45% de la materia seca suplementada). Los becerros amamantados suplementados recibieron 0.50 kg diarios de suplemento mientras que los becerros destetados suplementados recibieron 0.91 kg de suplemento al día. Durante el período de conducción del experimento los becerros destetados y los amamantados apacentaron el rebrote de las praderas subirrigadas. Los ensayos se condujeron del 17 de octubre al 18 de noviembre de 1995 y del 5 de septiembre al 4 de noviembre de 1996. El consumo de leche se midió mediante la técnica de peso-amamantamiento-peso. Las muestras de la dietas, colectadas de becerros con cánula ruminal y después de la evacuación del rumen, promediaron 12.5% de proteína cruda y 54.8% de digestibilidad in vitro de la materia orgánica. No se detectaron interacciones ( $P > 0.18$ ) entre la suplementación y los sistemas de destete. Los becerros amamantados tuvieron mayores ganancias de peso (0.95 vs 0.59 kg día<sup>-1</sup>;  $P = 0.001$ ) y menores consumos de forraje que los becerros destetados (2.36 kg día<sup>-1</sup> vs 2.96 kg día<sup>-1</sup>;  $P = 0.009$ ). La suplementación de proteína-no degradada aumentó las ganancias diarias de peso ( $P = 0.03$ ) de los becerros suplementados en comparación con los no suplementados 0.88 vs 0.66 kg día<sup>-1</sup> respectivamente. El consumo de forraje expresado como porcentaje del peso vivo tendió a ser mas alto en los becerros sin suplementar ( $P = 0.09$ ). Sin embargo, el consumo total (forraje + suplemento) expresado como porcentaje de peso vivo tendió a ser mayor en los becerros suplementados ( $P = 0.14$ ). El consumo total (kg día<sup>-1</sup>) fue mayor ( $P = 0.01$ ) en los becerros suplementados con proteína no-degradada. El consumo de leche no difirió entre becerros con y sin suplemento ( $P > 0.52$ ). Concluimos que el rebrote de las praderas subirrigadas estuvo limitado en proteína metabolizable y que la leche representa una importante fuente de proteína metabolizable para los becerros en apacentamiento.

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Milk represents an important source of nutrients for the nursing calf (Blaxter and Wood 1952, Baker et al. 1976, Le Du et al. 1976, Wyatt et al. 1977, Sowell et al. 1996). As a result of the esophageal groove reflex, milk bypasses rumen fermentation and is digested and absorbed in the abomasum and small intestine (Ruckebusch 1988). The protein in milk represents an important contribution to the metabolizable protein supply of the nursing calf. The nursing calf has higher relative protein requirements than more mature animals, because greater amounts of protein are needed for lean growth, relative to fat accretion (NRC 1996).

When cattle graze growing or vegetative cool-season grasses, ruminal ammonia concentrations generally do not limit microbial growth and fermentation. However, because the protein in these grasses is readily degradable in the rumen (Lardy 1997), large amounts of nitrogen can be absorbed as ammonia before reaching the duodenum (Beever and Siddons 1986). Therefore, metabolizable protein may be limiting in these forages despite their relatively high crude protein contents, especially when metabolizable protein requirements of the grazing ruminant are high (e.g., growth or lactation). Undegraded intake protein was limiting for nursing calves grazing native Sandhills range during summer (Hollingsworth-Jenkins 1994).

Numerous studies have evaluated the effects of early weaning on the performance of cows and calves, (Lusby et al. 1981, Harvey and Burns 1988, Grimes and Turner 1991a, 1991b). In these studies, early weaned calves were generally fed large amounts of grains, in a non-grazing setting. Lamb et al. (1997) reported that weaned calves gained  $0.56 \text{ kg day}^{-1}$  vs.  $1.09 \text{ kg day}^{-1}$  for calves nursing cows grazing subirrigated meadow in September through October. Our objectives were to evaluate the effects of milk and supplemental undegraded intake protein on calf body weight gain, forage intake, and forage digestibility by weaned and nursing calves grazing subirrigated meadow regrowth in the Nebraska Sandhills.

## Materials and Methods

The study was conducted at the University of Nebraska-Lincoln Gudmundsen Sandhills Laboratory (elevation 1,073 m, 42°05' N, 106° 26' W) near Whitman, Nebr. Forty March and April-

**Table 1. Number of steer and heifer calves assigned to weaning and supplement treatments in 1995 and 1996.**

Item	Treatment			
	Nursing no supplement	Nursing with supplement	Weaned no supplement	Weaned with supplement
<b>1995</b>				
Steers	5	5	5	5
Heifers	6	4	5	5
<b>1996</b>				
Steers	7	7	5	5
Heifers	3	4	4	5

born crossbred (1/4 Hereford, 1/4 Angus, 1/4 Simmental, and 1/4 Gelbvieh) steer and heifer calves were assigned in 1995 and 1996 to 2 weaning and 2 supplementation treatments as shown in Table 1. In 1995 the trial was initiated 5 September, but calves did not readily consume supplements until mid-October; therefore, the data are reported from 17 October to 18 November. In 1996, calves consumed supplements readily from the outset, and the trial lasted from 5 September to 4 November. Calves grazed subirrigated meadow regrowth after haying in July each year. Weaning treatments were: 1) weaning 1 September, or 2) nursing throughout the trial. Supplementation treatments were: 1) no supplementation, or 2) supplemental undegraded intake protein. Supplement composition is listed in Table 2 and it was formulated using a

**Table 2. Ingredients, crude protein (CP), undegraded intake protein (UIP) and invitro organic matter digestibility (IVOMD) of supplement fed to weaned and nursing calves (dry matter basis).**

Item	%
Sulfite Liquor Treated Soybean Meal	80.0
Feather Meal	20.0
CP	57.3
IVOMD	79.5
UIP, % CPI	78.8

<sup>†</sup>Determined using ammonia release procedure (Britton et al. 1978).

blend of sulfite-liquor-treated soybean meal (Cleale et al. 1987) and feather meal. Weaned calves that received supplement were individually fed 0.91 kg of supplement daily, whereas nursing calves received 0.50 kg of supplement daily (dry matter basis). Supplement amounts were based on the metabolizable protein requirement calculated as described by Wilkerson et al. (1993) and metabolizable protein supply calculated as described by Burroughs et al. (1974). Body weight was

estimated to be 189.5 kg and average daily gain was estimated to be  $1.1 \text{ kg day}^{-1}$  (Lamb et al. 1997). Metabolizable protein requirement for maintenance was  $3.8 \text{ g of metabolizable protein/kg of body weight}^{0.75}$  ( $3.8 \times 189.5^{0.75}$ ) = 194 g; metabolizable protein requirement for gain was  $305 \text{ g of metabolizable protein/kg gain}$  ( $305 \times 1.1$ ) = 348 g, and total metabolizable protein requirement was  $194 \text{ g} + 348 \text{ g} = 542 \text{ g day}^{-1}$  (Wilkerson et al. 1993). Subirrigated meadow regrowth was estimated to be 12% crude protein, 1.1% undegraded intake protein, and 60% TDN (Lardy 1997). Forage intake by nursing calves was estimated to be 1.5% of body weight or 2.84 kg (Hollingsworth-Jenkins 1994). Net synthesis of bacterial crude protein was assumed to be 13% of the TDN intake (Burroughs et al. 1974). Consequently, bacteria would supply 142 g of metabolizable protein ( $2.84 \text{ kg of organic matter intake} \times 60\% \text{ TDN} \times 13\% \text{ efficiency} \times 80\% \text{ digestibility} \times 80\% \text{ true protein}$ ). Milk intake by nursing calves was estimated to be  $8.2 \text{ kg day}^{-1}$  (NRC 1996) which would supply 223 g metabolizable protein ( $8.2 \text{ kg} \times 3.4\% \text{ CP} \times 80\% \text{ digestibility}$ ). Forage was estimated to supply 25 g of metabolizable protein ( $2.84 \text{ kg} \times 1.1\% \text{ undegraded intake protein} \times 80\% \text{ digestibility}$ ). Hence, total metabolizable protein supply for the nursing calf would be 390 g, with a resulting calculated deficiency of 152 g of metabolizable protein ( $542 \text{ g requirement} - 390 \text{ g supply}$ ). For weaned calves, forage intake was estimated at 2.5% of body weight (Le Du et al. 1976, Boggs et al. 1980). Resulting supply of metabolizable protein from bacteria was estimated to be 237 g. Forage supply of metabolizable protein was estimated to be 42 g, resulting in a metabolizable protein supply of 279 g ( $237 \text{ g} + 42 \text{ g}$ ). For the weaned calf, the resulting deficiency would be 263 g ( $542 \text{ g requirement} - 279 \text{ g supply}$ ). The sulfite liquor-treated soybean meal:feather meal supplement was estimated to be 52% crude protein and 70% of the crude protein was estimated to

be undegraded intake protein. Actual values for the trial are reported in Table 2. Hence, resulting feeding levels for weaned and nursing calves based on estimated deficiencies in metabolizable protein were 903 g and 522 g calf<sup>-1</sup> day<sup>-1</sup>, respectively. Calculations based on data from the trial resulted in a deficiency of 175 g and 285 g of metabolizable protein for nursing and weaned calves, respectively.

Cows and calves grazed a 33 ha pasture during the trial. Standing herbage was estimated to be 2,250 kg/ha (dry basis) at the beginning of the trial.

Calves were gathered daily at 0730 hours, sorted into individual pens (0.76 m X 2.54 m), and individually fed supplements. A small sample of supplement was collected weekly and composited for each year. In 1995, to prevent nursing by weaned calves, the subirrigated meadow pasture was split into 2 pastures. Nursing calves grazed on one side and weaned calves on the other. Each day following supplementation, nursing and weaned calves rotated pastures, so that over the course of the trial each group of calves grazed each side a similar number of days. In 1996, nursing and weaned calves were pastured together and observed several times in the a.m. daily for cross nursing. No nursing by weaned calves was observed.

The subirrigated meadow soils were classified as Gannet-Loup fine sandy loam (course-loamy mixed mesic Typic Haplaquoll). Dominant vegetation on the subirrigated meadow site was smooth brome grass (*Bromus inermis* Leyss.), red-top (*Agrostis gigantea* Roth), timothy (*Phleum pratense* L.), slender wheatgrass [*Elymus trachycaulum* (Link) Gould ex Shinn.], quackgrass [*Elytrigia repens* (L.) Nevski.], 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* var. *gerardii* Vitman), indiagrass [*Sorghastrum nutans* (L.) Nash], and switchgrass (*Panicum virgatum* L.). Red clover (*Trifolium pratense* L.) was the most abundant forb.

Calves were weighed on 17 October and 18 November 1995 and 5 September and 4 November 1996. Milk intake by nursing calves was determined by weigh-suckle-weigh on 4 November 1995 and 19 October 1996. The day before the weigh-suckle-weigh procedure, calves were separated from cows at 1400 hours, allowed to nurse at 1800 hours, and separated overnight. At 0700 hours the next day

calves were weighed, allowed to nurse, and weighed again. Twenty-four hour milk intakes were calculated by dividing overnight milk intake by 13 and multiplying by 24.

Fecal output by steer calves was determined 30 October through 3 November 1995 and October 14 through 18 1996. Each steer calf was dosed with an intraruminal continuous chromium (Cr) releasing device<sup>1</sup> 5 days before the 5-day fecal collection period. Fecal grab samples were obtained from each steer calf at approximately 0800 hours each day of the collection period. Six steers in 1995 (avg. body weight = 236 ± 17.5 kg) and 5 steers in 1996 (avg. body weight = 175 ± 19.3 kg) were used to perform total fecal collections. Steers used for total fecal collections had been weaned and received no supplement. Steers used for total collections were dosed with the same intraruminal continuous Cr releasing device as the steers on the trial and fitted with fecal collection bags for total fecal collection to obtain a correction factor for fecal output (Adams et al. 1991a, Hollingsworth et al. 1995). The correlation factor was 0.731 for 1995 and 0.897 for 1996. Feces collected in fecal collection bags was weighed, mixed, subsampled (300 to 500 g), and emptied. In 1995, bags were emptied daily at 0800. In 1996, fecal bags were emptied twice daily at 0800 and 1700 during the 5-day fecal collection period.

Forage diet samples were collected with 3 esophageally fistulated cows and 3 ruminally fistulated nursing calves. Calves were fistulated in late July before initiation of the trial. Cows had been fistulated 2 to 4 years previously as described by Adams et al. (1991b) with modifications for adult cattle. Surgical preparations and post-surgical procedures were reviewed and approved by the University of Nebraska Institutional Animal Care and Use Committee. Esophageal masticate samples were collected in screen-bottom bags and immediately frozen. Ruminant contents were evacuated, and the rumen was wiped with a damp sponge to remove digesta in order to prevent contamination of diet samples. Calves were allowed to graze for 45 to 60 minutes, and diet samples were collected via the ruminal cannula and immediately frozen.

All fecal and extrusa samples were stored frozen until chemical analyses were performed. Extrusa and fecal samples

were freeze dried. Fecal and supplement samples were ground to pass a 1-mm screen in a Wiley Mill. Extrusa samples were ground to pass a 2-mm screen in a Wiley Mill for analysis of diet protein degradability. Extrusa samples were ground to pass a 1-mm screen in a Wiley Mill for analysis of dry matter, organic matter, crude protein, neutral detergent fiber (NDF), acid detergent fiber (ADF), and in vitro organic matter digestibility (IVOMD). Dry matter, organic matter, and crude protein of extrusa and supplement were determined by standard methods (AOAC 1990). Extrusa NDF was determined according to Van Soest et al. (1991), and extrusa ADF by the method of Van Soest (1963). In vitro organic matter digestibility of extrusa and supplement samples was determined by the modified procedures of Tilley and Terry (1963) with the addition of 1 g of urea to the inoculum-buffer mixture (Weiss 1994). Fecal samples were analyzed for Cr concentration by atomic absorption spectrophotometry using an air-plus-acetylene flame (Williams et al. 1962). Forage organic matter intake was calculated by dividing fecal organic matter output by the in vitro organic matter indigestibility of esophageal extrusa after subtracting the indigestible contribution of the supplement (IVOMD, Table 2) from fecal output.

Undegraded intake protein of extrusa samples was determined as described by Mass et al. (1996) with the following modifications. Briefly, 1.25 g samples were placed in dacron bags<sup>2</sup> and incubated in a ruminally cannulated steer fed a smooth brome grass hay (8% crude protein) at 1.8% of body weight. Samples were incubated for 2, 12, and 96 hours. Three separate incubation runs were performed in the same animal. Bags were washed according to Wilkerson et al. (1995) and subjected to analysis of neutral detergent fiber nitrogen. Amounts of neutral detergent fiber nitrogen remaining after incubation were natural log transformed and a rate of degradation was calculated. Undegraded intake protein was calculated using the following formula:  $UIP = B \times (k_p / (k_d + k_p)) + C$ ; where B is the pool size or potential undegraded intake protein calculated from the intercept of the natural log transformation of degradation,  $k_p$  is the rate of passage and  $k_d$  is the rate of degradation of neutral detergent fiber nitrogen, and C is the undegradable fraction (Broderick 1994). Passage rates were determined in a sepa-

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

<sup>2</sup>Ankom, Inc., Fairport, N.Y.

**Table 3. Crude protein (CP), undegraded intake protein (UIP), neutral detergent fiber (NDF), acid detergent fiber (ADF), and in vitro organic matter digestibility (IVOMD) of diet samples collected from cows and calves grazing subirrigated meadow regrowth in 1995 and 1996.**

Date	Type	CP	% of Organic Matter			IVOMD
			UIP	NDF	ADF	
27 Oct. 1995	Cow	10.0	1.94	84.4	57.2	53.1
27 Oct. 1995	Calf	10.9	2.45	83.9	55.9	50.1
3 Nov. 1995	Calf	11.5	2.21	76.3	53.0	56.1
15 Oct. 1996	Cow	11.1	1.78	68.0	53.2	46.5
16 Oct. 1996 <sup>1</sup>	Calf	13.7	2.91	76.9	63.0	50.6

Mean of samples collected 15 and 16 October.

rate research project at the Gudmundsen Sandhills Laboratory during the 1994 growing season (Lamb 1996). Undegraded intake protein of the supplement fed in this study was determined using the ammonia release procedure of Britton et al. (1978).

Data were analyzed using the MIXED procedures of SAS (1990) with a 2 x 2 factorial treatment design. Sex and year served as blocking factors. Individual calf served as the experimental unit. For weight and weight gain data, year X weaning X supplementation X sex was considered random and was used to test year, supplementation, weaning, sex, supplementation X weaning, sex X weaning, sex X supplementation, and weaning X supplementation X sex. When no significant ( $P > 0.15$ ) interactions were detected, data were pooled and only main effects presented. For intake data, year X weaning X supplementation was considered random and was used to test year, weaning, supplementation, and weaning X supplementation. Because only steer calves were used to measure intake, sex was not included as a variable when intake data were analyzed.

## Results and Discussion

Year effects were significant for initial weight ( $P = 0.06$ ) and average daily gain ( $P = 0.04$ , respectively). Initial weights averaged 217 and 193 kg in 1995 and 1996, respectively, and were greater in 1995 because the trial was started later than anticipated due to the difficulties in getting calves to consume supplements. Daily gains averaged 0.69 and 0.85 kg day<sup>-1</sup> in 1995 and 1996, respectively, and again were likely influenced by the starting date of the trial.

Calves and cows selected diets that were similar in quality (Table 3). Diets collected with ruminally cannulated calves averaged 12.5% crude protein and 54.8% in vitro organic matter digestibility (Table 3). Lamb et al. (1997) reported similar values to our crude protein but higher in vitro organic matter digestibility for diets collected from esophageally cannulated cows grazing meadow regrowth during the fall. In addition, Lamb et al. (1997) reported similar gains by nursing and weaned calves grazing meadow regrowth. Based on in vitro organic matter digestibility of diet samples reported by Lamb et al. (1997) and the diet data reported here (Table 3), gains would be expected to be

lower because our in vitro organic matter digestibilities are lower than those reported by Lamb et al. (1997). Calves selected diets that averaged 2.6% undegraded intake protein, whereas cows grazing meadow regrowth selected diets averaging 1.9% undegraded intake protein (Table 3). Hollingsworth-Jenkins (1994) reported that calves grazing native range selected diets higher in crude protein and undegraded intake protein and similar in digestibility compared to cows grazing the same pastures.

No supplementation by weaning management interactions were detected for initial weight, final weight, or average daily gain ( $P = 0.83, 0.75, 0.92$ , respectively). No supplementation by weaning management interactions were detected for forage intake, total intake, forage intake as a percentage of body weight, or total intake as a percentage of body weight ( $P = 0.18, 0.81, 0.18, 0.94$ , respectively). Therefore, only main effects will be presented and discussed.

Nursing calves had greater average daily gains and heavier final weights ( $P = 0.001$ ) than weaned calves (Table 4). These findings agree with those of Lamb et al. (1997) for weaned and nursing spring-born calves grazing subirrigated meadows. Lusby et al. (1981) found that early weaned calves had similar weight gains to calves weaned at 7 months; however, early weaned calves were managed in drylot and fed a concentrate diet rather than consuming a grazed diet. When early weaned calves were managed on pasture with a creep feed, gains were 20 kg lower than nursing calves (Lusby et al. 1981). Sowell et al. (1996) found that calves restricted from suckling the cow's rear udder for 4 weeks had lower weight gains than calves that were not restricted.

Milk represents an important source of nutrients for the growing calf, as represented by the magnitude of the response in

**Table 4. Effect of weaning and undegraded intake protein (UIP) supplementation on initial weight, final weight, average daily gains (ADG), forage intake (kg day<sup>-1</sup>), total intake (kg day<sup>-1</sup>), forage intake (kg/100 kg body weight), and total intake (kg/100 kg body weight) of calves grazing subirrigated meadow regrowth.**

	Main Effects <sup>1</sup>						SEM <sup>2</sup>
	Weaning Management			UIP Supplementation			
	Weaned	Nursing	P-value	Non-Suppl.	Supplemented	P value	
Initial weight (kg)	196.3	213.8	.2072	207.6	202.5	.7560	7.49
Final weight (kg)	222.6	258.6	.0099	238.2	243.0	.6847	8.29
ADG (kg day <sup>-1</sup> )	0.59	0.95	.0009	0.66	0.88	.0306	.046
Forage intake (kg day <sup>-1</sup> )	2.96	2.36	.0090	2.73	2.59	.3257	.093
Total intake (forage + Supplement, kg day <sup>-1</sup> )	3.41	2.61	.0040	2.73	3.30	.0111	.092
Forage intake (kg/100 kg body weight)	1.29	0.89	.0074	1.17	1.02	.0927	.040
Total intake (forage + supplement, kg/100 kg body weight)	1.48	0.99	.0048	1.17	1.30	.1388	.037

<sup>1</sup>All supplement by weaning management interactions were nonsignificant  $P > 0.15$ . Data pooled over 2 years.

<sup>2</sup>SEM = standard error of mean.

daily gain. Nursing calves gained 0.36 kg day<sup>-1</sup> more than weaned calves. In production systems where calves are sold at weaning, this should result in an increase in gross returns to the producer. The effect of lactation on weight and body condition score changes in the cow were not investigated in this trial. Lamb et al. (1997) reported that lactating cows grazing meadow during the fall maintained body condition, while dry cows gained body condition. This finding has implications for production systems in which cows are wintered on low quality forages, because increases in body condition are not expected when cows graze low quality forages with or without proper supplementation (Villalobos et al. 1997). Thinner cows have greater energy requirements than fatter cows during the winter (Thompson et al. 1983).

Calves receiving undegraded intake protein supplementation had greater ( $P = 0.03$ ) daily gains than non-supplemented calves (Table 4). Weaned and nursing calves responded to supplemental undegraded intake protein in a similar fashion (e.g., no significant supplementation X weaning management interactions), which indicates the undegraded intake protein was likely limiting for both weaned and nursing calves. McCann et al. (1991) reported that gains by steers grazing wheat-annual ryegrass pastures were increased when supplemental undegraded intake protein (fish meal-dried distillers grains) was provided. ZoBell and Goonewardene (1989) reported that nursing calves that had access to a canola (*Brassica napus* L.)-soybean (*Glycine max* L. Merr.) meal creep while grazing native range had higher weight gains than calves receiving no creep feed. Hollingsworth-Jenkins (1994) found that nursing calves grazing native Sandhills range had increased average daily gains when supplemented with undegraded intake protein (treated soybean meal-feather meal) than calves receiving no supplement or supplemental energy (soyhulls-protected fat). Karges et al. (1992) found that yearling steers grazing native Sandhills range responded in a linear fashion to supplemental undegraded intake protein (treated soybean meal-feather meal).

Forage intake and total intake, when expressed either as a percentage of body weight or as kg/day were greater ( $P = 0.01$ ) by weaned than by nursing steers (Table 4). Boggs et al. (1980) found that milk intake was negatively correlated with forage intake in nursing calves. Le Du et al. (1976) reported that bottle-fed calves fed low quantities of milk consumed more

forage than calves fed high quantities of milk. Lusby et al. (1976) found calves that consumed more milk consumed less forage. Contradictory to these findings, Peischel (1980) found that level of milk intake did not affect forage dry matter intake. Even though weaned calves compensated for lack of milk intake by increasing forage intake, this compensation was not enough to increase weight gains to levels of nursing calves.

Forage intakes we report here appear to be low based on forage quality and cattle performance. Ansotegui et al. (1991) reported fecal outputs for calves grazing native range similar to what we observed (data not shown). External marker methodologies may have contributed to our relatively low estimates of intake (Galyean et al. 1986).

No differences were found in forage intake (kg day<sup>-1</sup>) between supplemented or non-supplemented steers ( $P = 0.33$ ) which contradicts results of Cremin et al. (1991), who found that forage intake was negatively correlated with consumption of creep feed. Intake of forage and supplement was greater ( $P = 0.01$ ) by supplemented than nonsupplemented steers. Forage intake, as a percentage of body weight, tended to be greater ( $P = 0.09$ ) for nonsupplemented than supplemented steers. Total intake, expressed as a percentage of body weight, tended to be greater ( $P = 0.14$ ) for supplemented calves.

Milk consumption averaged 5.8 and 6.6 kg milk day<sup>-1</sup> for supplemented and non-supplemented calves, respectively, and were not different ( $P = 0.52$ ). This agrees with the findings of Cremin et al. (1991) who reported that level of creep feed intake did not affect milk intake. Assuming that milk is 3.4% protein (NRC 1996), these milk intakes would supply 197 and 211 g of metabolizable protein, respectively. For the nursing calves not receiving the undegraded intake protein supplement, this represents over 50% of the metabolizable protein supply. However, based on the increased daily gain from supplemental undegraded intake protein, milk may not supply adequate metabolizable protein to meet the requirements of grazing beef calves.

Commonly accepted practices of creep feeding cereal grains to nursing calves may not correct metabolizable protein deficiencies in high quality forages. Creep feeding with small amounts of protein supplements that are high in undegraded intake protein may increase weight gains in nursing and weaned calves grazing high quality forages.

## Conclusions

High quality forages, such as subirrigated meadow regrowth, may be limiting in metabolizable protein for growth potential of weaned and suckling calves. Even though milk represents an important source of metabolizable protein, milk intake in late lactation may not be sufficient to support potential growth.

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# Comparative rumen and fecal diet microhistological determinations of European mouflon

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## Abstract

The population of European mouflon (*Ovis musimon* Pallas) established on an island of the sub-Antarctic Kerguelen archipelago is characterized by a demographic cycle. Every 2–5 years, there is a massive winter mortality due to food shortage. A good knowledge of food resources utilization appeared essential to understand the population growth dynamics. We investigated the validity of the microhistological analysis of feces by a comparative analysis of 30 paired rumen and fecal samples collected in winter. Sixteen and 17 food items were identified respectively in rumen and fecal samples. Most fragments could be accurately determined because plant diversity was low. Both methods gave similar results. Though quantitative differences appeared between methods for some items, the same 4 major food constituents were identified in relatively close proportions in both rumen and fecal samples. There is a risk of slight overestimation of annual meadow-grass (*Poa annua* L.) and mosses in feces, and of *Azorella selago* Hook. f. in the rumen.

**Key Words:** diet analysis, rumen, feces, *Ovis musimon*.

The population of European mouflon (*Ovis musimon* Pallas) present on Ile Haute (6.5 km<sup>2</sup>; 49°24'S 69°56'E), in the sub-Antarctic Kerguelen archipelago, originated from a pair introduced in 1957 (Léssel 1967). Since the end of the 1970's, the population has followed a cyclical demographic pattern during which population size fluctuated between approximately 250–300 and 700 individuals, with periodic die-offs due to undernutrition occurring every 2–5 years (Boussès et al. 1992, Réale 1996). The analysis of food resources utilization is thus central to understanding the population dynamics. It was however necessary to develop a non-invasive method to avoid disturbances of the population dynamics. The population diet was studied during 5 years using the fecal microhistological analysis. This method is limited in the analysis of complex diets (e.g. Stewart 1967, Scotcher 1979, Holechek and Gross 1982a, McInnis et al. 1983, Putman 1984), which often preclude identification to the species level. Moreover, the representation of diets obtained from feces and stomach content analyses can differ significantly (Anthony and Smith 1974, Hanley et al. 1985, Holisova et al. 1986, Lewis 1994). In this

## Résumé

La population de mouflon (*Ovis musimon* Pallas), établie dans une île de l'archipel de Kerguelen, présente une évolution cyclique de sa démographie. Tous les 2 à 5 ans, une mortalité massive des individus intervient par manque de nourriture. L'analyse de l'utilisation des ressources trophiques est essentiel pour expliquer la dynamique de la population. Dans ce but, la validité de la méthode basée sur l'analyse micrographique des fèces a été testée par la comparaison des contenus des panes et des fèces de 30 mouflons prélevés en hiver. Seize des 17 items consommés ont été trouvés respectivement dans les rumens et dans les fèces. La plupart des fragments peuvent être précisément identifiés en raison de la faible diversité en espèces végétales disponibles. Les deux méthodes donnent des résultats similaires, les 4 principales espèces consommées ayant été identifiées dans des proportions très proches dans les panes et les fèces. Cependant des différences quantitatives apparaissent pour quelques items dont la graminée *Poa annua* L. et les mousses, surestimées dans les fèces et *Azorella selago* Hook. f., surestimé dans les panes.

paper we examine the hypothesis that the fecal microhistological analysis is representative of the diet on Ile Haute by comparing it with rumen contents.

## Materials and Methods

The island landscape is a treeless area dominated by rocky and bare soils (68% of the area) while swards and meadows represent only 26% and peat bogs 6%. The number of native vascular plant species is limited to 31 in the Kerguelen archipelago (Greene and Walton 1975), of which only 10 are common on Ile Haute. These species include 3 grasses, *Agrostis magellanica* Lam., *Deschampsia antarctica* Desv. and *Festuca contracta* T. Kirk., a rush *Juncus scheuchzerioides* Gaud., some forbs *Azorella selago* Hook. f. (abundant), *Cotula plumosa* Hook. f., *Galium antarcticum* Hook. f., *Ranunculus biternatus* Smith, *R. pseudotrullifolius* Skottsberg, a dwarf shrub *Acaena magellanica* Vahl. and a fern *Blechnum penna-marina* Kuhn. Mosses are abundant in wetland areas. Some alien grasses (annual meadow-grass, *Poa annua* L., mainly) and forbs (*Cerastium fontanum* Baumg., *C. glomeratum* Thuill., *Sagina procumbens* L., *Taraxacum officinale* Wiggers) increased the carrying capacity of

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the island (Chapuis et al. 1994). On the seashore, 3 abundant algae species are available at low tide, *Ulva lactuca* L., *Durvillea antarctica* (Cham.) Har. and *Macrocyctis pyrifera* L.

For the purpose of this study, 30 mouflon ewes were shot on the island during the austral winter of 1994, from 21 July to 21 September. The rumen content was thoroughly mixed and one liter was collected, frozen in the field and then oven-dried at 65°C in the laboratory. Approximately 20 fecal pellets were obtained per mouflon and preserved in a 5% formalin solution. Biases due to differential plant fragmentation in rumen and fecal samples were overcome by dry-milling the rumen samples through a 2 mm screen (Sparks and Malechek 1968). After a 30 second maceration in sodium hypochlorite (Abbas 1988), rumen or fecal samples were washed through a 0.2 mm mesh sieve to eliminate small unidentifiable fragments (Sparks and Malechek 1968). No stain was used and subsamples were spread out on slides under 22 mm<sup>2</sup> cover slips. For each rumen and fecal sample, 4 microscope slides were prepared and plant fragments were counted in 25 microscope fields per slide at 100 magnification. An extensive photomicrographic reference collection of epidermal tissue from Ile Haute plant species was prepared and used to identify plant fragments. Isolated trichomes were not considered. The mean number of fragments examined per rumen and fecal sample was  $506 \pm 58$  (n = 60). Most epidermal fragments were identified to a species level. There were a few species with very similar epidermis (*Deschampsia antarctica*-*Agrostis magellanica*) and others we could only identified at a genus level (e.g. *Cerastium* spp., *Ranunculus* spp.). All the analysis were performed by the same trained observer, who practiced the technique for several years and previously determined the diet of various herbivores implanted in the Kerguelen archipelago.

We used the similarity index of Sørensen (1948) for qualitative comparison and the Schoener's Index (Schoener 1968) was applied to each individual mouflon's samples for quantitative comparison between rumen and fecal contents. Difference between rumen and fecal contents was tested using the Wilcoxon test (non parametric method for paired data, Sokal and Rohlf 1981). The relationships between data obtained from rumen and fecal materials were determined by least square linear regression (arcsin transformed) for food items with a normal dis-

Sørensen's Index

$$QS = 2a/b+c$$

Schoener's Index

$$PS = 1 - 0.5 \sum |p_i - q_i|$$

a: number of food items common to rumen and fecal contents

b: number of food items presents only in the feces

c: number of food items presents only in the rumen

p<sub>i</sub>: proportion of item i in the rumen

q<sub>i</sub>: proportion of item i in the feces

tribution, and by Spearman' rank correlation when the data were non-normal.

## Results and Discussion

Sixteen food items were identified in rumen samples and 17 in fecal samples (Table 1). The difference was due to the infrequent observation (1 to 3 fragments), of *Cotula plumosa* in only 6 fecal samples. All plant species identified in the rumen contents were also identified in the fecal samples. Thus, the list of plants consumed by the mouflons was slightly more complete in fecal than ruminal samples, a trend observed in many other studies (e.g. Owaga 1977, Hanley et al. 1985, Wallage-Drees et al. 1986) though some opposite results were also obtained (Smith and Shandruk 1979). As a result, the fecal analysis appeared to be appropriate for a qualitative study of the mouflon diet on Ile Haute. Moreover, the paired analysis of rumen and fecal contents of mouflons showed that the mean number of food items observed in the feces ( $12.1 \pm 2.0$ ) was significantly greater than in the rumen contents ( $10.1 \pm 2.2$ ;  $z = -3.98$ ,  $P < 0.001$ ). This result is usually attributed to the fact that fecal samples correspond to longer feeding periods than stomach contents (Anthony and Smith 1974, Wydeven and Dahlgren 1982, Lewis 1994). Consequently, and apart from the fact that animal sacrifice is not required, a major advantage of the fecal approach consists in the fewer sample sizes required to obtain a fixed level of qualitative precision. The mean Sørensen's Index (QS) between rumen and fecal samples was  $0.77 \pm 0.10$ . This index reached  $0.87 \pm 0.09$  when we considered only food items representing more than 1% of the plant fragments, and  $0.98 \pm 0.05$  when the representation level was elevated to 2%. This rapid increase of the QS index indicate that both methods were almost equivalent with regard to the major diet constituents.

The Schoener's Index (PS =  $80.8 \pm 6.7$ , range from 66.3 to 93.4) indicates both methods gave very similar results. In particular the 4 major items identified were the same in rumen and fecal contents: annual meadow-grass, *Azorella selago*,

*Juncus scheuchzerioides*, mosses (Table 1). Together, they represented more than 87% of the plant fragments identified in the feces and more than 91% of those found in the rumens. These dominant items were detected in all the fecal samples and in most rumen samples. The frequency of occurrence in fecal and rumen samples ranged from 7 to 97% (Table 1).

The paired comparison of the relative abundance of each item showed significant differences between rumen and fecal contents for 12 food items (Wilcoxon tests, Table 1). Most of these food items were more abundant in feces, especially annual meadow-grass (13.1% in feces versus 5.9% in rumens) and mosses (5.8% versus 2.8%). Exceptions were *Azorella selago* (61.1% versus 75.2%) and algae (0.4% versus 1.2%). The greater proportion of *Azorella selago* in rumen could be due to the particularly high fiber content of this plant, that increases the retention time in the rumen (Gaare et al. 1977, Owaga 1977). Nevertheless, *Azorella selago* remained by far the most abundant species by both methods, while the magnitude of differences between rumen and fecal samples was relatively small for the annual meadow-grass (6% and 13% respectively). Todd and Hansen (1973) suggest small statistical differences might be of little biological significance. Generally, grasses and mosses are over-represented in fecal materials, while forbs are under-represented (Batzli and Pitelka 1971, Neal et al. 1973, Anthony and Smith 1974, Vavra et al. 1978, Hanley et al. 1985, Wallage-Drees et al. 1986, Lewis 1994). The over-estimation of grasses is commonly attributed to the resistance of epidermis to digestive processes (Neal et al. 1973, Bartolome et al. 1995). The over-representation of mosses is linked to the fact that they fragment more than other plants during the digestive process and have very microscopically discernible epidermis. Consequently, minute fragments which are easily identified (Dearden et al. 1975) may be over-represented.

The relative abundance of food items in rumen and fecal samples were highly correlated (Spearman,  $Rho = 0.81$ ), especially for the 4 most highly consumed food items (Table 1): *Azorella selago* ( $r = 0.82$ ), annual meadow-grass ( $r = 0.73$ ), *Juncus scheuchzerioides* ( $r = 0.87$ ), Bryophytes ( $r$

**Table 1. Relative abundance (mean  $\pm$  SE), percent frequency of occurrence (% Freq.) and correlation coefficients (simple correlation when appropriate or Spearman' rank correlation) of food items in 30 rumen and fecal samples from mouflon ewes collected in winter 1994 on Ile Haute, Kerguelen archipelago. Differences between relative abundance in feces and rumen were tested using Wilcoxon tests.**

Plant species/taxon	Feces analysis (n=30)			Rumen analysis (n=30)			Wilcoxon test		Simple correlation (R)	Spearman' rank correlation	
	Mean	±SE	% Freq.	Mean	±SE	% Freq.	Z	P		Rho	P
Monocotyledons											
<i>Deschampsia/Agrostis</i>	2.15	2.10	90.0	2.16	2.07	96.7	0.39	NS	0.81	***	
<i>Festuca contracta</i>	0.57	1.03	63.3	0.69	1.06	53.3	0.75	NS	0.70	***	
<i>Poa annua</i>	13.14	8.75	100.0	5.89	4.85	100.0	4.68	***	0.73	0.73	***
Unidentified Graminaea	0.27	0.25	66.7	0.41	0.46	73.3	1.72	NS	0.10	NS	
<i>Juncus scheuchzerioides</i>	7.65	6.39	100.0	7.24	6.53	100.0	1.06	NS	0.87	0.88	***
Dicotyledons											
<i>Acaena magellanica</i>	0.02	0.06	13.3	0.01	0.05	6.7	0.41	NS	0.25	NS	
<i>Azorella selago</i>	61.14	14.36	100.0	75.17	10.64	100.0	4.64	***	0.82	0.82	***
<i>Cerastium</i> spp.	1.67	1.83	80.0	0.20	0.28	46.7	4.32	***	0.50	**	
<i>Cotula plumosa</i>	0.06	0.13	20.0	—	—	—	2.21	*	-		
<i>Galium antarcticum</i>	0.57	0.73	63.3	0.21	0.40	30.0	3.76	***	0.70	***	
<i>Ranunculus</i> spp.	0.22	0.47	40.0	0.04	0.09	20.0	1.99	*	0.10	NS	
<i>Sagina procumbens</i>	1.24	1.12	86.7	0.09	0.13	36.7	4.37	***	0.05	NS	
<i>Taraxacum officinale</i>	1.37	1.13	93.3	1.03	1.31	66.7	1.69	NS	0.50	**	
Unidentified Dicotyledons	1.57	1.28	90.0		1.00	1.12	76.7	2.68	**	0.63	***
Pteridophytes											
<i>Blechnum penna-marina</i>	1.12	1.26	83.3	0.32	0.67	50.0	3.98	***	0.54	**	
Bryophytes											
Algae	5.79	7.68	100.0	2.84	4.18	93.3	3.84	***	0.82	0.80	***
Unknown	0.36	0.78	33.3	0.95	1.20	63.3	2.17	*	-0.49	**	
	1.10	0.91	93.3	1.75	1.06	100.0	2.97	**	0.10	NS	

\*, \*\*, \*\*\* Significant at the 0.05, 0.01 and 0.001 levels respectively. NS: non significant.

= 0.82). Among other items, a high correlation existed for *Festuca contracta*, *Deschampsia/Agrostis* and *Galium antarcticum* (Spearman' rank correlation, Table 1). The only exceptions were 3 plant species which had a very low representation (*Acaena magellanica*, *Ranunculus* spp., *Sagina procumbens*) as well as the undetermined fragments.

## Conclusion

An accurate comparison between rumen and fecal methods requires 1) identical treatments of rumen and fecal samples by trained technicians (Westoby et al. 1976, Holechek and Gross 1982b); 2) correct samples size; 3) and the determination of most plant fragments. In our study, fecal and rumen samples were prepared similarly and examined by the same experienced person (point 1). Point 2 was also guaranteed by counting more plant fragments (approximately 500) per sample than the methods recommended. These usually range from 200 to 300 per sample (Chapuis 1980, Abbas 1988). Accurate determination of plant fragments was also obtained: 86.8% of the fragments observed were determined to a species level in feces and 90.6% in rumen samples. Most remaining fragments were determined to a genera or placed in broader categories (algae, bryophytes...). The proportion of totally

undetermined fragments was only  $1.1 \pm 0.9\%$  in the feces and  $1.8 \pm 1.1\%$  in the rumen. This result indicates that the micrographic method represents a significant improvement compared to the macroscopic volumetric method of rumen examination, which often result in a high proportion (up to 95%) of undetermined material (Edwards and Ritcey 1960, Bergerud and Russell 1964, Kessler et al. 1981). More importantly, the undetermined fraction is also reduced compared to many micrographic studies of herbivore diet (Zyznar and Urness 1969, Batzli and Pitelka 1971, Neal et al. 1973, Kessler et al. 1981, Homolka and Heroldova 1992, Lewis 1994). These results were due to the low diversity of food resources which limits misidentification of epidermal fragments.

It appears that both methods gave quite similar results on Ile Haute. All plant species identified in rumen were observed in fecal pellets, validating the fecal microhistological analysis from a qualitative viewpoint. Quantitative results from both methods were also very similar, particularly in regard to the major constituents of the diet. The microhistological analysis of feces seems thus applicable to a long term monitoring of diet variations of the mouflon population. In interpreting these results, we must however be aware that mosses and annual meadow-grass are probably slightly overestimated while

*Azorella selago* is underestimated by fecal studies compared to rumen analysis. The method will allow us to determine the relative temporal variations of species one to another, and thus to focus on important seasonal trends in the mouflons' diet.

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# Herbage response to precipitation in central Alberta boreal grasslands

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## Abstract

The dependence between grassland herbage production and precipitation within the Boreal region of central Alberta was evaluated. Additional objectives were to compare current year growing season (e.g., April or May, to August) precipitation with 12 and 16 month water year (e.g., dormant and growing season) precipitation for use in predicting herbage growth, and determine whether lowland and upland grasslands differ in their response to precipitation. Lowland herbage production averaged 6,053 kg ha<sup>-1</sup>, nearly twice the 3,153 kg ha<sup>-1</sup> found on upland grasslands during the study. In general, herbage production correlated significantly with precipitation, but the magnitude and direction of that relationship varied depending on grassland type. Uplands displayed a positive linear relationship with precipitation ( $r = 0.76$ ;  $p < 0.01$ ), while lowland communities displayed a negative curvilinear ( $R^2 = 0.65$ ;  $p < 0.05$ ) relationship. Furthermore, while herbage production on uplands was better predicted by current year precipitation, lowland production appeared more heavily dependent on precipitation falling during the water year, the latter of which included fall and winter moisture recharge. We hypothesize that these differences are linked to water redistribution within the landscape, along with subsequent soil temperature regimes and the length of effective growing season. Given the influence of topography in regulating water availability and use, rangeland managers within the Boreal region should use caution when determining rangeland carrying capacity from meteorological data.

**Key Words:** current year precipitation, lowlands, production, regression, uplands, water year

Maximum allowable stocking rates on rangeland are primarily determined by forage availability, which in turn is influenced by growing conditions. Although factors such as soil development can affect rangeland production (Cannon and Nielson 1984, Epstein et al. 1997), precipitation is perhaps the single most important determinant of forage production (Clarke et al. 1947, Coupland 1958, Lauenroth and Sala 1992). In particular, variability in forage production has been linked to fluctuations in precipitation within numerous studies conducted on both Shortgrass and Mixed Prairies (e.g., Rogler and Haas 1947, Smoliak 1956, 1986, Rauzi 1964, Hulett and Tomanek 1969, Epstein et al. 1997).

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## Resumen

Se evaluó la dependencia entre la producción de forraje del pastizal y la precipitación dentro de la región Boreal de la parte central de Alberta. Objetivos adicionales fueron comparar la precipitación de la estación de crecimiento del año actual (esto es, Abril o Mayo a Agosto) con la precipitación de 12 y 16 meses de agua año (esto es, estaciones de crecimiento y dormancia) para usarlos en predecir el crecimiento del forraje y determinar si los pastizales de tierras bajas y altas difieren en su respuesta a la precipitación. Durante el estudio la producción de forraje en tierras bajas promedió 6,053 kg ha<sup>-1</sup>, casi el doble de los 3,153 kg ha<sup>-1</sup> registrados en los pastizales de tierras altas. En general la producción de forraje se correlaciono significativamente con la precipitación, pero la magnitud y dirección de esa relación varió dependiendo del tipo de pastizal. Las tierras altas mostraron una relación lineal positiva con la precipitación ( $R^2 = 0.76$ ;  $p < 0.01$ ) mientras que las comunidades de tierras bajas mostraron una relación curvilínea negativa ( $R^2 = 0.65$ ;  $p < 0.05$ ). Además, mientras la producción de forraje en las tierras altas fue predicha mejor con la precipitación del año actual, la producción de las tierras bajas pareció ser más dependientes de la precipitación caída en el año agua, el cual incluye la recarga de humedad de otoño e invierno. Hipotetizamos que estas diferencias están ligadas a la redistribución del agua dentro del paisaje junto con los subsecuentes regímenes de temperatura del suelo y la longitud de la estación efectiva de crecimiento. Dada la influencia de la topografía en regular la disponibilidad y uso del agua, los manejadores de pastizales dentro de la región Boreal deben tener cuidado cuando determinen la capacidad de carga del pastizal a partir de datos meteorológicos.

Furthermore, these climatic influences may continue to regulate standing crop levels despite the application of various mechanical improvements (Haferkamp et al. 1993). The ultimate utility of precipitation data for explaining changes in primary production may be linked, however, to annual variation in the pattern of rainfall including its timing and frequency of occurrence (Ballard and Ryerson 1973).

The Boreal region is the largest forested zone in central Canada, covering up to 75% of the country (Rowe 1959). Nearly 40% of Alberta falls into the Dry and Central Boreal Mixedwood Ecoregions alone (Strong 1992), with upland vegetation dominated by trembling aspen (*Populus tremuloides* Michx\*), paper birch (*Betula papyrifera* Marsh.), and white spruce (*Picea glauca*

\*Nomenclature follows E.H. Moss (1983), Flora of Alberta, Univ. of Toronto Press.

[Moench] Voss). Jackpine (*Pinus banksiana* Lamb.) are common on sandy soils, and black spruce (*Picea mariana* [Mill.] BSP.), willows (*Salix* spp.) and sedges (*Carex* spp.) thrive in poorly drained areas. In general, open grasslands are confined to lowlands (e.g., wet meadow vegetation), or uplands where topographic and soil conditions, coupled with disturbances such as fire and grazing, restrict the encroachment of forest vegetation (Willoughby et al. 1996). Although only a small fraction of the typical boreal landscape consists of open grasslands, these areas produce a disproportionately large amount of the herbaceous forage available for ungulates. In British Columbia alone, wetlands have been estimated to provide up to 50% of the total forage needs for 25% of the beef cow herd (Van Ryswyk et al. 1995). As a result, these areas are the focus of considerable attention for both livestock and wildlife managers.

Despite the documented importance of the link between precipitation and productivity in prairie grasslands, little information exists on the relationship between precipitation and herbage production within grassland environments of the boreal region. Boreal rangelands, being dominated by forested vegetation and having precipitation:evapotranspiration (P:E) ratios equal or greater than 1.0 (Strong 1992), are often perceived as being non-limiting in moisture. This notion is untested, however, and additionally appears to make the assumption that drought management within the region is less of a concern during rangeland planning. Better information on the relationship between precipitation and herbage production would address this notion, as well as provide greater insight into the ecological response of these plant communities to climatic factors. Ultimately, this information could improve the ability of rangeland managers to use climatic variables such as precipitation to predict herbage growth, set appropriate long-term stocking rates, as well as anticipate potential shortages in forage availability.

Specific objectives of this study were to, (1) determine the effect of precipitation on boreal grassland herbage production, (2) compare the effects of current year and water year precipitation on herbage production, and (3) differentiate between the response of upland and lowland herbage production to inter-annual variation in precipitation.

## Study Area

Elk Island National Park (EINP) was chosen as the site to address the above

objectives. The park is situated near the southern limit of the Lower Boreal Mixedwood ecoregion (Strong 1992), directly adjacent to the Aspen Parkland. This area was chosen because data were readily available for individual plant communities from a long-term herbage monitoring program initiated in 1984 to assess carrying capacity throughout the Park. Furthermore, assessment of the relationship between precipitation and herbage production has direct relevance for Park managers given the relationship of herbage production to carrying capacity.

EINP is the only fenced National Park in Canada, and combined with the absence of large predators and abundant populations of bison, deer, elk, and moose, this Park faces the unique challenge of intensively managing ungulate populations (Telfer 1972). To avoid the die-offs that have historically occurred, surplus animal numbers are identified through annual aerial surveys, and removed with live trapping during the winter (Blyth and Hudson 1987). All of these management actions, however, are predicated on an accurate assessment of carrying capacity within the Park, as well as an understanding of how carrying capacity may fluctuate between years. Changes through time are particularly important as the greatest limitation in available forage occurs during winter (Bork et al. 1997), which is determined primarily by the success of plant growth the previous summer.

Given the need for detailed information regarding the status of available forage resources, a plan was implemented in 1984 that involved the annual monitoring of grassland composition and production from a fixed set of rangeland plant communities over time. This monitoring plan had 2 major objectives: provide an indication as to the extent of degradation in grasslands associated with potential overgrazing, and document changes in grassland carrying capacity through time so that animal numbers may be adjusted appropriately. The detection of significant reductions in total forage availability might allow Park managers sufficient opportunity (if necessary) to reduce ungulate populations. More recent reductions to manpower within the Park, however, have threatened the continuation of this rangeland monitoring program. As a result, alternative methods are being sought to reliably predict forage availability, including the use of climatic variables. This information would enable managers to bypass the labor intensive and expensive task of sampling individual plant commu-

nities throughout the Park, while still tracking short-term changes in ungulate carrying capacity.

Elk Island National Park is situated within the Beaver Hills (53°35'N, 112°50'W) of central Alberta, approximately 40 km east of Edmonton, Alberta, Canada. The Beaver Hills are part of the Cooking Lake Moraine, a terminal moraine deposited during Keewatin glaciation (Blyth and Hudson 1987). Vegetation in the region is considered to be an outlier of the Lower Boreal Mixedwood ecoregion directly to the north (Strong 1992). The area is characterized by strongly undulating topography and is approximately 60 m higher in elevation than the surrounding plains.

Soils are variable throughout the Park, but are mostly Orthic Grey Luvisols on uplands having developed under deciduous forest. Gleysolic and organic soils are common in depressional wetlands, with the latter associated with flooded fens and bogs (Crown 1977). In addition, a smaller region of Solonchic soil exists.

Although the majority of the Park is forested with *Populus tremuloides* and *P. balsamifera* L., numerous grasslands remain within the Park. Upland grasslands are dominated primarily by invasive grasses such as *Poa pratensis* L., *Bromus inermis* Leyss., and *Agropyron repens* (L.) Beauv., with *Trifolium repens* L. and *Taraxacum officinale* Weber co-dominant forbs. Native species include *Agropyron trachycaulum* (Link) Malte, *Calamagrostis canadensis* (Michx.) Beauv., and *Puchinellia nuttalliana* (Schult.) A.S. Hitchc. Lowland grasslands are dominated almost exclusively by *Calamagrostis canadensis* and various wetland *Carex* spp., including *C. atherodes* Spreng. and *C. aquatilis* Wahlenb. Solonchic soils are dominated by *Koeleria macrantha* (Ledeb.) and *Beckmannia syzigachne* (Steud.) Fern. (Blyth and Hudson 1987).

## Methods

To develop the relationship between precipitation and herbage production, data from the long-term rangeland monitoring sites distributed throughout the Park's 194 km<sup>2</sup> were used. Although the data available for upland range sites is nearly continuous for the years spanning the monitoring period 1984 to 1996, no data was available from 1986 because of Park staffing changes at that time. In addition, because 'year' was considered to be the experimental unit in this investigation, only those sites for which production data



was consistently available over all years were used in the analysis (i.e., intra-annual herbage production was averaged across all range sites). This process excluded several sites from the investigation that were added or removed at intermediate stages during the monitoring period. Two additional upland monitoring sites were excluded from the investigation due to poor range condition associated with excessive grazing (Blyth et al. 1993): one due to excessive ungulate use and the other to Richardson's ground squirrels (*Spermophilus richardsonii*). Both sites were removed before any analysis was conducted and only after consultation with Park staff regarding the condition of sites.

Monitoring sites were approximately evenly distributed between upland grasslands and lowland sedge meadows. At each site, a minimum of 4 range cages, 1.5 by 1.5 m in size, were used to exclude ungulate herbivory for the growing season, with peak production clipped annually the first 2 weeks of September. Other work within the Park (unpublished data) indicates that 4 plots are sufficient to stabilize individual estimates of herbage production within sampled grasslands. Range cages were re-randomized to new locations on each site every spring prior to the onset of vegetation green-up.

Original clip sizes were 1 m<sup>2</sup>, but were reduced to 0.25 m<sup>2</sup> (50 by 50 cm) in 1993 to improve sampling efficiency. All current annual vegetative growth was clipped at ground level and sorted into herbage and shrub components. Shrub growth was minimal and therefore excluded from the analysis. All clips samples were oven-dried at 75°C for 24 hours, and weighed to determine mean herbage production (kg ha<sup>-1</sup>) for each site, with all sites averaged to determine overall rangeland herbage production per year for the entire Park.

## Data Analysis

Data were analyzed separately for upland and lowland areas due to the different dominant plant species, soil types, moisture regimes, and microclimates found within each area. The collection of lowland production data did not begin until the late 1980's, and as such, was pooled from 5 sites within each year for the period 1988 to 1996, inclusive (n = 9 years). Upland productivity data were also pooled for 5 sites in each of the years from 1984 to 1996, inclusive, but excluded 1986 (n = 12 years).

In addition to the upland grasslands, 2 additional sites were examined separately from the rest as they were located on

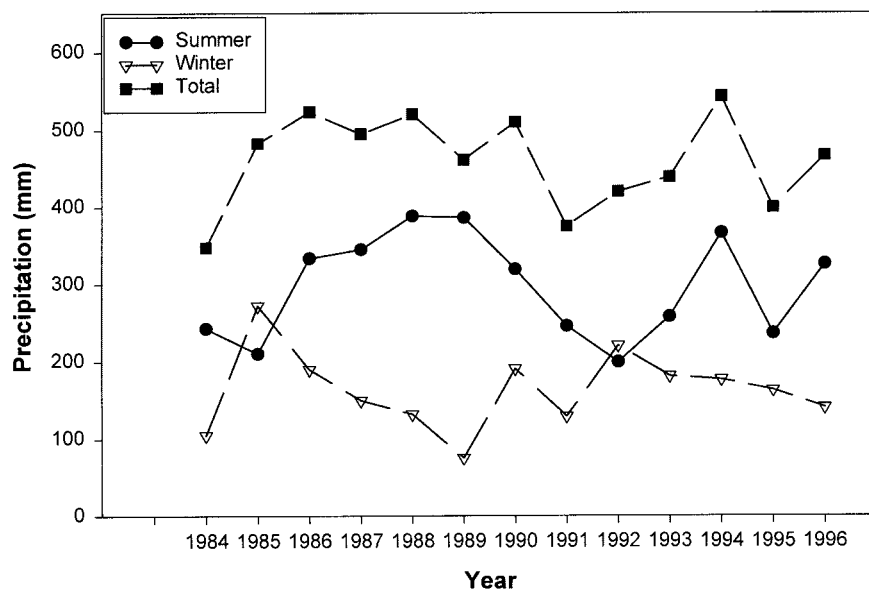


Fig. 1. Winter (Sept. to April), summer (May to August), and total (Sept. to August) precipitation for Elk Island National Park, from September 1983 to August, 1996.

Solonchic soils within the Park (n = 8 years). These areas, because of their unique soil features and obvious limitations in terms of plant growth, were of additional interest to Park managers and thus, included within the analysis.

Precipitation data was obtained from an Environment Canada weather station centrally situated within the Park. The maximum linear distance of the most distant sampling site from the station was approximately 16 km, with most sites within a radius of 12 km. For the analysis, 4 time intervals were chosen: 2 current year periods including May to August (4 month current growing season) and April to August (5 month extended growing season), as well as 2 water year periods. The latter included the preceding September to current August (12 month) period, as well as the preceding May to current August (16 month) period. These were chosen to assess the importance of previous year moisture recharge in affecting herbage production, as several studies have highlighted the importance of recharge moisture in contributing to forage production (e.g., Noller 1968, Smoliak 1986). Actual precipitation data for the area over the duration of the study are shown in Figure 1, with the precipitation variables summarized in Table 1. Four month growing season precipitation averaged 322 mm, ranging from 200 to 389 mm during 1984 to 1996. In contrast, 12 month water year precipitation averaged 477 mm, varying from 375 to 557 mm.

Initially, linear regression of precipitation with herbage yield was used to assess

the predictability of forage production (dependent variable) from precipitation. Second order regressions were also performed, with increases in R<sup>2</sup> evident for the lowland data (e.g., increases in R<sup>2</sup> ranged from 0.04 to 0.27). Significance parameters were used to assess the reliability of all resulting regressions, facilitating comparisons between upland and lowland data sets, as well as between data sets involving current year and water year precipitation.

## Results and Discussion

Average herbage production for all sites in each year are shown in Table 1. Lowlands yielded nearly twice the herbage from upland sites. This difference is likely due to the shortage of water that occurs on uplands in mid to late summer after soil moisture reserves are depleted and rainfall is unable to meet evapo-transpiration demands. The Solonchic sites sampled yielded slightly more than the upland sites, but well below the lowland sites (Table 1). These areas benefit from being lower in elevation than upland sites and therefore, have an increased susceptibility to spring flooding, but suffer from the presence of a clay hardpan and elevated salt levels, which limit plant growth and overall productivity.

Absolute linear correlation coefficients among the 12 regressions varied from 0.35 to 0.76 (Table 2). The greatest correlations with herbage production were evident for upland grasslands using current year precipitation data (Table 2; Fig. 2a). Both 4 and 5 month current year (e.g., growing season) precipitation exhibited significant positive relationships (p < 0.01) with

**Table 1. Average grassland herbage yields and precipitation levels for EINP from 1984 to 1996.**

Year	Average Annual Forage Yield			Current Year Precipitation		Water Year Precipitation	
	Upland (n=12)	Solonetz (n=8)	Lowland (n=9)	May - Aug. (4 month)	April - Aug. (5 month)	Prev. Sept.- Aug. (12 month)	Prev. May - Aug. (16 month)
	----- (kg.ha <sup>-1</sup> ) -----			---- (mm) ----		---- (mm) ----	
1984	3174			243	258	426	735
1985	1080			211	253	483	726
1986*	n/a			334	358	557	767
1987	2931			345	346	495	829
1988	3278	2891	5111	389	414	521	866
1989	4554	4901	4595	387	397	502	890
1990	3218	3390	5030	320	345	511	897
1991	2721	2373	7889	246	264	375	694
1992	2318	2372	5474	200	241	420	666
1993	3207	3180	5889	258	301	439	639
1994	4287	4780	6113	367	374	543	801
1995	2722	4536	6418	236	263	400	766
1996	3954		7954	326	362	467	703
Mean	3120	3553	6053	291	322	477	775
SD	920	1047	1201	67.8	57.9	56.8	84.9

\*No data was collected in 1986 from the monitoring sites.

upland herbage production (Table 2). In contrast, water year precipitation was a poorer predictor of herbage production on upland grasslands within the Park.

Overall, these correlations are lower than those reported by researchers conducting similar studies within the northern plains. For example, in SE Kansas, Shiftlet and Dietz (1974) found May to September (inclusive) precipitation was highly correlated with total growing season production ( $r = 0.893$ ). Working in southern Alberta, Smoliak (1956) also found a high correlation ( $r = 0.859$ ) for May and June precipitation with production. Both of these studies, however, were conducted in prairie environments, where production is expected to depend heavily on growing season precipitation. The results found in our study suggest that similar to the Mixed Prairie, Boreal upland grassland production is heavily dependent on summer pre-

cipitation, and as a result, these areas remain prone to significant variations in forage production with summer drought. Spatial separation between forage sampling sites and the precipitation monitoring station may also have contributed some error into the regression relationships (Perry 1976).

The relatively poor relationship observed between water year precipitation and upland herbage production is contrary to the findings of Smoliak (1986) and Johnston et al. (1969), who found that Dry Mixed Prairie production in southern Alberta was best explained by incorporating fall precipitation. This may be due to the topographical differences found within Boreal and Mixed Prairie landscapes. Dormant season moisture recharge would only be expected to enhance forage production if contributing to soil moisture availability. Boreal environments, to

which the park is no exception, often consist of steeply sloped topography (e.g., gradients of 5–15%). Coupled with deeply frozen ground for 6 months or more during the winter, any snow falling and melting during the dormant season is likely to run off from these areas. Furthermore, snow is more likely to be redistributed from uplands to low-lying topographic positions during the winter months with drifting, rendering it inaccessible when spring growth resumes. Although runoff losses have been cited as one of the potential factors limiting the effectiveness of heavy summer rainfall in prairie environments (e.g., Albertson and Weaver 1942), the Dry Mixed Prairie landscapes of southern Alberta are generally flatter than those in the Boreal region. Coupled with milder and shorter winters, opportunities for water infiltration are likely greater, which may make these rangelands less susceptible to seasonal water re-distribution in the landscape.

Upland grasslands within the Park have been documented as generally in poor to fair range condition (Blyth et al. 1993, Bork et al. 1997). As a result, there is the possibility that part of the sensitivity of herbage production to precipitation variability is attributable to range condition. Despite this, other studies correlating production with precipitation indicate that while degradation associated with overgrazing may exacerbate forage reductions during drought years, productivity often continues to be more sensitive overall to changes in precipitation than grazing intensity (e.g., Milchunas et al. 1994). In addition, it must be noted that the poor condition ratings in the Park are primarily due to the abundance of undesirable introduced (e.g., exotic) plant species such as Kentucky bluegrass (*Poa pratensis* L.), rather than actual declines in plant vigor or

**Table 2. Results of the regression of precipitation on herbage production for EINP.**

Area:	Years:	Precipitation Variable*:	Simple Correlation		Second-Order Regress.	
			(r):	p-value:	Model R <sup>2</sup> :	p-value:
Uplands	1984-1996 (omitting '86) (n=12)	CY—May to August	0.76	p<0.01	—	—
		CY—April to August	0.74	p<0.01	—	—
		WY—Sept. to Aug.	0.45	p=0.20	—	—
		WY—May to Aug.	0.41	p=0.25	—	—
Solonetz	1988-1995 (n=8)	CY—May to August	0.50	p=0.21	—	—
		CY—April to August	0.44	p=0.28	—	—
		WY—Previous Sept. to Aug.	0.45	p=0.27	—	—
		WY—Previous May to Aug.	0.50	p=0.21	—	—
Lowlands	1988-1996 (n=9)	CY—May to August	– 0.35	p=0.36	0.36	p=0.26
		CY—April to August	– 0.35	p=0.35	0.23	p=0.46
		WY—Previous Sept. to Aug.	– 0.54	p=0.14	0.33	p=0.30
		WY—Previous May to Aug.	– 0.61	p=0.08	0.64	p<0.05

\* CY - denotes current year precipitation; WY - denotes water year precipitation, which includes the previous summer and/or dormant season recharge period.

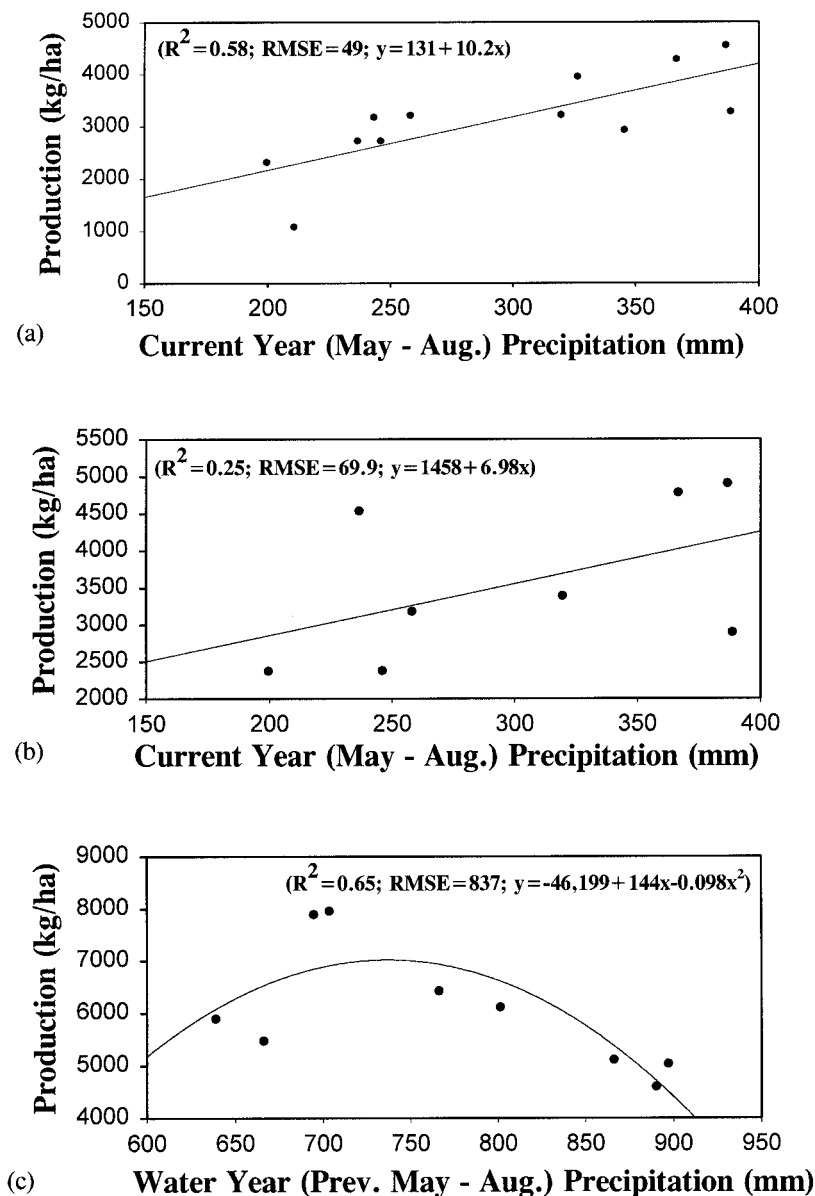


Fig. 2. Regressions of the leading climatic variable with herbage production for each of the (a) upland grasslands, (b) Solonchic sites, and (c) lowland grasslands.

site degradation such as soil erosion. Repeated grazing in the past may also have altered the effectiveness of nitrogen cycling on uplands, particularly within a National Park where intensive management (e.g., fertilization) never occurs. Repeated vegetation removal coupled with nutrient redistribution and losses from animal waste (Parton and Risser 1980), may have produced soil N-impooverished plant communities limited in their ability to respond to increased rainfall.

Separate regression analysis of the 2 sampling sites on Solonchic soils showed a weak positive relationship ( $p = 0.21$ ) for each of the 4 precipitation variables inves-

tigated (Table 2, Fig. 2b). Solonchic soils are characterized by a highly compacted clay pan B-horizon, which impedes water and air penetration as well as root development. Perched water tables are common above the B horizon, and high sodium levels may further limit the water available to plants. Plant growth is spatially patchy, with production probably linked to a complex of factors, including species composition, opportunities for root development, and moisture availability. Salt concentrations, which can reach levels that inhibit growth, vary widely over short distances (Cairns and Bowser 1977). Spatial heterogeneity within these areas is also likely to

complicate the accurate assessment of herbage production. The weak positive correlation between herbage production and current year precipitation on Solonchic soils (Fig. 2b) may arise from enhanced moisture availability within the perched water table, as well as the direct dilution of salts (Donahue et al. 1977).

Similar to upland areas, lowland herbage production displayed a significant ( $p < 0.05$ ) relationship with precipitation (Table 2). Unlike the uplands, however, this relationship followed a negative curvilinear function (Fig. 2c). This suggests that within the Boreal environment, levels of precipitation above a specific threshold impede rather than enhance plant growth within wetlands.

The negative response of lowland herbage to high precipitation is most likely linked to soil temperatures. Average growing seasons within the Boreal region are less than 90 days (Strong 1992). Wet or saturated soils take longer to warm in the spring than well-drained uplands, delaying and slowing plant growth throughout the spring and into summer (Donahue et al. 1977). The length of the effective growing season within these areas may fall to levels well below 90 days. Excess moisture may also create a soil environment that is oxygen deficient, lowering root respiration and subsequent plant growth.

The negative effect of precipitation on lowland herbage production also appears to be linked to the timing of precipitation. Overall, water year precipitation resulted in improved relationships with herbage production than current year precipitation (Table 2). When regressed as a second order polynomial against herbage production, 16 month water year precipitation produced a superior fit to all other precipitation variables (Fig. 2c). These results are likely attributable to lowlands accumulating much of the redistributed snow and surface runoff (e.g., meltwater) deposited the previous fall and winter. Hence, greater overwinter precipitation is more likely to delay spring growth. Rumberg and Sawyer (1965) tested the production response of native wet meadows to flooding and found similar results. They concluded that while shallow flooding increased total production, flooding depths equal or greater than 5 inches (12.5 cm), and which were 50 days or longer in duration, actually reduced yields. The relatively greater dependency of lowland production on 16 month water year demonstrated here may indicate that moisture recharge begins either well in advance of the previous fall, or that elevated sequential grow-

ing season and dormant season precipitation may compound one another to further restrict lowland herbage growth the following year.

Overall, these results indicate that Boreal grassland production is very site (e.g., topographic position) specific, a trend which has been observed in prairie ecosystems by other researchers (Wight et al. 1984). As a result, generic relationships relating precipitation to forage production should be avoided. For example, it has been shown that different soil types with differing production capabilities are not directly applicable to other areas (Sneva and Hyder 1962). In this study, topographic position interacted with precipitation to effect herbage production. This supports the notion that production models should not be used for sites and environmental conditions beyond that from which they were developed. These findings agree, however, with the conclusion of Collins and Weaver (1978), that precipitation levels can be an effective determinant of herbage production, provided it is recognized that the actual response will depend heavily on the timing and nature of the precipitation, as well as the potential of the specific plant community to respond to increased moisture.

## Conclusion

Contrary to the frequently held notion that moisture is non-limiting for plant growth within the boreal region, upland herbage production within boreal grasslands is directly dependent on precipitation, particularly that which falls during the growing season (May to August). These results parallel those found for the major prairie rangeland ecosystems in western Canada, and have implications for ranchers and rangeland managers working within boreal ecosystems.

Although upland production is positively correlated with precipitation, lowland meadows appear to be negatively effected by high levels of precipitation. In these situations, the accumulation of excessive moisture, particularly during the previous dormant season when precipitation and snowmelt may accumulate within lowlands, appears to reduce herbage production. These results indicate that topographic position is an equally important factor to consider in the modeling of herbage production in relation to precipitation, particularly within boreal environments.

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# The nutritive quality of cholla cactus as affected by burning

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## Abstract

Cholla cactus may serve as an emergency feedstuff for livestock when forage availability is low. A study was conducted at the Corona Range and Livestock Research Center to evaluate the nutritive quality of cholla cactus (*Opuntia imbricata*) after spine removal. Six samples were collected for each treatment in a completely randomized design. Treatments consisted of spine removal by burning with a propane torch (BURN), or leaving spines intact (UN). Each sample consisted of 2 burned and 2 unburned cladodes from each of 5 plants. One sample from each treatment was weighed immediately after collection and used solely for dry matter (DM) determination. Remaining samples were evaluated for crude protein (CP), organic matter (OM), neutral detergent fiber (NDF), and mineral composition. Rate and extent of ruminal DM and OM disappearance were estimated in situ for 20 and 68 hours in the rumen of each of 2 cannulated cows grazing native rangeland. Dry matter contents of burned and unburned cholla were 12.7% and 12.4% respectively. Crude protein was not affected by burning ( $P > 0.6$ ; 13.0% UN, 13.6% BURN,  $SE \pm 0.7$ ). Burning reduced OM (82.4% UN, 81.0% BURN;  $SE \pm 0.4$ ) and NDF (48.6% UN, 39.2% BURN;  $SE \pm 1.8$ ) content ( $P < 0.03$ ). Reduced NDF contributed to increased rate and extent of ruminal OM disappearance for burned cholla ( $P < 0.03$ ). Mineral content was minimally affected by burning. Measurements indicate that cholla has relatively high nutrient quality, but the high moisture content would require large amounts to be fed as an emergency feed source.

**Key Words:** drought forages, mineral content, emergency feeding

Drought is a frequent and recurring situation on western rangelands. A major problem created by drought is depletion of quantity and quality of forage available for livestock. Dormant forage is often limiting in both total and available crude protein (Krysl et al. 1987) and the lack of new forage growth combined with continued forage demand may create a shortage of grazeable forage. This situation must be addressed by removal of livestock, provision of emergency feedstuffs, or some combination thereof.

Characteristics of ideal emergency feedstuffs include adequate nutritive quality to meet realistic production goals, abundant and available supplies, and minimal cost. Hay and grains may not contain an adequate nutrient balance to meet animal requirements; additionally, these sources may be in short supply or prohibitively expensive during drought situations. An alternative to these "traditional" emergency feeds is the feeding of cactus.

## Resumen

La "Cholla" una especie cactácea puede servir como alimento de emergencia para el ganado cuando la disponibilidad de forraje es baja. En el Centro Corona de Investigación en Pastizales y Ganado se condujo un estudio para evaluar la calidad nutritiva de la "Cholla" (*Opuntia imbricata*) después de remover las espinas. Se colectaron 6 muestras por tratamiento bajo un diseño completamente al azar. Los tratamientos consistieron en: 1) la remoción de la espina con fuego utilizando un soplete de gas propano (quemado) y 2) dejando intactas las espinas (sin quemado). Cada muestra consistió de 2 cladodios quemados y 2 sin quemar colectados en 5 plantas. Una muestra de cada tratamiento se pesó inmediatamente después de colectada y fue utilizada únicamente para determinar materia seca (MS). En las muestras restantes se determinó la proteína cruda (PC), materia orgánica (MO), fibra neutro detergente (FND) y la composición mineral. La tasa y cantidad de desaparición ruminal de la materia orgánica y materia seca se estimó in situ a las 20 y 68 h, la estimación se realizó en el rumen de cada una de 2 vacas canuladas apacentando pastizal nativo. Los contenidos de MS de la "Cholla" quemada y sin quemar fueron 12.7% y 12.4% respectivamente. La proteína cruda se afectó por la quema ( $P > 0.6$ ; 13.0% sin quema, 13.6% con quema  $SE \pm 0.7$ ). La quema redujo el contenido de MO (82.4% sin quema; 81.0% con quema  $SE \pm 0.4$ ) y la FND (48.6% sin quema y 39.2% con quema  $SE \pm 0.7$ ). El bajo contenido de FND contribuyó a aumentar la tasa y cantidad de desaparición de la MO de la "Cholla" quemada ( $P < 0.03$ ). El contenido mineral fue afectado minimamente por la quema. Las mediciones indican que la "Cholla" tiene una calidad nutritiva relativamente alta, pero por su alto contenido de humedad se requerirían grandes cantidades para ser una fuente de alimento de emergencia.

Cactus has been used as an emergency feedstuff for many years (Griffiths and Hare 1906; Wooten 1911) and may meet the criteria of availability on rangelands where large stands of cacti exist. Providing cactus as an emergency feed may be less expensive than feeding hay (Hanselka and Paschal 1990). Most reports have concentrated on prickly pear cactus, and little current information is available on the nutritive quality of cholla cactus, which is more abundant than prickly pear on central New Mexico rangelands (Pieper et al. 1974). Early reports concerning the feeding of cacti describe both burning and chopping as methods of provision (Griffiths and Hare 1906, Thornber 1911). Therefore, the objectives of this study were to describe the nutritive quality of cholla cactus during a drought, and to evaluate the effects of burning on measures of nutritive quality.

## Materials and Methods

### Study Area

The experiment was conducted at New Mexico State University's Corona Range and Livestock Research Center located 15 km east of Corona (Lat 34.26°N, Long 105.41°W). Elevation at the site is 1900 m and average annual precipitation is 400 mm with a majority occurring during the summer months as brief but intense convectional thunderstorms. Total precipitation from June 1994 through May 1996 (i.e., the 24 months preceding sampling) was 518 mm (Fig. 1). Average precipitation over this time span is 794 mm (Krysl et al., 1987), so that only 65% of normal precipitation had been received during this period. Major forage species include blue grama (*Bouteloua gracilis* (H.B.K.) Lag. Ex Steud.) and wolf tail (*Lycurus phleoides* H.B.K.) with minor components of other species. Walkingstick cholla (*Opuntia imbricata* (Haw.) D.C.) can be an important part of the plant community, sometimes forming dense stands.

### Sampling Methods

Sampling was conducted during June 1996. This sampling time occurred after a long period of below average precipitation, and is reflective of drought conditions under which cholla would likely be utilized as a feedstuff. A transect was marked in a randomly chosen direction across a large stand of cholla. The cholla in this stand ranged from 30 cm to 200 cm in height. Plants were from 1 m to 5 m apart.

Clippings were obtained from plants intersecting the transect. Clippings consisted of terminal cladodes from the intersected plant (excluding buds) and were considered representative of portions cattle might naturally select based upon observation of rumen digesta in cannulated animals. Two paired clippings were collected from each of 25 plants. One of each pair was burned with a propane torch until all spines had been removed (BURN), but little or no singeing of the green plant material had occurred. The spines of the remaining clipping from each pair were left intact (UN). Burned and unburned clippings from each of 5 plants were combined to form 1 sampling unit, so that in total 5 samples were collected for BURN and UN. An additional sample was collected in a similar manner and used solely for determination of dry matter content.

### Chemical Analyses

After collection, the sample collected for dry matter determination was immediately weighed, diced, and then dried in a forced air oven at 100°C for 24 hours. All remaining samples were diced and dried in a forced air oven at 40°C to a constant weight and ground through a Wiley mill to pass a 2 mm screen. Samples were analyzed for crude protein content by micro Kjeldahl methods (AOAC 1990) and for neutral detergent fiber content (Goering and Van Soest 1970). Samples were analyzed for ash content by ignition in a muffle furnace at 500°C for 6 hours.

To determine ruminal degradability (as a measure of digestibility), equal amounts

of each sample were composited within treatment. Three grams dry matter (DM) of composited material was placed into each of 8 Dacron bags (10 cm X 20 cm, 44 mm average pore size; Ankrom Technology Corp., Fairport, N.Y.) per treatment. Four bags from each treatment were incubated in the rumen of each of 2 cannulated cows grazing native rangeland pastures at the Corona Research Center. Two bags were removed from each cow after 20 hours and 68 hours of incubation. Bags were frozen immediately to cease fermentation. Frozen bags were thawed at room temperature and rinsed with cool tap water until effluent was clear. Bags were then dried in a forced air oven 40°C to a constant weight to determine ruminal DM disappearance. A sample of the residue from each bag was ashed as previously described to determine organic matter (OM) disappearance.

Mineral composition was determined by an independent laboratory using ICP methodology (Agricultural Analytical Services Laboratory, University Park, Penn.). Minerals assayed were P, K, Ca, Mg, Mn, Cu, Al, and Zn. Crude protein and neutral detergent fiber content, mineral composition, and ruminal degradability were used as estimators of nutritive quality.

### Statistical Analysis

Results of the dry matter determination were not subjected to statistical analysis since the sample was not replicated. The DM values obtained are therefore used for descriptive purposes only. Other data were analyzed by analysis of variance using the General Linear Models procedures of the Statistical Analysis System (SAS 1992) for a completely randomized design. Chemical composition data were analyzed with treatment (BURN or UN) as the only effects in the model. Ruminal dry matter and organic matter disappearance data were analyzed by time with cow and treatment as effects in the model. The shorter incubation is reflective of the rate of ruminal degradation, while the longer incubation describes potential extent of ruminal degradation.

## Results and Discussion

Sample collection was conducted in June following 2 years of low precipitation (Fig. 1). Early summer represents a time when managerial decisions concerning drought management strategies are often implemented, and the sampling time was reflective of conditions in which cac-

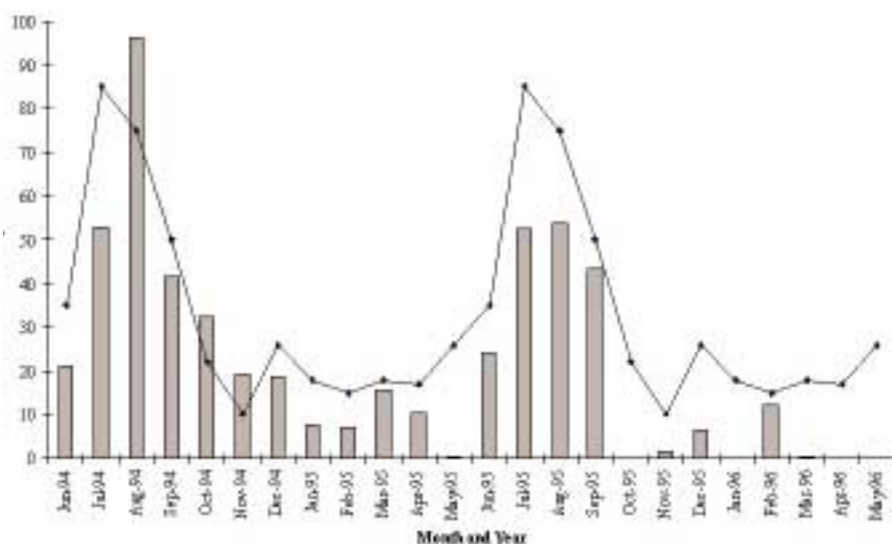


Fig. 1. Precipitation (mm) by month from June 1994 through May 1996 (bars) and long term average monthly precipitation (line) at the Corona Range and Livestock Research Center.



**Table 1. Crude protein (CP), neutral detergent fiber (NDF), organic matter (OM) and dry matter percentages for burned and unburned cholla cactus.**

Item	Unburned	Burned	SE <sup>a</sup>	OSL <sup>c</sup>
	----- (%) -----			
CP <sup>b</sup>	13.0	13.6	0.7	P > 0.59
NDF <sup>b</sup>	48.6	39.2	1.8	P < 0.005
OM <sup>c</sup>	82.4	81.0	0.4	P < 0.03
DM <sup>d</sup>	12.4	12.7	--	--

<sup>a</sup>n = 5

<sup>b</sup>expressed as a percentage of OM

<sup>c</sup>expressed as a percentage of DM

<sup>d</sup>as fed basis

<sup>e</sup>observed significance level

tus feeding might be employed. Dry matter content of sampled cholla cactus averaged 12.5% (Table 1). Samples were collected 1 week following a 55 mm rainfall event, and increased soil moisture may have affected the moisture content of the cholla. Griffiths and Hare (1906) demonstrated up to a 9% increase in moisture content in prickly pear cactus sampled 1 year apart when the rainfall 3 months prior to sampling increased. Shoop et al. (1977) reported DM values for prickly pear ranging from 14.6% in June to 45.8% in February in Colorado. Dry matter content of cholla cactus in New Mexico was lowest (16% to 20%) during the summer and increased to 38% during February (Pieper et al. 1974). For several species of cactus, DM content ranged from 8% to 33.5% (Griffiths and Hare 1906). These authors reported an average DM content of 12% for walkingstick cholla, while Vinson (1911) reported a DM content of 22% and Vega-Villasante et al. (1997) reported 20% DM for walkingstick cholla and *Opuntia cholla*, respectively.

Although most reports agree that the DM content of cactus reaches a nadir in the summer months, moisture content is always relatively high. Feeding high moisture feeds may be beneficial in situations when the diet is of low quality (as in drought conditions). Pasha et al. (1994) found that as moisture content of the diet increased, ruminal passage rate increased. When available forages contain a high level of indigestible constituents, increasing passage rate may increase intake (Van Soest 1994). While intake may be impaired if the DM content of the diet is less than 25% (Arnold 1962, Minson 1966) it is unlikely that enough of the diet would consist of cholla to achieve such an effect.

Cacti in general are slow growing perennials, and do not appear to exhibit dramatic fluctuations in nutrient quality with changing season (Shoop et al. 1977) when

determined on a DM or OM basis. The fluctuation in moisture content may affect total DM intake, but does not affect the nutrient composition of the plant; therefore, temporal variation is probably not an important consideration when evaluating the nutritive quality of cholla for potential use as an emergency feedstuff within a given location, although large variation in quality may exist between species of cacti.

Crude protein content was not affected by spine removal in cholla cactus (P > 0.5; Table 1). These values are higher than most others reported for prickly pear cactus or cholla. Values for prickly pear cactus range from 5.9% to 6.5% (OM basis; Bath et al. 1995, NRC 1970, Shoop et al. 1977). The estimates from Bath et al. (1995) and NRC (1970) are composite values based on a large number of samples, and the value reported by Shoop et al. (1977) is similar to these composite estimates. In another study, Meyer and Brown (1985) reported a much higher crude protein level in prickly pear cactus of 14.1%. This single value appears to be well outside the range of other reported values, and illustrates the potential variation among locations. Griffiths and Hare (1906) reported a range of CP values across several species of cacti at various locations in New Mexico, Arizona, and northern Mexico from 1.75% to 10.7%, while Vinson (1911) reported a mean CP value for cholla of 7.5%. More recently, Vega-Villasante (1997) observed CP content of 3.8% in *Opuntia cholla* Weber, although this species is from Baja California. As with prickly pear, location and species may be important determinants of cholla quality. The crude protein levels observed in this study are at the high end of the range of reported values; however cholla cactus in general contains a higher amount of CP than prickly pear (Griffiths and Hare 1906, Wooten 1911) at a given location.

Mature beef cows in mid lactation (early summer in a spring calving herd) require between 8.5% and 10% CP in the diet (NRC 1996). Cow diets sampled from a pasture near the study site at the Corona Range and Livestock Research Center were 6.3% CP 2 weeks before this study (Sawyer et al. 1997). Since the majority of reported values for prickly pear are below 7% CP, cattle that are maintained for long periods on dormant forage/prickly pear diets require protein supplementation (Hanselka and Paschal 1990). However, if 45%–55% of the diet could be supplied as cholla, cows could be maintained without protein supplements. If this proportion of

cholla in the diet could not be achieved, the protein contribution of the cholla would still reduce the amount of additional supplement required to maintain cattle as compared to prickly pear.

Burning the spines off of cholla cactus reduced the NDF content of cholla (P < .01; Table 1). The NDF content for burned cholla is comparable to the 34.0% NDF reported by Shoop et al. (1977) for burned prickly pear. This low value indicates that cholla contains a high amount of soluble carbohydrates and that it may be a source of rapidly fermentable energy. In situ disappearance of OM supports this premise (Table 2). Burned samples had a greater in

**Table 2. Ruminal organic matter disappearance of burned and unburned cholla cactus after 20 hours or 68 hours of incubation.**

Time	OM Disappearance		SE <sup>a</sup>	OSL <sup>b</sup>
	Unburned	Burned		
(hours)	----- (%) -----			
20	66.3	77.3	2.4	P < 0.03
68	77.0	86.9	1.3	P < 0.005

<sup>a</sup>n = 4

<sup>b</sup>observed significance level

situ disappearance at 20 hours (P < 0.05) as well as after 68 hours of incubation (P < 0.05). This indicates that the rate and extent of ruminal degradation were enhanced by spine removal. When prickly pear cactus was incubated in situ for 48 hours, 66.4% of the DM disappeared (Shoop et al. 1977) while Meyer and Brown (1985) reported an IVDMD of 75.7% for prickly pear.

The ash content of cacti in general is variable and often quite high. The organic matter content of cholla was slightly reduced by burning (P < 0.05; Table 1). Although this difference was statistically significant, it is of doubtful biological significance. Organic matter content of prickly pear ranges from 79.8% (Meyer and Brown 1985) to 86.5% (Shoop et al. 1977). Griffiths and Hare (1906) determined the OM of walkingstick cholla to be 78.9%. In contrast, *Opuntia cholla* from Baja California was reported to have an ash content of only 5.1% (Vega-Villasante et al. 1997).

The high ash content of cacti is reflected by an accumulation of minerals. The content of selected minerals in burned and unburned cholla cactus is shown in Table 3. Spine removal decreased the amount of aluminum and zinc in cholla cactus (P < 0.07) but did not affect any other minerals examined.

**Table 3. Selected mineral composition of burned and unburned cholla cactus, and suggested mineral requirements and tolerances for beef cows.**

Mineral (units)	Treatment		SE <sup>a</sup>	OSL	Req. <sup>b</sup>	Max. <sup>b</sup>
	Burned	Unburned				
Calcium (%)	4.85	4.56	0.13	P>.14	.20-.30	—
Phosphorus (%)	0.17	0.16	0.01	P>.50	.18-.22	—
Potassium (%)	2.19	2.08	0.13	P>.56	.6-.7	3.0
Magnesium (%)	0.66	0.61	0.02	P>.13	.1-.2	.5
Manganese (ppm)	73.0	75.20	4.78	P>.75	20-40	1000
Copper (ppm)	4.8	5.00	0.26	P>.60	10-12	100
Aluminum (ppm)	91.8	115.60	8.15	P=.07	—	1000
Zinc (ppm)	10.6	24.40	3.39	P=.02	30-40	500

<sup>a</sup>n = 5

<sup>b</sup>adapted from NRC, 1996.

The phosphorus contained in cholla approaches the dietary requirement of a beef cow (NRC 1996). Since dormant forage is generally low in P, it is likely that additional P would need to be supplemented since cholla would not comprise the entire diet. Additionally, the high accumulation of calcium in the cactus creates a Ca:P ratio of 29:1. Other authors have reported an accumulation of Ca by cacti (Shoop et al. 1977, Hanselka and Paschal 1990) with Ca:P ratios potentially exceeding 20:1 (Griffiths and Hare 1906). The maximum acceptable ratio of Ca:P in cattle diets is approximately 10:1 (NRC 1996), therefore additional P supplementation would be necessary if large amounts of cholla are to be fed.

Potassium in cholla is well above animal requirements, but is below maximum tolerable levels, indicating that cholla is a good source of K in the diet. Potassium in dormant forage at this location was well below animal requirements (0.29%; Knox 1998), so that feeding cholla would improve K supplies. Magnesium in cholla is above the maximum tolerable level for beef cows; however, dormant forage at this location was very low in magnesium (0.05%; Knox 1998). Additionally, high potassium levels reduce the absorption of Mg, so that high K levels may offset high Mg levels. It is possible that the relatively high amounts of K and Mg, coupled with the high moisture content of the cactus, could be responsible for the diarrheic condition often observed in animals fed cactus (Vinson 1911, Shoop et al. 1977, Hanselka and Paschal 1990), but it is doubtful that a toxic condition would be observed.

Manganese levels are well above required amounts, but well below maximum tolerable levels. Copper and zinc are both deficient in cholla to meet requirements for beef cows, so that additional supplementation of these minerals is warranted when feeding cholla cactus. Each of these minerals was found to be deficient in dormant forage at this location (Mn, 17

ppm; Cu, 1 ppm; Zn, 11 ppm; Knox 1998) and are commonly limiting in dormant forages, so that it is likely that these minerals would be supplied under normal management. Although no requirements have been established for aluminum in beef cow diets, this mineral can exasperate other deficiencies and may create toxic effects at high levels; however, the amount contained in cholla is well below this level.

"Pearmouth," a condition occasionally observed in sheep accustomed to consuming prickly pear cactus, is probably not a major concern when feeding cholla. This affliction, characterized by lesions of the lips, tongue, and gastro-intestinal tract, is caused by penetration of the tissues by the glochids subtending the main spines of prickly pear and subsequent infection (Ueckert et al. 1990). Since cholla has few if any glochids similar to those in prickly pear, it is doubtful that pearmouth would occur after feeding cholla.

Informal observations indicate that cholla cactus is most heavily consumed by grazing cattle during the early spring, when new growth is present. The emerging buds of cholla do not have hardened spines, and cattle appear to actively seek these buds. Ruminant contents of cows under these conditions have been found to contain as much as 75% cholla if animals were allowed to graze in an area with large amounts of available plants; 10–20% of the contents is more common. Although consumption is highest during the spring, cattle consume some amount of cactus throughout the year. Animals are frequently observed "checking" cholla for grazable portions. It is also common to see animals with pieces of cholla stuck on their muzzles, indicating that they have been attempting to browse the plants. These observations indicate that even without spine removal, cholla is a highly desirable browse species.

## Conclusions

Cholla cactus may be a suitable feedstuff for emergency situations such as drought. Cholla is a highly degradable source of energy and contains an adequate amount of crude protein to maintain productive animals with little or no additional protein supplementation. Burning to remove the spines from cholla improves the digestibility of the cactus without reducing protein content, and therefore may be preferred over chopping as a method of providing cholla to livestock.

The primary drawbacks to feeding cholla as an emergency feed are its excessive moisture and ash contents. The high mineral (ash) content of cholla may create problems such as diarrhea or excessive imbalances in mineral intake, especially calcium and phosphorus. These effects can be managed by supplementation with an appropriately formulated salt-mineral supplement to mediate deficiencies and imbalances.

High moisture content dictates that large amounts of cholla must be provided to achieve adequate levels of dry matter intake. This limitation may be offset if feeding begins before other forage resources (i.e., grasses) are completely exhausted, or if large and dense enough stands of cholla are available. Testimonial reports from Texas indicate that enough prickly pear can be burned in 20–30 minutes to feed 8–10 cows (Hanselka and Paschal 1990). If a similar provision rate can be attained with cholla, and labor is less expensive than alternative feed sources such as hay or grain, then feeding cholla may be cost effective.

Cholla cactus may be an acceptable alternative feedstuff, and could be a valuable drought/survival management tool for livestock producers, both to maintain livestock and to decrease the costs of drought management.

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# Remote sensing of redberry juniper in the Texas rolling plains

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## Abstract

Redberry juniper (*Juniperus pinchotii* Sudw.) is a noxious shrub or small tree that invades rangelands in northwest Texas. Field reflectance measurements showed that redberry juniper had lower visible and higher near-infrared (NIR) reflectance than associated species and mixtures of species in February. The low visible reflectance of redberry juniper was due to its darker green foliage than associated species, whereas its high NIR reflectance was attributed to its greater vegetative density than associated vegetation. Redberry juniper had a distinct reddish-brown image tonal response on color-infrared aerial photographs obtained in February. Computer analysis of a color-infrared photographic transparency showed that redberry juniper infestations could be quantified. An accuracy assessment performed on the classified image had a user's accuracy of 100% and a producer's accuracy of 94% for redberry juniper.

**Key Words:** color-infrared photography, reflectance, digital image analysis, accuracy assessment, *Juniperus*

Redberry juniper (*Juniperus pinchotii* Sudw.) is a sprouting, evergreen shrub or small tree rarely reaching a height of 7 m that occurs on rangelands in Oklahoma, New Mexico, Arizona, and Texas (Correll and Johnston 1979). Historically, west Texas populations of redberry juniper were restricted primarily to buttes and escarpments but since the 1860's have expanded into grasslands (Ellis and Schuster 1968, West 1991). Redberry juniper is a major invader of fertile lowland ranges in northwest Texas, particularly those below, or associated with rough shallow-soiled rangeland (Scifres 1980). Ansley et al. (1995) estimated that redberry juniper had increased its range by 61% from 1948 to 1982, and occurred on 4.1 million ha of Texas rangelands. Its fairly recent expansion in range is blamed on suppression of naturally occurring fires, severe overgrazing, and recurrent droughts (Smeins 1980, 1990).

On some sites redberry juniper has value as a soil stabilizer and furnishes cover for wildlife. However, it is considered a low value browse for both livestock and wildlife (Scifres 1980). Several methods have been used to control redberry juniper including bulldozing, broadcast sprays and pelleted herbicides, and fire (Scifres 1980, Steuter and Britton 1983, Steuter and

## Resumen

El "Redberry juniper" (*Juniperus pinchotii* Sudw.) es un arbusto o árbol pequeño nocivo que invade los pastizales del Noroeste de Texas. Las medidas de reflectancia de campo muestran que en febrero el "Redberry juniper" tiene una menor reflectancia visible y una mayor reflectancia cercana al infrarrojo (NIR) que las especies asociadas y las mezclas de especies. La baja reflectancia visible del "Redberry juniper" se debió a que su follaje es de color verde más oscuro que el de las especies asociadas, mientras que su alta reflectancia NIR se atribuyó a que tenía una mayor densidad vegetativa que la vegetación asociada. En las fotografías aéreas infrarrojas de color obtenidas en febrero el "Redberry juniper" tuvo una respuesta de imagen tonal rojiza-café distinta. El análisis de computadora de una transparencia fotográfica infrarroja de color mostró que las infestaciones de "Redberry juniper" pudieron ser cuantificadas. Para el caso de "Redberry juniper", una evaluación de la exactitud realizada en la imagen clasificada tuvo una exactitud del usuario del 100% y una exactitud del productor del 94%

Wright 1983).

Due to the generally great expanse and inaccessibility of many rangeland areas, rapid and low-cost evaluation procedures are needed to acquire information for proper management of these areas. This information would be useful to range managers and individual land owners. Remote sensing techniques offer the advantage of rapid acquisition of data with generally short turnaround time and a procedure considerably less costly than ground surveys (Tueller 1982, Everitt et al. 1992). Plant canopy reflectance measurements have been used to distinguish noxious brush and weed species, and color-infrared aerial photography has been used extensively to remotely detect these undesirable species in rangeland areas (Gausman et al. 1977, Myhre 1987, Everitt et al. 1995, Driscoll et al. 1997, Anderson et al. 1999).

The objectives of this study were: (a) to establish the plant canopy reflectance characteristics of redberry juniper to facilitate its detection on remotely sensed imagery; and (b) to evaluate color-infrared aerial photography for distinguishing redberry juniper on northwest Texas rangelands.

## Materials and Methods

This study was conducted in northwest Texas. Study sites were located near Justiceburg (32° 59'N 101° 12'W), Dickens (33° 31'N 100° 36'W), Quanah (34° 10'N 99° 52'W), Maryneal (32° 17'N

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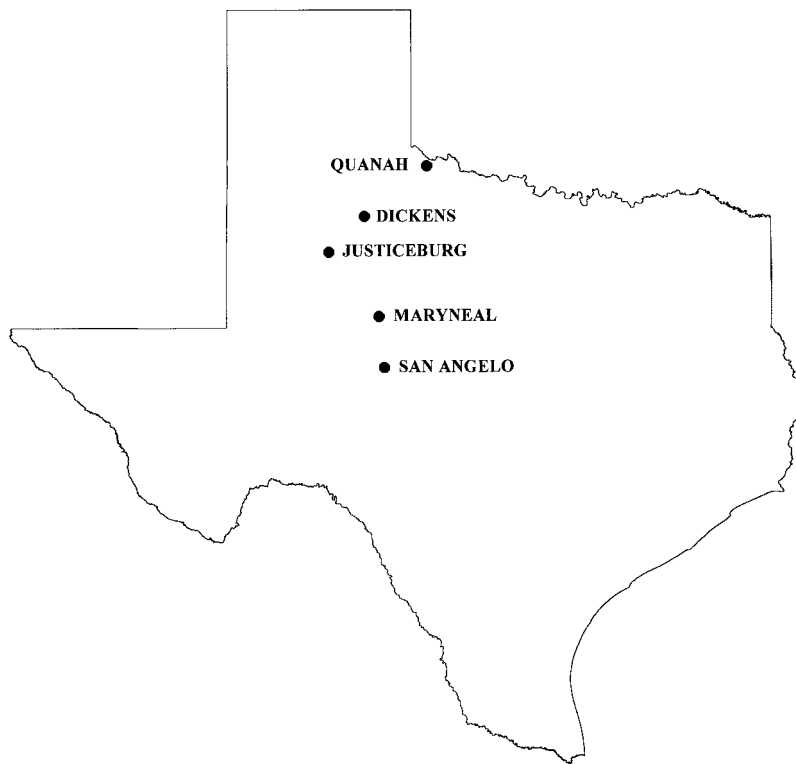


Fig. 1. Locations of study sites in Texas.

100° 29W), and San Angelo 31° 38N 100° 32W) in the Rolling Plains resource area (Hatch et al. 1990) (Fig. 1). Aerial photography, radiometric reflectance measurements, computer image analysis, and ground truth observations were conducted for this study. Reflectance measurements were made to establish the spectral characteristics of redberry juniper, associated plant species, and soil to help interpret

aerial photographs. Ground observations were made to verify the aerial photographs. Aerial photographs and reflectance measurements of redberry juniper were obtained at different dates over the year to study it under various growing conditions. The dates and locations these data were obtained are summarized in Table 1.

Table 1. Dates and locations that field reflectance measurements and aerial photography were acquired in northwest Texas.

Location	Reflectance	Photography <sup>1</sup>
Justiceburg	30 June <sup>2</sup> 1998; 23 Feb. <sup>3</sup> 28 June <sup>4</sup> , 18 Aug. <sup>4</sup> , & 22 Sept. <sup>4</sup> , 1999	30 June 1998, 23 Feb., 29 July, & 22 Sept. 1999
Maryneal	18 Aug. <sup>5</sup> 1999	
Dickens		30 June 1998, 23 Feb. & 22 Sept. 1999
San Angelo		9 July 1998 23 Feb. & 22 Sept. 1999
Quannah		9 July 1998; 23 Feb. & 22 Sept. 1999

<sup>1</sup>Photographs were taken at scales of 1:1,200, 1:2,500, 1:4,000, 1:5,000, 1:6,000, 1:7,500, and 1:8,500.

<sup>2</sup>Reflectance measurements were made on redberry juniper, honey mesquite, yucca, plains prickly pear, tobosa grass, mixed herbaceous species (grasses and broadleaved herbs), and bare soil.

<sup>3</sup>Reflectance measurements were made on redberry juniper, yucca, plains prickly pear, tobosa grass, mixed herbaceous species, and bare soil.

<sup>4</sup>Reflectance measurements were made on redberry juniper, honey mesquite, yucca, plains prickly pear, tobosa grass, annual broomweed, mixed herbaceous species, and bare soil.

<sup>5</sup>Reflectance measurements were made on redberry juniper, honey mesquite, yucca, plains prickly pear, mixed herbaceous species, and bare soil.

Reflectance measurements were made on each of 10 randomly selected plant canopies of each species or species mixture and soil surfaces with a Barnes<sup>1</sup> modular multispectral radiometer (Robinson et al. 1979). Measurements were made in the visible green (0.52 to 0.60  $\mu$ m), visible red (0.63 to 0.69  $\mu$ m), and NIR (0.76 to 0.90  $\mu$ m) spectral bands with a sensor that had a 15-degree field-of-view placed 1.0 to 1.5 m above each plant and soil target.

The area within the sensor field-of-view ranged from 0.26 to 0.39 m. Reflectance measurements were made between 1100 and 1500 hours Central Standard Time under sunny conditions. Measurements of redberry juniper and honey mesquite (*Prosopis glandulosa* Torr.) were usually made from a stepladder. Honey mesquite was not measured in February 1999 because it is deciduous (Table 1). Annual broomweed (*Amphicaryis dracunculoides* DC.) was not measured in June 1998 and February 1999 because it was not available in sufficient amounts and was not present, respectively. Overhead vertical photographs were obtained of the plant canopies and bare soil measured with the radiometer to help interpret the reflectance data. Radiometric measurements were corrected to reflectance using a barium sulfate standard (Richardson 1981).

Green, red, and NIR reflectance data were analyzed using analysis of variance techniques. Duncan's multiple range test was used to test statistical significance at the 0.05 probability level among means (Steel and Torrie 1980).

Kodak Aerochrome color-infrared (0.50 to 0.90  $\mu$ m) type 2443 film was used for aerial photographs. Color-infrared film is sensitive in the visible green (0.50 to 0.60  $\mu$ m), visible red (0.61 to 0.75  $\mu$ m), and NIR (0.76 to 0.90  $\mu$ m) spectral regions. Photographs were obtained with a Fairchild type K-37 large format (23 cm x 23 cm) mapping camera. The camera was equipped with a 305 mm lens with an aperture setting of f11 at 1/250 sec. A fixed-wing aircraft, equipped with a camera port in the floor, was used for obtaining aerial photography. The camera was maintained in a nadir position during all image acquisition. Aerial photographs were acquired between 1130 and 1400 hours Central Standard Time under sunny conditions.

Two color-infrared photographic transparencies (1:5,000 scale) of a study site near Justiceburg obtained on 23 February

<sup>1</sup>Trade names are included for the benefit of the reader and do not imply endorsement of or a preference for the product listed by the USDA.

and 29 July 1999, respectively, were digitized to perform a computer classification and accuracy assessment on each photograph. A Trimble differential global positioning system (GPS) Pathfinder Pro XRS system that provided submeter accuracy was used in the field to establish control points on the digitized photographic transparencies. The transparencies were scanned at 600 dpi and had a pixel resolution of 0.40 m. Erdas Imagine software (Version 8.3) was used to georeference the transparencies. The images were subjected to an Iterative Self-Organizing Data Analysis (ISODATA) which performs unsupervised classifications on the basis of specified iterations and recalculates statistics for each iteration (Erdas 1997). The ISODATA technique uses minimum spectral distance to assign a cluster for each selected pixel. It begins with arbitrary cluster means, and each time the clustering repeats, the means of these clusters are shifted. The new cluster means are used for the iteration. Initially the unsupervised classification created 10 classes at the 99% convergence threshold (the maximum percentage of pixels cluster assignments go unchanged between iterations). Some of the initial categories were combined resulting in 4 final categories. The classes consisted of redberry juniper, mixed vegetation, bare soil, and honey mesquite. Honey mesquite was defoliated in the February photograph. For accuracy assessment, 100 points were assigned to the 4 classes in a stratified random pattern. The geographic coordinates of these points were determined and the GPS was used to navigate to the points in ground truthing. The ground sampling sites for all classes had an area much larger than the image pixel size or GPS error.

## Results and Discussion

### Reflectance measurements

Mean light reflectance measurements of redberry juniper, associated plant species and mixtures of species, and bare soil at 3 wavelengths from 6 sampling dates near Justiceburg and Maryneal are shown in Table 2. In June 1998 at the Justiceburg site, bare soil (sand and rock) had higher green, red, and NIR reflectance than the associated plant species. Redberry juniper had lower green reflectance than the other plant species, mixtures of species, and soil. At the red wavelength, redberry juniper and honey mesquite had similar reflectance values. The NIR reflectance of redberry juniper did not differ from that of

honey mesquite and yucca (*Yucca angustifolia* Trel.).

Differences in visible reflectance among the plant species and mixtures of species was primarily attributed to differences in foliage color and subsequent plant pigments (Myers et al. 1983, Gausman 1985). Foliage colors varied from dark green for redberry juniper and honey mesquite, to light green for plains prickly pear (*Opuntia polyacantha* Haw.) and yucca, to various shades of light green and gray-green for mixed herbaceous species and tobosa grass [*Hilaria mutica* (Buckl.)

Benth.]. Plants with darker green foliage (higher chlorophyll concentrations) reflected less of the green light and absorbed more of the red light than plants with lighter green or gray-green foliage (lower chlorophyll concentrations) (Gausman 1985). Differences in NIR reflectance among the plant species was primarily due to differences in their vegetative density. Near-infrared reflectance in vegetation is highly correlated with vegetation density (Myers et al. 1983, Everitt et al. 1986). An overhead view of the plant species and mixtures of species showed

**Table 2. Mean light reflectance of redberry juniper, associated species and mixtures of species, and bare soil on 6 dates for the visible green, visible red, and near-infrared wavelengths. Measurements were made near Justiceburg and Maryneal, Tex.**

Location and date	Plant species, mixture, or soil	Reflectance values <sup>1</sup> for 3 wavelengths		
		green	red	near-infrared
June 1998 Justiceburg	Honey mesquite	5.6 d	3.7 e	25.8 b
	Plains prickly pear	7.2 c	7.0 c	17.1 d
	Redberry juniper	4.3 e	3.0 e	24.0 bc
	Yucca	7.2 c	6.1 d	23.3 c
	Tobosa grass	9.6 b	9.7 b	16.5 d
	Mixed herbaceous species	9.0 b	9.2 b	18.4 d
	Bare soil	14.4 a	17.7 a	28.2 a
February 1999 Justiceburg	Honey mesquite	— <sup>2</sup>	—	—
	Plains prickly pear	5.9 d	5.4 c	14.3 b
	Redberry juniper	4.3 e	3.0 d	23.3 a
	Yucca	6.9 c	6.2 c	14.9 b
	Tobosa grass	7.9 b	7.6 b	13.2 b
	Mixed herbaceous species	7.9 b	7.6 b	14.1 b
	Bare soil	12.2 a	13.7 a	23.8 a
June 1999 Justiceburg	Annual broomweed	6.7 de	4.5 e	33.0 a
	Honey mesquite	4.9 f	3.0 f	8.8 b
	Plains prickly pear	7.2 cd	6.5 cd	18.4 e
	Redberry juniper	4.6 f	3.1 f	24.8 c
	Yucca	6.0 e	5.3 de	24.2 c
	Tobosa grass	8.0 bc	7.3 bc	21.6 d
	Mixed herbaceous species	8.7 b	8.3 b	24.9 c
	Bare soil	13.8 a	16.7 a	29.2 b
August 1999 Justiceburg	Annual broomweed	7.7 cd	5.6 c	29.7 a
	Honey mesquite	5.3 ef	3.2 d	28.0 a
	Plains prickly pear	6.6 de	6.0 c	20.0 c
	Redberry juniper	4.4 f	3.1 d	24.3 b
	Yucca	7.5 cd	6.1 c	28.1 a
	Tobosa grass	8.5 bc	8.2 b	18.2 c
	Mixed herbaceous species	9.3 b	9.4 b	24.0 b
	Bare soil	14.7 a	16.3 a	28.5 a
August 1999 Maryneal	Honey mesquite	5.3 c	3.4 d	28.8 a
	Plains prickly pear	7.4 b	6.9 c	17.5 c
	Redberry juniper	5.2 c	3.2 d	25.1 b
	Yucca	7.9 b	5.8 c	29.8 a
	Mixed herbaceous species	8.5 b	8.3 b	22.6 b
	Bare soil	17.1 a	17.2 a	29.2 a
September 1999 Justiceburg	Annual broomweed	6.1 cd	3.9 de	29.3 ab
	Honey mesquite	5.9 cd	3.9 de	26.5 c
	Plains prickly pear	6.6 c	5.4 c	19.3 e
	Redberry juniper	4.7 d	2.9 e	23.4 d
	Yucca	6.2 cd	4.9 cd	30.0 a
	Tobosa grass	8.3 b	7.7 b	17.3 e
	Mixed herbaceous species	7.9 b	7.5 b	18.1 e
	Bare soil	14.8 a	16.0 a	27.7 bc

<sup>1</sup>Values within a column at each sampling date followed by the same letter do not differ significantly at the 5% probability level, according to Duncan's multiple range test.

<sup>2</sup>Honey mesquite is deciduous and consequently was not measured in February.



that honey mesquite, redberry juniper, and yucca had greater vegetative density and less gaps (sun flecks) in their canopies than plains prickly pear, tobosa grass, and mixed herbaceous species. Internal leaf structure measurements were not made, but this could also contribute to the NIR reflectance measurements (Gausman 1974). The high visible reflectance of bare soil was due to its light gray-brown color, whereas its high NIR reflectance was attributed to sand and rocky surface particles (Bowers and Hanks 1965, Gerbermann et al. 1987).

In February 1999 at Justiceburg, redberry juniper had lower green and red reflectance than the associated plant species and mixtures of herbaceous species, and bare soil. At the NIR wavelength, redberry juniper and bare soil had similar reflectance values; however, redberry juniper had higher NIR reflectance than the associated plant species and mixtures of species. The lower visible and higher NIR reflectance of redberry juniper in February was due to its darker green foliage and greater vegetative density, respectively, than that of the associated plant species and mixtures of species. The lower vegetative density of the associated species and mixtures of species was attributed to their winter dormancy.

Reflectance data for June 1999 at Justiceburg indicated that redberry juniper could not be distinguished spectrally from honey mesquite at both the green and red wavelengths. At the NIR wavelength, redberry juniper, yucca, and mixed herbaceous species had similar reflectance values.

At the Justiceburg site in August 1999, the green and red reflectance of redberry juniper did not differ from that of honey mesquite. The NIR reflectance values of redberry juniper and mixed herbaceous species could not be separated. Reflectance measurements made at the Maryneal site in August 1999 showed that redberry juniper and honey mesquite had similar reflectance values at both the green and red wavelengths, whereas at the NIR wavelength the reflectance values of redberry juniper and mixed herbaceous species did not differ.

Spectral measurements made at Justiceburg in September 1999 indicated that the green reflectance of redberry juniper could not be distinguished from that of annual broomweed, honey mesquite, and yucca. At the red wavelength, redberry juniper had similar reflectance to that of annual broomweed and honey mesquite. The NIR reflectance of redberry juniper differed from that of the other associated plant species, mixtures of species, and bare soil in September.

These findings indicate that the optimum time to spectrally distinguish redberry juniper from associated species was in February when other species are dormant. Redberry juniper had much greater NIR reflectance than the other associated species in February. Thus, the discrimination of redberry juniper on color-infrared aerial photos should be best at this time.

### Aerial photography

Figures 2A and 2B show color-infrared positive photographic prints obtained on 29 July and 23 February 1999, respectively, of a rangeland area infested with redberry juniper near Justiceburg. Both prints are portions of 23 cm photographs (1:5,000 scale). The arrow on the February photograph (Fig. 2B) points to the conspicuous reddish-brown image tone of redberry juniper. Redberry juniper has a similar tonal response throughout the image. Dormant mixed herbaceous species have variable blue-gray tones, whereas bare soil, rocky soil areas, and roads have a whitish-gray tone. Dormant deciduous honey mesquite plants have a dark blue-gray image response. In the July photograph (Fig. 2A) the vegetation is in vigorous growing condition follow-

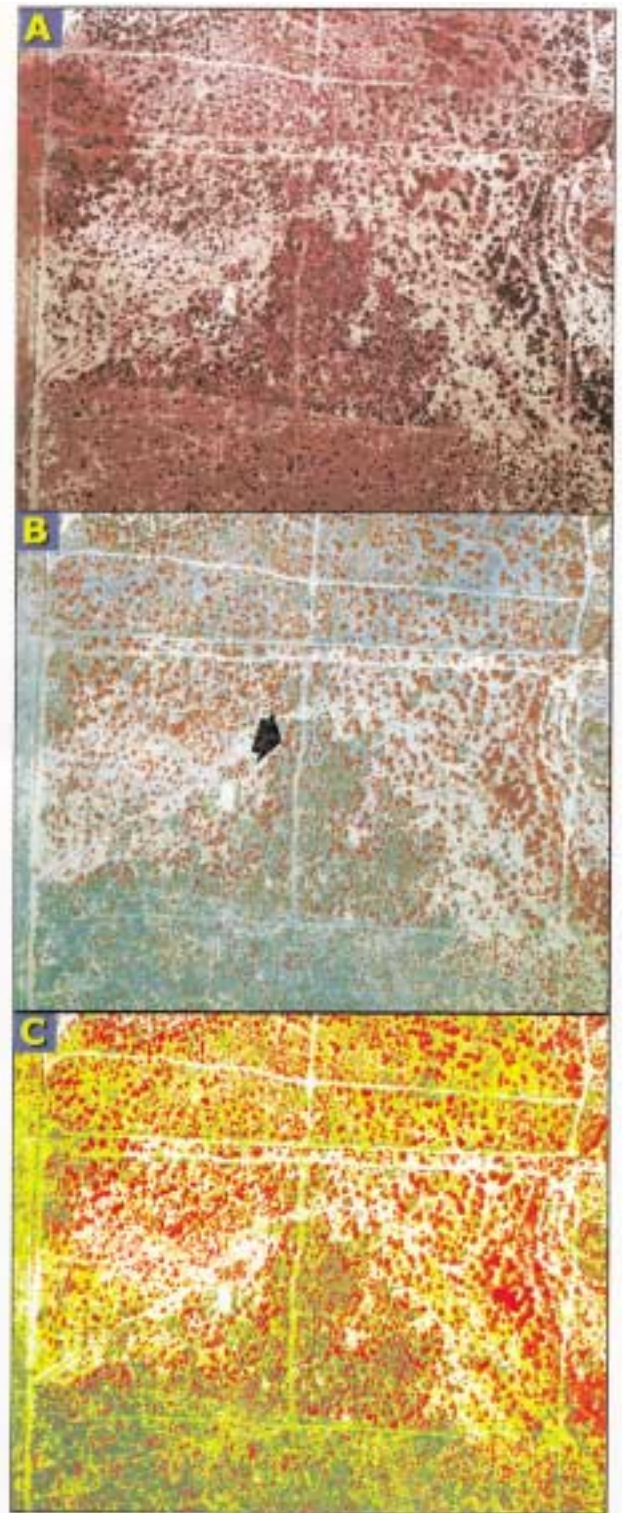


Fig. 2. Color-infrared photographic prints obtained on 29 July (print A) and 23 February (print B), 1999 of a rangeland area near Justiceburg, Texas. Both photos had an original scale of 1:5,000 and the area shown here is 590 x 500 m. The arrow on print B points to the reddish-brown image tonal response of redberry juniper. Unsupervised computer classification (C) of print B. Color codes for the various landuse types are: red = redberry juniper, yellow = mixed vegetation, green = dormant honey mesquite, and white = bare soil.



ing optimum rainfall in June and early July. Consequently, most of the vegetation has high chlorophyll levels which contributes significantly to its various red and magenta tones on the color-infrared photograph. Redberry juniper and honey mesquite both have dark red image tones in the July photograph that can not be separated. This is apparent in the lower-center portion of the photograph where a moderate stand of honey mesquite occurs. The various red to magenta tones (background) of associated herbaceous vegetation also hinder the detection of redberry juniper in the July photograph.

Qualitative analysis and ground truth reconnaissance of additional color-infrared photographs acquired of 13 scattered rangeland areas near San Angelo, Justiceburg, Dickens, and Quanah in February 1999 showed that redberry juniper could be readily distinguished at all locations. It had a similar color-infrared image response to that shown in Figure 2B and could be distinguished at various photographic scales (1:1,200 to 1:8,500), but the best scales were 1:1,200 to 1:6,000. Redberry juniper could not be readily distinguished from honey mesquite in color-infrared photographs obtained in June and July 1998, and June, July, and September 1999 at San Angelo, Justiceburg, Dickens, and Quanah. The inability to separate redberry juniper from honey mesquite during the growing season was attributed to their comparable visible reflectance values (Table 2).

The unsupervised computer classification of the February color-infrared photograph (Fig. 2B) is shown in Figure 2C. Color codes and respective areas/percentages for the various land-use types are: red = redberry juniper (29.9%), yellow = mixed vegetation (39.2%), green = dormant honey mesquite (15.5%), and white = bare soil (15.4%). Mixed herbaceous species, tobosa grass, yucca, and plains prickly pear were included in the mixed vegetation class. All of these species and mixtures had similar NIR reflectance in February (Table 2). Shadow was not a problem in the classification. This was primarily attributed to obtaining the aerial photographs at mid-day. The generally short stature (< 3 m) of the woody species also contributed minimal shadowing problems in the photographs. A qualitative comparison of the computer classification to the photograph shows that the computer did a good job in identifying redberry juniper. This technique can provide a means of quantifying redberry juniper infestations.

**Table 3. An error matrix generated from classification data and ground data for the 23 February 1999 color-infrared photograph of the Justiceburg study site.**

Classified Category	Actual Category				Total	User's Accuracy
	Juniper	Mesquite	Mixed Vegetation	Bare Soil		
Juniper	30	0	0	0	30	100%
Mesquite	1	8	7	0	16	50.0%
Mixed Vegetation	1	1	37	0	39	94.9%
Bare Soil	0	0	1	14	15	93.3%
Total	32	9	45	14	100	
Producer's Accuracy	93.8%	88.9%	82.2%	100%		

Overall accuracy = 89.0%. Kappa = 0.841.

Table 3 shows the error matrix by comparison of the classified data with the ground data for the 100 observations within the Justiceburg study area for the 23 February 1999 image. The overall classification accuracy was 89%, indicating that 89% of the category pixels in the image were correctly identified in the classification map. The user's accuracy ranged from 50% for honey mesquite to 100% for redberry juniper, whereas the producer's accuracy for individual categories ranged from 82.2% for mixed vegetation to 100% for bare soil. Redberry juniper was the easiest class to identify due to its distinct image response. The lower accuracy of honey mesquite was due to its confusion with mixed vegetation. The inability to separate defoliated honey mesquite plants from mixed vegetation was attributed to their similar image tonal responses. Another accuracy measure, the kappa estimate for this study, was 0.841, indicating the classification has achieved an accuracy that is 84.1% better than would be expected from random assignment of pixels to the categories.

An accuracy assessment performed on the classification map of the 29 July 1999 color-infrared photograph of the Justiceburg study area had an overall accuracy of 54%. Both the producer's accuracy and user's accuracy were lower for the 4 categories, compared to the 23 February 1999 classification map. As for the ability to classify redberry juniper, the 29 July classification resulted in a producer's accuracy of 87.5% and a user's accuracy of 50%. In other words, although 87.5% of the redberry juniper areas were correctly identified as redberry juniper, only 50% of the areas called redberry juniper were actually redberry juniper. The low accuracy was primarily due to significant confusion in discriminating redberry juniper from honey mesquite and mixed vegetation as revealed on the July 29 photograph (Fig. 2A).

## Conclusions

Our results indicate that color-infrared aerial photography can be a useful tool for distinguishing redberry juniper infestations on the Texas Rolling Plains in winter due to its evergreen foliage. Other associated plant species that are confused with redberry juniper during the growing season are dormant during winter. Ground reflectance measurements support these findings. The optimum photographic scales for distinguishing redberry juniper were 1:1,200 to 1:6,000. Computer image analysis of a color-infrared film transparency (1:5,000 scale) obtained in February showed that redberry juniper infestations could be differentiated quantitatively from associated vegetation and soil. An accuracy assessment of the classification showed that the user's accuracy was 100% and the producer's accuracy was 93.8% for redberry juniper. The capability to remotely distinguish redberry juniper infestations on rangelands should be useful to range resource managers who are interested in infestation monitoring and control of noxious woody plants on rangelands. Aerial photographs provide a record that can be stored and examined for comparative purposes at any time and provide the highest resolution and capture the spatial essence of the scene with greater fidelity than any other procedure. Disadvantages of aerial photography include cost of repeated coverage for change detection, costs of film and processing, and the limited spectral sensitivity (Tueller 1989).

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# Characteristics of nest sites of northern bobwhites in western Oklahoma

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## Abstract

Previous authors have described nesting habitat of the northern bobwhite (*Colinus virginianus*) throughout its range, but few have compared structural or compositional differences of vegetation between nest sites and random non-use sites, and successful and non-successful nests. From 1996–1998, we compared cover and structure of 85 plant species from 80 nest sites of northern bobwhite in western Oklahoma. Nest sites were consistently associated with greater structural complexity than what was available at random. Bobwhites selected nest sites with a greater coverage of grass (ca. 50%) and woody (ca. 20–30%) vegetation with a relatively low percentage of bare ground, presumably because these attributes maximize their chance for successful reproduction by providing protection against weather and predators. Successful nests were more concealed during 1996 and 1997 (12.37 and 10.74% visibility, respectively) than non-successful nest sites (21.6 and 27.65% visibility), but levels of concealment did not differ during 1998. We found no significant differences in vegetation composition or structure between successful and non-successful nest sites.

**Key Words:** bobwhite, *Colinus virginianus*, gallinaceous, habitat, northern, quail, upland game.

Ground-nesting birds in shrub and grassland habitats suffer greater nesting mortality than other species, and many are documented to be in long-term population declines (Martin 1993a). Declining populations of northern bobwhite (*Colinus virginianus*) are no exception and have been well documented (Klimstra 1982, Church et al. 1993). Oklahoma experienced a 16% decrease from 1961 to 1988 (Brennan 1991). Although reasons for these declines remain unknown, successful reproduction is an important factor of bobwhite ecology that depends on adequate nesting

## Resumen

Anteriormente otros autores han descrito el hábitat de anidamiento del “Northern bobwhite” (*Colinus virginianus*) a través de su rango de adaptación, pero pocos han comparado las diferencias estructurales y de composición de la vegetación entre sitios de anidamiento y sitios aleatorios de no- uso y el éxito y fracaso de los nidos. De 1996 a 1998 comparamos la cobertura y estructura de 85 especies de plantas de 80 sitios de anidamiento del “Northern bobwhite” en el oeste de Oklahoma. Los sitios de anidamiento fueron consistentemente asociados con una mayor complejidad estructural que la que estuvo disponible al azar. Los “Bobwhite” seleccionaron sitios de anidamiento con una mayor cobertura de zacate (50%) y vegetación leñosa (20–30%) y con un porcentaje relativamente bajo de suelo desnudo, presumiblemente porque estos atributos maximizan sus probabilidades de una reproducción exitosa al proveer protección contra el clima y los predadores. Durante 1996 y 1997 los nidos exitosos estuvieron más ocultos (12.37 y 10.74% de visibilidad respectivamente) que los nidos no exitosos (21.6 y 27.65% de visibilidad), pero los niveles de ocultamiento no difirieron en 1998. No encontramos diferencias significativas en la composición o estructura de la vegetación entre sitios de anidamiento exitosos y no exitosos.

and brood rearing habitat (Berner and Gysel 1969). Previous studies have described the macrohabitat of bobwhite nest sites throughout their range (Klimstra and Roseberry 1975, Lehmann 1984, Roseberry and Klimstra 1984, Taylor 1991), but few have compared structure and composition of vegetation between nest sites vs. random non-use sites and successful vs. non-successful nest sites. Our study was designed to determine whether nest-site selection by bobwhites is related to specific site characteristics and whether such characteristics influence likelihood of nest success.

## Study Area

Research was conducted at the Packsaddle Wildlife Management Area (35° 52' N 99° 40' W) in western Oklahoma. This 6,475-ha area of mixed-prairie habitat is located 40 km north

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of Cheyenne, Okla., where elevation ranged from 579 to 762 m above mean sea level. The area was season long grazed (April 15–September 15) with stocker cattle at a rate of 6.5 ha/AU (light-moderate based on NRCS recommendations). Mean precipitation throughout the breeding season (April–September) was 11.3 cm in 1996, 9.4 cm in 1997 and 4.3 cm in 1998. Precipitation was greater than normal in 1996 (4.4 cm) and 1997 (3.5 cm), but was below normal in 1998 (–2.7 cm). Ambient temperatures averaged 2.1°C during winter and 27.0°C in summer (Cole et al. 1966). Soils consisted of sandy Nobscot (Loamy, mixed, superactive, thermic Arenic Paleustalfs)–Delwin (Fine-loamy, mixed, active, thermic Typic Paleustalfs) and Eda (Mixed, thermic Lamellic Ustipsamments)–Tivoli (Mixed, thermic Typic Ustipsamments), moderately sandy Hardeman (Coarse-loamy, mixed, superactive, thermic Typic Haplustepts)–Likes (Mixed, thermic Aridic Ustipsamments)–Devol (Coarse-loamy, mixed, superactive, thermic Typic Haplustalfs) and Eda (Mixed, thermic Lamellic Ustipsamments)–Carwile (Fine, mixed, superactive, thermic Typic Argiaquolls), and loamy Quinlan (Loamy, mixed, superactive, thermic, shallow Typic Haplustepts)–Woodward (Coarse-silty, mixed, superactive, thermic Typic Haplustepts (Cole et al. 1966, USDA-NRCS Official Soil Series Descriptions 2000). Dominant species of grasses included sand bluestem (*Andropogon hallii* Hack), little bluestem (*Schizachyrium scoparium* (Michx.) Nash), indiagrass (*Sorghastrum nutans* (L.) Nash), switchgrass (*Panicum virgatum* L.), sand paspalum (*Paspalum stramineum* Nash), blue grama (*Bouteloua gracilis* (Kunth in H.B.K.) Lag.), hairy grama (*B. hirsuta* Lag.), and sand dropseed (*Sporobolus cryptandrus* (Torr.) Gray). Common forbs on the area included western ragweed (*Ambrosia psilostachya* DC.), croton (*Croton* sp. L.), and prairie sunflower (*Helianthus petiolaris* Nutt.). Woody vegetation included shinnery oak (*Quercus harvardii* Rydb.), sand sage (*Artemisia filifolia* Torr.), and sand plum (*Prunus angustifolia* Marsh.) (Cole et al. 1966).

## Methods

### Radio-telemetry

We trapped bobwhite using modified Stoddard funnel traps (Wilbur 1967) baited with sorghum throughout the year, and by nightlighting (Huempfer et al. 1975)

sessions prior to the nesting season (March–April). Captured birds were marked with radio transmitters (Holohill Systems Limited, Ontario, Canada and Wildlife Materials, Incorporated, Carbondale, Ill.) weighing < 7 g, sexed, aged and banded with aluminum leg bands (Webb and Guthery 1982). Birds were monitored at least once daily throughout the nesting and brood rearing season (May–October).

### Nesting Cover

Nest sites were marked and microhabitats characterized after parents permanently left the nests. Successful nests were defined by a hatch of  $\geq 1$  chick from each nest. Lost nests were characterized as either: (1) predated (mammal or snake) or (2) abandoned. We took additional habitat measurements at each of 2 plots: a plot centered directly over the nest and a plot 20 m from the nest selected at a random direction (Badyaev 1995). Ten, 0.10 m quadrats were used to characterize plant cover (Daubenmire 1959) in a 1-m<sup>2</sup> plot positioned directly over each nest site. Estimates of percent cover by plant species and bare ground were recorded using Daubenmire's coverage classes (Daubenmire 1959).

### Nesting Habitat Characteristics

Physiographic variables such as aspect (degree), slope (%) (Sieg and Becker

1990), distance to nearest shinnery oak stand, or any other noticeable abrupt change in macro-habitat cover type (edge), or major disturbance (roads, burns, food plots, etc.) were recorded. Diameter of the nest at the top, and depth and thickness of the nest lining were recorded (Lehmann 1984). Tradeoffs associated with nest-site selection between visibility (a bobwhite's view of its surrounding while incubating eggs) and concealment from predators were evaluated (Gotmark et al. 1995). Visual obstruction (simulating a bobwhite's view while sitting on the nest) was evaluated using a vertical profile board placed 3 m from each nest or non-use site (Nudds 1977) and measurements were taken in 4 different directions (Angelstam 1986): the first direction was random and subsequent directions were taken at 90° intervals. Obstruction was recorded at 4 heights: <0.25 m, 0.25–0.50 m, >0.50–1.00 m, and >1.00–2.00 m and percentage of vegetation cover was differentiated into 6 categories; <2.5%, 2.5–25%, >25–50%, >50–75%, >75–95%, and >95% (Schmutz et al. 1989).

Nest concealment from outside the nest (predator's view) was quantified by 9 points; 8 at 45° compass intervals 1 m from the nest and 1 overhead view taken at 0.5 m from the nest (Keppie and Herzog 1978, Martin and Roper 1988, Holway 1991, Gotmark et al. 1995). Concealment was quantified by placing a 10-cm disc

**Table 1. Nest-site selection by northern bobwhites based on percent ground cover of nest and random sites on PWMA, Ellis County Okla., 1996–1998.**

Year Coverage	Nest Site			Random Site			P
	n	$\bar{x}$	SE	n	$\bar{x}$	SE	
1996							
Bare ground	41	22.79	2.88	41	37.40	4.50	0.003
Leaf Litter	41	11.06	2.22	41	12.66	3.43	0.679
Grasses	41	49.72	2.95	41	32.82	3.35	0.001
Forbs	41	6.36	1.45	41	8.88	2.06	0.365
Woody plants	41	19.58	3.05	41	9.55	2.12	0.015
Sedges	41	0.13	0.05	41	0.26	0.10	0.585
Legumes	41	1.15	0.57	41	0.64	0.23	0.294
1997							
Bare ground	21	5.64	2.34	21	28.00	5.12	0.001
Leaf Litter	21	15.03	2.22	21	12.36	3.55	0.623
Grasses	21	49.47	5.15	21	36.33	5.32	0.056
Forbs	21	9.65	2.92	21	13.60	3.08	0.310
Woody plants	21	28.63	5.14	21	15.62	3.90	0.023
Sedges	21	0.68	0.63	21	0.01	0.01	0.052
Legumes	21	0.54	0.37	21	0.71	0.34	0.792
1998							
Bare ground	18	14.35	3.22	18	18.44	5.79	0.575
Leaf Litter	18	19.26	4.77	18	15.88	4.24	0.563
Grasses	18	49.78	4.78	18	46.42	6.34	0.648
Forbs	18	6.83	1.41	18	12.10	4.32	0.211
Woody plants	18	29.78	4.78	18	15.04	4.00	0.017
Sedges	18	0	0	18	0	0	
Legumes	18	0.04	0.03	18	0.10	0.08	0.939

divided into 5 equivalent sections and each section was assigned a visibility percentage as follows: 0 = 0%, 1 = 20%, 2 = 40%, 3 = 60%, 4 = 80%, 5 = 100% (Holway 1991). Because bobwhites in western Oklahoma primarily nest in old growth little bluestem, we quantified little bluestem patch density around the nest and non-use site within 1 m<sup>2</sup> and at 1 m, 2 m, and 5 m radii (Martin and Roper 1988). This density was compared with nest success in relation to predation.

We measured shrub densities at 1 m, 2 m, and 5 m radii around each nest and non-use site. Shrubs were defined as woody vegetation >0.50 m in height and with a stem diameter <2 cm (Holway 1991). Effective plant height directly over the nest was measured using a meter tape (Higgins et al. 1994).

### Statistical Analyses

We compared percent plant cover and nest characteristics between nest sites vs. random non-use sites, and successful and non-successful nests with analysis of variance (SAS Institute, Incorporated 1996). Sources of variation were distributed among main factor effects (site and year) and the interaction terms (site by year). If there were significant interaction terms ( $P \leq 0.05$ ), main effects were compared separately by each year.

## Results

### Vegetative Cover

Our analysis of plant species composition associated with 80 bobwhite nest sites yielded few differences. As a result, we summarized vegetation cover in the following categories: bare ground, leaf litter, grasses, forbs, woody plants, sedges and legumes. Bobwhites selected nest sites associated with greater coverage of woody and grass vegetation and less coverage of bare ground than what was available at random. During 1996 and 1997, cover of grass and woody vegetation, respectively, was greater at nest sites than at random non-use sites (Table 1). During 1998, woody vegetation was also greater at nest sites than at random non-use sites. Coverage of bare ground was 1.6-fold greater in 1996 ( $P = 0.003$ ) and 5-fold greater in 1997 ( $P = 0.001$ ) at random non-use sites than at nest sites. Coverage of plant species did not differ between successful and non-successful nest sites (Table 2).

**Table 2. Percent ground cover of successful and non-successful nests sites on PWMA, Ellis County Okla., 1996–1998.**

Year Coverage	Successful			Non-Successful			P
	$\bar{x}$	SE	n	$\bar{x}$	SE		
	(%)			(%)			
1996							
Bare ground	23	15.53	2.83	18	32.06	4.72	0.001
Leaf Litter	23	13.23	3.14	18	8.29	3.06	0.288
Grasses	23	53.36	4.62	18	45.07	3.01	0.206
Forbs	23	8.03	2.22	18	4.22	1.62	0.227
Woody plants	23	22.76	4.41	18	15.51	3.97	0.274
Sedges	23	0.12	0.05	18	0.14	0.09	0.968
Legumes	23	1.71	0.99	18	0.43	0.23	0.149
1997							
Bare ground	12	8.29	3.94	9	2.11	0.87	0.346
Leaf Litter	12	11.54	2.83	9	19.67	3.07	0.212
Grasses	12	49.33	7.44	9	49.67	7.23	0.971
Forbs	12	12.05	4.94	9	6.44	1.63	0.204
Woody plants	12	24.56	6.93	9	34.06	7.72	0.306
Sedges	12	1.11	1.11	9	0.11	0.08	0.136
Legumes	12	0.90	0.64	9	0.06	0.06	0.494
1998							
Bare ground	7	14.18	5.77	11	14.45	4.01	0.969
Leaf Litter	7	27.00	8.99	11	14.34	5.11	0.078
Grasses	7	46.04	8.57	11	52.16	5.84	0.542
Forbs	7	5.54	1.95	11	7.66	1.97	0.660
Woody plants	7	30.11	9.12	11	29.57	5.64	0.958
Sedges	7	0	0	11	0	0	
Legumes	7	0.04	0.04	11	0.05	0.05	0.994

### Nesting Characteristics

Bobwhites selected nest sites associated with dense vegetation cover and greater densities of little bluestem. Density of little bluestem at 1 m and visual obstruction estimates (0–1 m high) were consistently greater at nest sites than at random non-use sites (Table 3). During 1996, little bluestem density within 1 m<sup>2</sup> of nest sites ( $\bar{x} = 7.07$ ,  $SE = 0.47$ ) was greater than that of random non-use sites ( $\bar{x} = 4.07$ ,  $SE = 0.47$ ;  $P < 0.001$ ), but it did not differ during 1997 or 1998.

We found no differences in structure of vegetation characteristics between successful and non-successful nest sites (Table 4). However, nest concealment was related to nest success. Successful bob-

white nests were less visible than non-successful nests in 1996 ( $P = 0.026$ ) and 1997 ( $P = 0.012$ ) but did not differ in 1998 ( $P = 0.536$ ; Fig. 1), presumably because of below average rain fall and poor plant growth.

## Discussion

Nest-site selection can be a critical factor in determining reproductive success of bobwhites. Individuals that select nest sites in more favorable environments are likely to increase successful reproduction (Martin 1993b). Bobwhites selected nest sites that consisted primarily of old growth little bluestem at a height of 84 cm, slight-

**Table 3. Nest site selection based on a comparison of vegetation characteristics of bobwhite nest sites and their respective random sites on PWMA, Ellis County Okla., 1996–1998.**

Characteristic	Nest Site			Random Site			P
	n	$\bar{x}$	SE	n	$\bar{x}$	SE	
Shrub Stem Count, 1 m	80	39.53	4.01	80	34.43	3.85	0.336
Shrub Stem Count, 2 m	80	93.59	10.14	80	71.45	7.13	0.142
Shrub Stem Count, 5 m	80	228.98	22.80	80	172.16	17.20	0.064
Little Bluestem Patch, 1 m	80	12.06	0.62	80	9.83	0.64	0.036
Little Bluestem Patch, 2 m	80	22.43	1.18	80	19.24	1.12	0.140
Little Bluestem Patch, 5 m	80	46.25	2.47	80	43.61	2.78	0.828
Visual Obstruction, 0-0.25 m	80	65.90	1.11	80	58.15	2.01	0.005
Visual Obstruction, 0.25-0.50 m	80	46.51	2.26	80	34.23	2.21	0.001
Visual Obstruction 0.50-1.00 m	80	29.99	2.57	80	17.59	1.77	0.001
Visual Obstruction, .00-2.00 m	80	8.06	1.74	80	4.84	1.13	0.285

ly taller than vegetation heights reported by Klimstra and Roseberry (1975) in Illinois (50 cm) and Taylor et al. (1999) in Kansas (52 cm).

Microhabitat selection is best described by a nonrandom distribution of nest sites within dense vegetation (Gloutney and Clark 1997). Bobwhite nests were consistently associated with greater structural complexity than what was available at random. Meseke (1992) documented that nest site selection by bobwhites on Conservation Reserve Program (CRP) fields in Illinois did not differ from random sites. In contrast, our data was collected on native rangeland where landscape composition tends to be more heterogeneous (Patten and Ellis 1995, Fuhlendorf and Smeins 1999) than grassland monocultures typically found in CRP fields. As a result, bobwhites in western Oklahoma apparently select nest sites that have a greater coverage of grass and woody vegetation with a relatively low percentage of bare ground.

Taylor et al. (1999) documented that bobwhite nest sites, in Kansas, were associated with taller vegetation, greater visual obstruction and more litter cover than what was available at random. Nest sites associated with 20–30% woody and 50% grass vegetation may provide bobwhites greater protection from predators throughout the breeding season in western Oklahoma. Sites associated with dense vegetation are thought to be less vulnerable to predation (Rands 1988, Filliater et al. 1994) because these sites presumably offer superior cover that helps prevent pre-

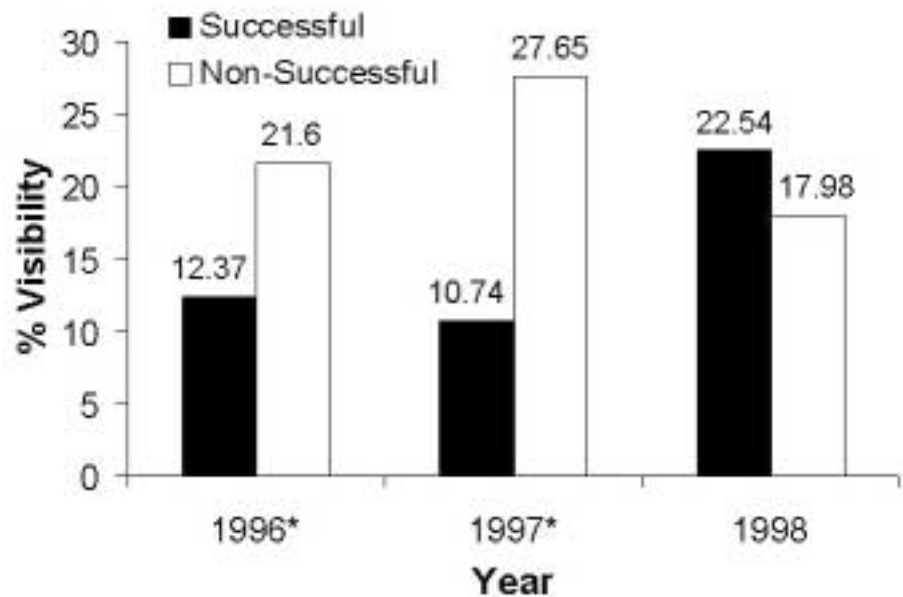


Fig. 1. Mean estimates of nest concealment for successful and non-successful bobwhite nest sites at PWMA, Ellis County, Okla. 1996–1998 (\* =  $P < 0.05$ ).

dation by inhibiting chemical, auditory, or visual clues (Martin and Roper 1988) and protects incubating bobwhites from weather and other disturbances (Colwell 1992, Riley et al. 1992). McKee et al. (1998) reported similar results in nest site selection of greater-prairie chicken (*Tympanuchus cupido pinnatus*). They documented litter and woody cover or forb and grass cover to be the best predictors of nest success of greater-prairie chickens.

Unlike McKee et al. (1998), plant cover around bobwhite nest sites was not a pre-

dicator of nest success. Martin and Roper (1988) hypothesized that increased density of nest-site foliage (within a habitat patch surrounding the nest) decreases a predator's chance of finding the nest. Bobwhite nest sites in western Oklahoma primarily were constructed within patches of little bluestem, but we found that the mean density of little bluestem patches at successful nest sites did not differ from non-successful nest sites. In addition, coverage of vegetation did not differ between successful and non-successful nest sites. Several studies on artificial ground-nest predation have supported our conclusions and have found that neither vegetation type nor coverage was associated with nest success (Byers 1974, Horkel et al. 1978, Yahner and Piergallini 1998).

Estimates of concealment have been documented to be another important component of nest success (Keppie and Herzog 1978, Riley et al. 1992). Bowman and Harris (1980) found spatial heterogeneity to be more important than concealment in reducing nest predation. Angelstam (1986) also documented greater predation rates on less concealed artificial ground nests. Similarly, we believe that bobwhites are primarily cuing on structural complexity associated with visual obstruction and coverage of woody vegetation, because we assume these attributes provide greater concealment from predators.

Table 4. Comparison of vegetation characteristics between successful and non-successful bobwhite nest sites at PWMA, Ellis County Okla., 1996–1998.

Characteristic	Successful			Non-Successful			P
	n	$\bar{x}$	SE	n	$\bar{x}$	SE	
Shrub Stem Count, 1 m	42	36.52	5.39	38	42.84	6.00	0.575
Shrub Stem Count, 2 m	42	102.81	15.72	38	83.39	12.41	0.467
Shrub Stem Count, 5 m	42	244.74	34.51	38	211.55	29.34	0.662
Little Bluestem Patch, 1 m	42	12.98	0.91	38	11.05	0.82	0.298
Little Bluestem Patch, 2 m	42	23.98	1.70	38	20.71	1.61	0.286
Little Bluestem Patch, 5 m	42	48.62	3.65	38	43.63	3.28	0.494
Visual Obstruction, 0-0.25 m	42	66.96	1.43	38	64.74	1.73	0.657
Visual Obstruction, 0.25-0.50 m	42	49.77	2.79	38	42.91	3.57	0.227
Visual Obstruction, 0.50-1.00 m	42	32.39	3.27	38	27.34	4.04	0.453
Visual Obstruction, 1.00-2.00 m	42	7.43	2.55	38	8.75	2.38	0.816
Total Height (cm)	41	85.01	4.06	37	83.19	2.51	0.737
Clump Width (cm)	41	80.30	5.29	37	79.00	4.72	0.815
Clump Length (cm)	41	67.75	4.94	37	66.70	3.42	0.847
Bowl Width (cm)	42	14.51	1.49	38	12.17	0.18	0.337
Bowl Length (cm)	42	14.32	1.25	38	12.36	0.25	0.372
Depth Dome (cm)	40	8.92	0.54	35	8.56	0.73	0.542
Depth Bowl (cm)	33	5.45	0.36	32	4.97	0.38	0.368
Lining Thickness (cm)	42	4.89	0.22	37	4.82	0.18	0.550

## Management Recommendations

Because nest predation is the primary cause of reproductive failure in many species of birds (Ricklefs 1969, Martin 1992), management practices should be designed to help maximize fitness by providing optimal nesting habitat. It is well established that bobwhites require highly variable habitats that are very patchy in productivity and composition (Ellis et al. 1969, Burger et al. 1990, Roseberry and Sudkamp 1998). Rangeland management practices that provide 50% grass and 20–30% woody vegetation will produce adequate bobwhite nesting habitat on western Oklahoma rangelands. Consequently, light to moderate stocking rates usually provide the proper proportions of bare ground, herbaceous quail foods, and woody cover that is required to sustain bobwhite populations on western Oklahoma rangelands.

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# Research Observation: Cattle preference for Lambert locoweed over white locoweed

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## Abstract

White (*Oxytropis sericea* Nutt. in T. & G.) and Lambert (*O. lambertii* var. *biglovii* Pursh) locoweed grow adjacent to each other on the foothills of the Rocky Mountains from southeastern Wyoming to northeastern New Mexico. Lambert locoweed matures later and flowers about 3–4 weeks after white locoweed, thus potentially increasing the critical period of poisoning when livestock graze areas infested by both species. The objective of this study was to evaluate cattle consumption of these 2 species as they progress phenologically. In 1998, 15 Hereford cows grazed a 32 ha pasture infested with both species from the time white locoweed flowered in mid June until both species were mature and senesced in August. In 1999, 4 cows were placed in a 5 ha pasture infested with both species for 4 days in each of the following periods: (1) flower stage of white locoweed, (2) flower stage of Lambert locoweed, immature pod at white locoweed, (3) immature pod stage of Lambert locoweed, mature pod while (4) mature pod and seed shatter stage respectively. Diets were estimated by bite-count. Lambert locoweed was preferred over white locoweed in the season-long grazing trial in 1998, and in each of the 4 intensive grazing trials in 1999. The cows consumed white locoweed as availability of Lambert locoweed declined in 1998, but little white locoweed was consumed in the 4 intensive grazing trials in 1999. The toxic locoweed alkaloid swainsonine ranged from 0.04 to 0.06% in white locoweed, but was not detected in Lambert locoweed in this study.

**Key Words:** *Oxytropis lambertii*, *Oxytropis sericea*, poisonous plant, cattle grazing, swainsonine

Locoweeds are the most wide-spread poisonous plant problem on western rangelands (Kingsbury 1964). White locoweed (*Oxytropis sericea* Nutt. in T. & G.; also known as silky crazyweed) is locally abundant on shallow rocky soils (Payne 1957) along the eastern foothills of the Rocky Mountains from Montana to northern New Mexico. It also occurs on mountain tops in the Great Basin and Colorado plateau. Lambert locoweed (*Oxytropis lambertii* var. *biglovii* Pursh; also known as Lambert crazyweed) occurs on sandy plains, sagebrush mesa and mountain sides from southern Wyoming southward along the foothills of the Rocky Mountains into New Mexico.

## Resumen

Las especies “white locoweed” (*Oxytropis sericea* Nutt en T. & G.) y “Lambert locoweed” (*Oxytropis lambertii* var. *Biglovii* Push) crecen adyacentes una de otra en las áreas de pie de monte de las montañas rocallosas desde el sudeste de Wyoming hasta el nordeste de New Mexico. “Lambert locoweed” madura más tarde y florece 3–4 semanas después que el “white locoweed”, lo que incrementa potencialmente el período crítico de envenenamiento cuando el ganado apacienta áreas infestadas con ambas especies. El objetivo de este estudio fue evaluar el consumo de estas dos especies por el ganado conforme progresan fenológicamente. En 1998, 15 vacas Herford apacentaron un potrero de 32 ha infestado con ambas especies, apacentaron desde que el “white locoweed” floreció, a mediados de Junio, hasta que ambas especies maduraron y senescieron en Agosto. En 1999, 4 vacas fueron colocadas en un potrero de 5 ha infestado con ambas especies y permanecieron en el por 4 días en cada uno de los siguientes períodos: (1) etapa de floración del “white locoweed”, (2) etapa de floración de “Lambret loco weed”, (3) etapa de vainas inmadura de “Lambert locoweed” y (4) etapa de vainas maduras y caída de semilla de ambas especies. Las dietas se estimaron mediante el conteo de mordidas. En el ensayo de apacentamiento estacional de 1998 el ganado prefirió el “Lambert locoweed” sobre “white locoweed” y la misma respuesta se obtuvo en cada uno de los 4 ensayos de apacentamiento intensivo conducidos en 1999. Las vacas consumieron “white locoweed” conforme la disponibilidad de “Lambert locoweed” disminuyó en 1998, pero poco “White locoweed” fue consumido en los 4 ensayos de apacentamiento intensivo de 1999. En este estudio el alcaloide tóxico swainsonina que contiene el “Locoweed” varió de 0.04 a 0.06% en “white locoweed” y no fue detectado en “Lambert locoweed”.

The taxonomy of these 2 species has been confusing. Marsh (1909) included both the white flowered (*O. sericea*) and the lavender flower (*O. lambertii*) in his description of the locoweed *Aragallus lambertii*. Later (Marsh 1919) he referred to the white locoweed as (*Astragalus lambertii*). Taxonomists have clearly separated the 2 species based on the color of their flowers (white to slightly yellow—*O. sericea*; purple violet or lavender—*O. lambertii*) and the dolabriform (ox head-like) pubescence that is unique to *O. lambertii* (Barneby 1952). Early toxicology research implicated both species in causing locoism.

Both species grow abundantly and adjacent to each other in southeast Wyoming and northcentral Colorado. However, they

differ in their phenology. White locoweed flowers in late May and early June, while Lambert locoweed flowers 3 weeks later in late June and early July. Grazing studies on short grass prairies of northeast New Mexico show that cattle readily graze white locoweed in the spring when it is green and growing rapidly and warm-season grasses are still dormant, but cease grazing it as it matures into the pod stage and warm-season grasses begin rapid growth in June (Ralphs et al. 1993, 1994, 1997). The later growing period of Lambert locoweed may cause additional management problems by extending the time cattle are likely to eat locoweeds into the summer grazing season. The objective of this study was to determine the amount of the 2 locoweed species grazed by cattle during their advancing phenological stages through the late spring and summer grazing season.

## Methods

The study was conducted at the Colorado State University Research Foundation Maxwell Ranch, located 40 km north west of Fort Collins (40° 56' N, 105° 15' W). White locoweed was abundant throughout the area on sandy loam to gravelly soils on gently sloping to steep ridges, while Lambert locoweed occurred on deeper loam soils in swales. Associated cool-season grasses included needleand-thread (*Stipa comata* Trin. & Rupr.), bottlebrush squirreltail (*Elymus elymoides* Raf. Swezey), prairie June grass (*Koeleria macrantha* (Ledeb.) Schultes) and western wheatgrass (*Pascopyron smithii* (Rydb.) A. Love). Warm-season grasses included blue grama (*Bouteloua gracilis* (H.B.K.) Lag. ex Steudel), and ring muhley (*Muhlenbergia torreyi* (Kwyth) M.E. Jones). Dominant forbs included penstemon (*Penstemon glaber* Persh), geranium (*Geranium caespitosum* James), rose pussytoes (*Antennaria parvifolia* Nutt), fringed sage (*Artemisia frigida* Willd.), and other nontoxic *Astragalus* spp..

In 1998, fifteen 2-year old Hereford cows and their calves were used for the grazing study. They had been used in a locoweed grazing study during the previous 5 weeks. The cows were placed in a 32 ha pasture and grazed from 19 June to 30 July. This corresponded to the time that white locoweed was in full flower, through the flowering period of Lambert locoweed, until both species matured and pods ripened. White and Lambert locoweed were present in equal propor-

**Table 1. Standing crop of forage classes at the beginning and end of the grazing trials in 1998 and 1999.**

Year	Time	Grass	Forb	White loco	Lambert loco	<i>Astragalus</i> spp.	Total
(kg/ha)							
1998	Begin	457 ± 64	302 ± 58	14 ± 9	26 ± 25	—	800 ± 70
	End	452 ± 72	166 ± 19	0	6 ± 5	—	624 ± 61
1999	Begin	429 ± 66	153 ± 29	165 ± 66	86 ± 23	—	833 ± 77
	End	219 ± 28	179 ± 25	50 ± 13	36 ± 13	37 ± 27	522 ± 65

tions, but neither were very abundant (Table 1).

Cattle diets were estimated using a bite count technique. Each cow was observed for 5 min periods during the morning and evening grazing periods. The number of bites of grass, forbs, white locoweed, and Lambert locoweed were counted and their percentage of the diet calculated. Each cow was observed for 5 min, then the observer rotated to another cow, so that each animal was observed at least once during each morning and evening grazing period. The percentage of bites of white and Lambert locoweed were compared by paired t-tests.

In 1999, 4 of the cows were selected for intensive grazing trials corresponding to the phenological development of the 2 locoweed species. Cows were placed in a 5 ha pasture for 4 days in each of the following periods: (1) flower stage of white locoweed (8–11 June), (2) flower stage of Lambert locoweed and immature pod stage of white locoweed (28 June–1 July), (3) immature pod stage of Lambert locoweed and mature pods of white locoweed (20–23 July), (4) mature pods and seed shatter of both species (17–20 Aug). White locoweed occurred in a patch covering about 15% of the pasture along a ridge. Lambert locoweed covered about 30% of the pasture in deeper soils of a swale. Bite counts were taken as described above by 2 observers so that 5 to 10 observations were obtained on each cow during each morning and evening grazing period. The amount of white and Lambert locoweed in diets was compared by t-tests.

Between the intensive grazing trials, the cows were grazed with a larger group of cows (the remainder from the 1998 trial) in an adjacent pasture. White locoweed was locally abundant in this pasture, but Lambert locoweed, and the other *Astragalus* species were scarce. Bite counts were taken on this group of cattle periodically to monitor locoweed consumption throughout the summer in a free-ranging setting.

Standing crop was estimated by clipping twenty, 1 x 0.25 m quadrats placed sys-

tematically along transects running the length or breadth of the pastures in both years. The vegetation was separated into forage classes of: grasses, white locoweed, Lambert locoweed, and other forbs; dried in a forced air oven at 60°C for 48 hours and weighed. The toxic alkaloid swainsonine was measured in composite samples of both species at the beginning of the 1998 trial, and at beginning and end of the 1999 trial, by gas chromatography (Molyneux et al. 1989).

## Results

In the previous grazing trial (Ralphs, unpublished data), cows consumed white locoweed for an average of 5% of their bites as it matured from the vegetative stage to full flower. When placed in the larger pasture of this study containing both white and Lambert locoweed, cows selected Lambert locoweed (up to 40 % of bites, Fig. 1), at the exclusion of white locoweed. Consumption of Lambert locoweed declined over the next 2 weeks due to the reduction in its availability. Cows began eating white locoweed as Lambert locoweed declined during the second week. Cows started selecting the immature pods of white locoweed, then progressed to selecting its leaves. A combination of decreasing availability, maturity, and drying of the leaves of the 2 species contributed to the cows ceasing to graze them after the third week of the trial. Cool-season grasses were beginning to form heads and comprised 76% of bites. Mean consumption of the 2 locoweed species for the first 3 weeks of the trial were 8 ± 1.1 % of bites for Lambert locoweed, compared to 3 ± 0.52 % for white locoweed (Table 2).

In the 1999 intensive grazing trial, cattle clearly preferred Lambert locoweed (Table 2). Only a small amount of white locoweed was consumed in the flower stage in the first trial. By the middle of the first trial, the cows selected Lambert locoweed when encountered. Three other *Astragalus* species were present in the pasture (*A. lax-*

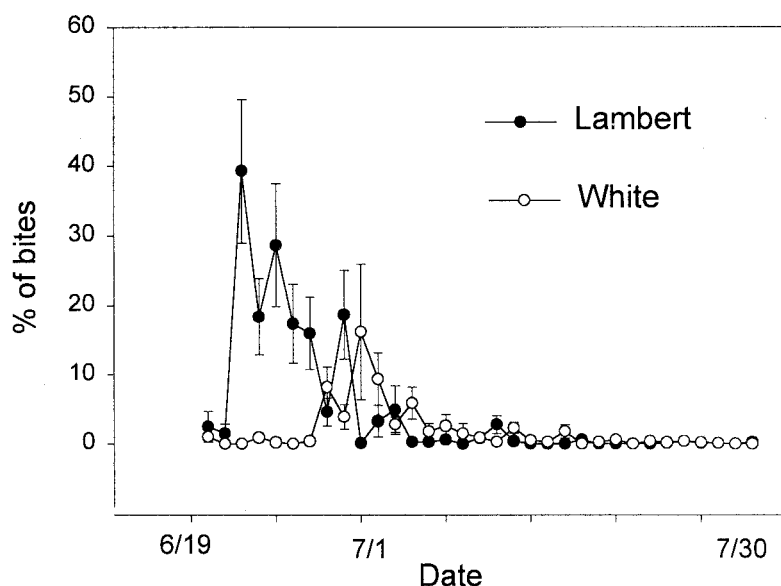


Fig. 1. Cattle consumption of Lambert and white locoweed over the grazing trial in 1998. White locoweed was in full flower at the beginning of the trial and Lambert locoweed was in the bud stage, but flowered by the first of July.

*mannii*, *A. wingatanus*, *A. drummondii*). These species were intermingled with Lambert locoweed in the swales and were highly preferred (Table 2).

Lambert locoweed was in full flower in Trial 2. The cows would seek it out (41% of bites, Table 2) and graze it along with the other *Astragalus* species. Cows consumed Lambert locoweed for 15% of bites in Trial 3, and readily grazed the other *Astragalus* species (Table 2). Cattle almost ceased grazing Lambert locoweed in Trial 4, due to its reduced availability and mature foliage. The other *Astragalus* species were also becoming mature and rank. Other forbs were abundant due to the plentiful rains and comprised a large part of the diet in the last 2 trials [sand lily (*Leucocrinum montana* Nutt.), western wallflower (*Erysimum asperum* Nutt.), western ragweed (*Ambrosia psilostachya* DC.)]. The cool-season grasses needleand-

thread, prairie junegrass and bottlebrush squirreltail dominated diets while cattle grazed uplands, and western wheatgrass, Kentucky bluegrass (*Poa pratensis* L.) and sedges (*Carex* spp.) dominated diets when cattle grazed the swales.

Between the intensive grazing trials, the 4 cows grazed in an adjacent pasture with the remainder of the original 15 cows. White locoweed was widely distributed in this pasture, Lambert locoweed was scarce, and other forbs were not as plentiful. The 4 cows consumed white locoweed for an average of 2% of bites during the intervening periods (Table 2). Between Trial 1 and 2, they consumed flowering heads of white locoweed for up to 16% of bites. They started grazing white locoweed leaves after Trial 2, and increased consumption of leaves (10–21% of bites) between Trial 3 and 4. Summer rains were frequent during 1999, and leaves of white

locoweed remained green and succulent throughout the summer, in contrast to drying up and senescing as it did in 1998.

The paradox of white locoweed being consumed in the intervening periods between the intensive grazing trials may be explained by the availability of other forage. The 5 ha pasture of the intensive grazing trial contained an abundance of cool- and warm-season forbs (including Lambert locoweed and *Astragalus* spp.), which the cows selected throughout the trial. About 1/3 of the pasture was considered swale or bottom land, and had adequate soil moisture to support growth of cool-season grasses throughout the summer. Apparently, the associated forages were more palatable than white locoweed in the intensive study pasture. Although the cattle preferred grazing in the swales, they did graze a considerable amount of time on the ridges, yet did not select white locoweed. The larger holding pasture contained more uplands with fewer forbs and more arid growing conditions. Here the succulent leaves of white locoweed were relatively palatable considering the alternative forages.

Concentration of the toxic alkaloid swainsonine in white locoweed was 0.06% in 1998 and 0.04% in 1999. However, we did not find swainsonine at detectable levels in Lambert locoweed. We also examined a sample of Lambert locoweed from Union County New Mexico and found no swainsonine. Fox et al. (1998) reported swainsonine in Lambert locoweed at concentrations of 0.026 in Mora County and 0.1% in Sierra County, N.M. Molyneux et al. (1989) measured swainsonine at 0.031% in Lambert locoweed on the Henry Mt. in southeastern Utah. There may be other indolizidine alkaloids in Lambert locoweed that were not detected by the chemical assay that account for its toxicity.

The cows in our study showed no visible signs of intoxication during the study. Locoweed poisoning is chronic, requiring animals to consume it for 15 to 20% or their diets for 3 to 4 weeks before signs of poisoning become apparent. Swainsonine inhibits glycoprotein metabolism, thus there would be no immediate post-ingestive consequence to be associated with consumption of the plant. Further, the low levels of swainsonine in locoweeds are probably below detection thresholds (Molyneux and Ralphs 1992), and thus would not affect palatability.

Table 2. Comparison of cattle consumption of white vs. Lambert locoweed.

Year	Trial	Growth stage White /Lamb.	Grass	Forb	White locoweed	Lambert locoweed	<i>Astragalus</i> spp.
----- (% of total bites) -----							
1998	1 <sup>st</sup> 3 weeks		76 ± 1.4	12 ± 1.0	3 ± 0.5 **	8 ± 1.1 **	-
1999	1	flower bud	56 ± 1.5	22 ± 1.2	0.2 ± 0.1**	11 ± 1.2**	11 ± 0.8
	2	pod flower	38 ± 2.2	15 ± 1.3	0 **	41 ± 2.4**	6 ± 0.6
	3	pod pod	43 ± 2.0	25 ± 1.7	0 **	15 ± 1.3**	18 ± 1.5
	4	seed pod	68 ± 3.0	30 ± 2.9	0 *	1 ± 0.5*	1 ± 0.5
	Mean		49 ± 1.1	22 ± 0.8	0.1 ± .04**	19 ± 1.0 **	10 ± 0.6
1999	Intervening periods		82 ± 1.5	15 ± 1.3	2 ± 0.7	0	1 ± 0.4

Difference in consumption of white and Lambert locoweed as determined by paired t-tests: \*\* P < 0.01, \* P < 0.05.

## Conclusion

Cattle consumed more Lambert locoweed than white locoweed throughout the June–August grazing season in both years, when both species were available within the same pasture. However, cattle readily consumed white locoweed before the comparison grazing trial in 1998, and in the intervening holding periods between the intensive grazing periods in 1999.

The lack of the toxic locoweed alkaloid swainsonine in Lambert locoweed in this study presents a quandary. Lambert locoweed populations at other locations have been reported to contain swainsonine. Further research is necessary to determine if Lambert locoweed contains other toxic alkaloids, and if there are seasonal and geographic differences in swainsonine content.

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# Antelope bitterbrush seed production and stand age

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## Abstract

Antelope bitterbrush (*Purshia tridentata* (Pursh) DC) is the most important browse species on many western mule deer (*Odocoileus hemionus*) ranges. Lack of antelope bitterbrush seedling recruitment is a critical problem, and therefore, the influence of livestock grazing on antelope bitterbrush seed production is an important issue. Seed production was compared in grazed and ungrazed communities during 1995 and 1996 at 2 locations in northeastern California and one location in northwestern Nevada. A system of seed traps was used to estimate seed production in relation to the size, age and grazing of antelope bitterbrush plants in the various stands. Antelope bitterbrush seed production was significantly ( $P \leq 0.01$ ) higher at one of the ungrazed sites. Significant ( $P \leq 0.05$ ) differences in shrub ages were also recorded between sites.

**Key Words:** *Purshia tridentata*, mule deer, shrub, browse, herbivory

Antelope bitterbrush (*Purshia tridentata* (Pursh) DC) is one of the most important browse species on many western ranges. Fire, excessive grazing, insects, drought, and other unfavorable weather conditions can all contribute to the deterioration of antelope bitterbrush communities (Hormay 1943). Antelope bitterbrush is a key browse species in the diets of many mule deer (*Odocoileus hemionus*) herds (Lassen et al. 1952, Dasmann and Blaisdell 1954, Leach 1956, Updike et al. 1989). This shrub is also an important source of digestible protein for cattle (*Bos taurus*) during late summer and fall. The influence of domestic livestock grazing on wildlife habitat is a very important issue in northeastern California and throughout the west, thus antelope bitterbrush is a focal point in deer and cattle competition.

Antelope bitterbrush flowers on second year wood. Excessive utilization of the current annual growth is reported to reduce flowering and seed production the next season (Hormay 1943). However, the effects of livestock grazing on antelope bitterbrush seed production is not well known. This study was initiated to determine whether sites grazed by domestic livestock differed in antelope bitterbrush seed production from paired ungrazed sites of the same potential.

## Resumen

El "Antelope bitterbrush" (*Purshia tridentata* (Pursh) DC) es la especie de ramoneo mas importante en muchos de los pastizales donde habita el "Western mule deer" (*Odocoileus hemionus*). La falta de establecimiento de plántulas de "Antelope bitterbrush" es un problema crítico, y por lo tanto, la influencia del apacentamiento del ganado en la producción de semilla de "Antelope bitterbrush" un problema importante. En 1995 y 1996 se comparó la producción de semilla en comunidades con y sin apacentamiento, la comparación se realizó en dos localidades del nordeste de California y en una localidad del noroeste de Nevada. Se utilizó un sistema de trampas semillas para estimar la producción de semilla en relación al tamaño, edad y apacentamiento en plantas de varias poblaciones de "Antelope bitterbrush". La producción de semilla del "Antelope Bitterbrush" fue significativamente mayor ( $P \leq 0.01$ ) en uno de los sitios sin apacentar. También se registraron entre sitios diferencias significativas ( $P \leq 0.05$ ) en la edad de los arbustos.

## Study Area

We used 2 sites in northeastern California, and 1 site in extreme northwestern Nevada. The Turtle Mountain site, 40 km northeast of Doyle, Calif., is at an elevation of 1,378 m, and has grazed and ungrazed communities. The ungrazed community is within a state wildlife management area that has been free from livestock grazing since 1948. The livestock-grazed community receives annual spring use by cattle. Both the grazed and ungrazed communities are dominated by antelope bitterbrush, big sagebrush (*Artemisia tridentata* ssp. *tridentata* Nutt.), and desert peach (*Prunus andersonii* A. Gray), with a cheatgrass (*Bromus tectorum* L.) understory. The soil is a gravelly, loamy, coarse sand. The site received 71 cm of precipitation from October of 1994 through October 1996, mostly during the winter months as recorded by rain gauges located on site.

The Buntingville, Calif., site is on private property 35 km south of Susanville, Calif. and received 150 cm of precipitation from October 1994 through October 1996, mostly during the winter months. The elevation is 1,345 m. The grazed community is dominated by antelope bitterbrush, big sagebrush, and cheatgrass and receives late season grazing. The ungrazed community, separated from the grazed habitat by U.S. 395, is dominated by antelope bitterbrush with a very sparse occurrence of cheatgrass. The soils are a coarse gravel with inclusions of mixed loamy sand.

Pilgrim Lake in northwestern Nevada is 682 km north of Reno, Nev. at an elevation of 2,067 m. The site has a three-way enclosure which was constructed in 1993 to protect 1 ha of habitat from livestock grazing. The site is dominated by antelope bitter-

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brush, mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana* Nutt.), and golden currant (*Ribes aureum* Pursh.), while the understory is dominated by Idaho fescue (*Festuca idahoensis* Elmer), bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Love.), and arrowleaf balsamroot (*Balsamorhiza sagittata* Pursh.). The site received 80 cm of precipitation from October 1994 through October 1996, mostly during the winter months. The soils are mostly clay with loamy inclusions. A 2 pasture deferred rest rotation grazing system by cattle is practiced on the unprotected habitat.

## Methods

Antelope bitterbrush seed production was sampled in 1995 and 1996 on 10 randomly selected antelope bitterbrush shrubs in each grazed and ungrazed community. The same shrubs were used for both 1995 and 1996 sampling. The height of the shrub and diameter of the canopy of each shrub was measured.

Seed collecting grates measuring 9.5 cm<sup>2</sup> surface area and 4.2 cm in depth were used to collect dispersed bitterbrush seeds for estimates of seed production. Four grates were evenly distributed under each bitterbrush shrub in the 4 cardinal directions (38 cm<sup>2</sup> seed collecting grate area/shrub), 60 cm within the edge of the shrub, during the end of May of each year and marked by shrub, grazing treatment, and site. The grates, which allowed for seed collection but did not allow for seed predation by birds, rodents, and other seed predators, were picked up in mid-August following seed dispersal. Antelope bitterbrush seeds within individual grates were counted and recorded by shrub, site, and treatment. The number of antelope bitterbrush seeds produced by each shrub was calculated by multiplying the number of seeds in the seed trap by the proportionate area sampled ( $N = n \times c$ , where  $N$ =total seed production,  $n$ =seeds in trap,  $c$  = canopy area sampled) using the seed trap method (Johnson and West 1988).

The height of the shrub, canopy (length x width), and basal diameter of the stem or trunk area of the 3 randomly selected antelope bitterbrush plants in each treatment were measured and the shrubs cut at the soil surface for age determinations. Growth rings were counted using a low power microscope to determine age (McConnell and Smith 1977).

A three-way, mixed Analysis of Variance model with repeated measures

**Table 1. Antelope bitterbrush mean seed production ( $\pm$  confidence interval) per shrub in 1995 and 1996 at 3 separate locations in grazed and ungrazed communities. Plants sampled per treatment = 10.**

Location/ Treatment	Year	$\bar{x}$ Seed Production (seeds/plant)	$\pm$ 95% Confidence Interval
Buntingville	Grazed	1995	8,700
		1996	24,000
	Ungrazed	1995	90,600
		1996	28,500
Turtle Mountain	Grazed	1995	6,200
		1996	6,600
	Ungrazed	1995	4,400
		1996	8,800
Pilgrim Lake	Grazed	1995	700
		1996	2,000
	Ungrazed	1995	900
		1996	2,500

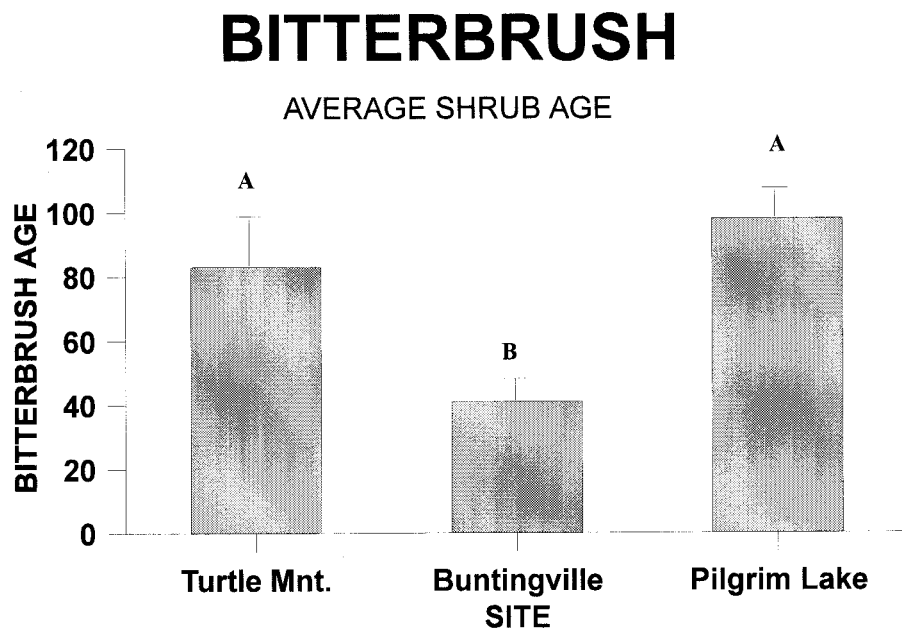
was used to analyze the effects of grazing, site, and year on seed productivity.

## Results

Antelope bitterbrush seed production was significantly greater ( $P \leq 0.01$ ) at the Buntingville ungrazed treatment in 1995 compared to all other sites and treatments (Table 1). The remaining treatments were not significantly different among treatments (grazed or ungrazed), and years, but

there was a significant ( $P \leq 0.05$ ) difference in seed production between sites. Antelope bitterbrush seeds at the Buntingville site produced significantly ( $P \leq 0.05$ ) more seeds than recorded at the Turtle Mountain and Pilgrim Lake sites, and Turtle Mountain significantly ( $P \leq 0.05$ ) produced more seeds than did the Pilgrim Lake site.

The age of antelope bitterbrush shrubs was significantly ( $P \leq 0.05$ ) older at the Pilgrim Lake and Turtle Mountain sites than the Buntingville site (Fig. 1). The



**Fig. 1. Average age of antelope bitterbrush shrubs. Sites with same letter are not significantly different ( $P > 0.05$ ).**

# BITTERBRUSH

## AVERAGE CANOPY SIZE

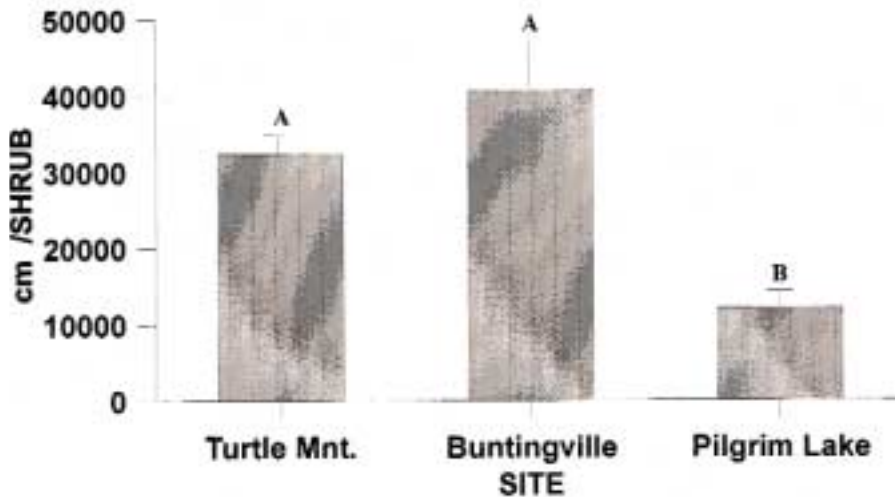


Fig. 2. Average canopy size of antelope bitterbrush shrubs. Sites with same letter are not significantly different ( $P > 0.05$ ).

Buntingville ungrazed habitat was significantly ( $P \leq 0.05$ ) younger ( $\bar{x} = 33$ ) than the other grazed and ungrazed habitats ( $n = 5$ ), including the Buntingville grazed habitat ( $\bar{x} = 49$ ).

There was no significant difference in the height of antelope bitterbrush shrubs between these sites and treatments. However, antelope bitterbrush shrubs had significantly ( $P \leq 0.05$ ) lower mean canopy diameter at the Pilgrim Lake site than that recorded at the Turtle Mountain and Buntingville sites (Fig. 2).

## Discussion

The Buntingville ungrazed community produced almost twice as much antelope bitterbrush seed per shrub monitored in 1995 than in 1996. This greater seed production was the only statistical difference in antelope bitterbrush seed production between treatments and years during the study. Precipitation is a major role player in antelope bitterbrush seed production (Nord 1965). The site received 74 cm of precipitation from October 1994 to October 1995, which is 45% more precipitation than it received from October 1995 to October 1996 (41 cm). The amount and periodicity of moisture received should generally effect the adjacent grazed and ungrazed treatments equally, but some confusing occurrences took place. Antelope bitterbrush plants flower on sec-

ond year wood, therefore precipitation the previous year is very important. Antelope bitterbrush shrubs in the grazed community at the Buntingville site produced 36% more seeds in the less favorable precipitation scenario of 1996 than it did in 1995 during a more favorable scenario. The Buntingville grazed site experienced improved seed production through the favorable precipitation scenario. The importance of this relation in interpreting the results of this study is that grazing did not reduce the excellent shoot growth in 1995 enough to depress seed production in 1996 at the Buntingville site. The height and crown diameter of the antelope bitterbrush plants at the Buntingville grazed site places much of the current annual twig growth out of the reach of grazing animals. This is one of the multitude of factors that influences the relative influence of livestock grazing on antelope bitterbrush seed production.

Appearance of antelope bitterbrush plants can be deceiving in terms of actual age. The Buntingville grazed and ungrazed communities appear to be very different in age, but based on analysis of trunk growth rings, the grazed community was 16 years older, 33 years of age in the ungrazed community and 49 years of age in the grazed community, respectfully. This 16 year difference in age should not play a major role in the difference in seed production between the two treatments at the Buntingville site we experienced, and

therefore may suggest that the level of grazing on antelope bitterbrush shrubs over time between the two treatments plays a larger role in the seed production results we recorded. Foliage production of antelope bitterbrush is reported by McConnell and Smith (1977) to peak at around 60 years of age with early season grazing. The Buntingville site was the only site under 60 years of age. The Turtle Mountain site averaged 83 years of age and the Pilgrim Lake site averaged 98 years of age. Using McConnell and Smith's (1977) estimates on the peak production of antelope bitterbrush, the age classes at two of our three sites were well past their peak in production. This can result in an inadequate seed source at the site, thus poor seedling recruitment may result, as is currently being reported.

The Buntingville site is in the heart of the antelope bitterbrush communities where the Lassen cultivar was selected. The once continuous stands of large statured plants have been broken into smaller units in the Buntingville area by increasing development of home sites. It is very possible the stands on adjoining sides of a major highway resulted from separate stand renewal processes, perhaps wildfires.

Great Basin tent caterpillar (*Malacosoma fragile*) infestations occurred at the Buntingville and Pilgrim Lake sites during 1996. This caterpillar periodically infests bitterbrush causing defoliation and sometimes death (Clark 1956, Furniss and Barr 1975). The stress these caterpillars inflicted upon these shrubs can result in significant loss of foliage and seed production. The accumulations of tent caterpillar webs and debris have a negative influence on herbivore preference for the browse. We assume the chances of infestation are equal between grazed and ungrazed sites, but in the case of the Buntingville site this may not be true, as we noted a heavier infestation of the tent caterpillar at the Buntingville ungrazed community in 1996 than that in the grazed habitat. This may have played a factor in the decreased seed production experienced at the Buntingville ungrazed community from 1995 to 1996.

The Buntingville ungrazed community was visually more vigorous than plants at the other sites or treatments (Fig. 3a and 3b.). This ungrazed community is also along U.S. 395, a very heavily traveled highway creating a barrier to mule deer movement. The combination of factors such as minimal herbivory, favorable precipitation, and younger age class may all





a



b

**Fig. 3.** Notice the leader length of this younger more vigorous antelope bitterbrush shrub (a) compared to an old decadent shrub (b).

help in making the Buntingville ungrazed community significantly more productive, although insect herbivory greatly curtailed this productivity in 1996.

This study suggests that grazing had an effect (negative effect) on antelope bitterbrush seed production at one site. This one site was also a younger more vigorous antelope bitterbrush community. But, the poor age distribution (older age class shrubs) of antelope bitterbrush shrubs suggests that recruitment of younger antelope bitterbrush shrubs into bitterbrush communities has been lacking for some time (80–100 years). Removal of livestock itself may not increase bitterbrush foliage production and second year growth, or seed production, but may rather add stress to the plant thus decreasing its years in sustainable production as reported by McConnell and Smith (1977). The Turtle Mountain and Pilgrim Lake grazed plant communities received light grazing during this study, while the Buntingville grazed community received moderate levels of use. Adams 1975, reported that in southern Oregon an antelope bitterbrush community that averaged 473 antelope bitterbrush shrubs per 0.4 hectares, required the establishment of 6.7 antelope bitterbrush plants per 0.4 hectares annually to propagate the community. He also reported that the establishment of antelope bitterbrush plants into the community from 1925 to 1975 was 0.7 plants per 0.4 hectares annually, resulting in old even-aged decadent

antelope bitterbrush communities.

Outside of seed production, other factors that influence the establishment of antelope bitterbrush plants into the community include seed damage by insects (Furniss 1972), seed predation by granivorous rodents (Clements 1994), seed dispersal by granivorous rodents (Vander Wall 1994), seedling competition with other plant species (Holmgren 1956), seedling predation by rodents (Clements and Young 1996) and insects (Hubbard 1956), and grazing by domestic and wild animals (McNulty 1947), to name a few.

The establishment of new antelope bitterbrush plants into the community is very complex, and with all the research done in the area of antelope bitterbrush ecology, researchers as well as resource managers are still unsure of the importance of the various factors on antelope bitterbrush seedling establishment. Bitterbrush is an opportunistic species, perhaps the propagation of this species is highly dependent on some form of habitat manipulation or combinations of manipulation. Senescent antelope bitterbrush shrubs lose vigor and provide little browse.

Leopold (1959) suggested to the Nevada Department of Fish and Game that to maintain high carrying capacities of mule deer, deliberate manipulation of habitat must be implemented. At both the Turtle Mountain and Pilgrim Lake sites, the age classes of antelope bitterbrush suggest that any form of natural disturbance for propa-

gating antelope bitterbrush has been absent for the past 80–100 years. The Buntingville site is of a younger age class and both the grazed and ungrazed communities are under private ownership. Though no absolute deliberate disturbance is documented, being under private ownership may have resulted in such a disturbance that favored antelope bitterbrush recruitment. The widespread concern over the lack of antelope bitterbrush recruitment on many western rangelands warrants further research on this problem. Further research into the effects of livestock as well as native herbivores on antelope bitterbrush seedlings, as well as investigating different methods of vegetation manipulation to reinvigorate bitterbrush and other brush communities is an area of research worth approaching.

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# Activated charcoal and experience affect intake of juniper by goats

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## Abstract

Goats consume juniper, but toxic terpenoids within the plant limit intake. Our objective was to determine if dosing goats with the adsorptive compound activated charcoal would increase juniper consumption. Twenty Boer-cross goats were placed in individual pens; at 0800 hours, 10 were dosed with 1 g kg<sup>-1</sup> body weight (BW) of activated charcoal in an aqueous solution, and 10 were not dosed. Dosing occurred daily for 10 days. Goats were offered redberry juniper (*Juniperus pinchotii* Sudw.) in Trial 1, ashe juniper (*Juniperus ashei* Buch.) in Trial 2, and a choice between redberry and ashe juniper in Trial 3. For each trial, juniper was offered to all goats for 2 hours after dosing with activated charcoal. In Trial 1, goats dosed with activated charcoal consumed more ( $P < 0.05$ ) redberry juniper during the first 5 days of exposure. In Trial 2, activated charcoal did not affect ashe juniper intake. In Trial 3, dosing with activated charcoal did not affect juniper intake. All goats preferred ashe to redberry juniper. Juniper intake increased across days of exposure for Trials 1 and 2, apparently because goats adapted to the terpenoids in juniper through repeated exposure. It appears that activated charcoal will only increase redberry juniper intake during initial exposures.

**Key Words:** *Juniperus*, *J. ashei*, *J. pinchotii*, *Capra*, experience, preference, toxicosis, feedback, aversions, browsing

Redberry (*Juniperus pinchotii* Sudw.) and ashe (*Juniperus ashei* Buch.) juniper are increasing over most of central and western Texas (Smeins et al. 1997). In the Rolling Plains region of Texas, redberry juniper is common while ashe juniper or a mixture of redberry and ashe juniper occur throughout the Edwards Plateau of Texas (Ansley et al. 1995, Smeins and Fuhlendorf 1997, Ueckert 1997). Control alternatives are available, but most are expensive and may adversely impact other desirable shrubs (Reinecke et al. 1997, Johnson et al. 1999). Recent efforts have focused on training goats to consume juniper (Launchbaugh et al. 1997, Pritz et al. 1997) or selecting replacements for the flock from goats that readily consume juniper (Jones et al. unpubl. data).

Intake of a particular plant species depends on the herbivore's ingestive and digestive abilities and familiarity with the forage

## Resumen

Los caprinos consumen el "Juniper", pero los terpenoides tóxicos que contiene la planta limitan su consumo. Nuestro objetivo fue determinar si la administración a los caprinos del compuesto adsorptivo carbón activado incrementaría el consumo de "Juniper". 20 cabras de cruce Boer se colocaron en corrales individuales a las 0800 horas, a 10 se les administró 1 g kg<sup>-1</sup> de peso vivo (PV) de carbón activado en solución acuosa y las 10 restantes no recibieron carbón activado. La administración del carbón activado fue diaria durante 10 días. En el experimento 1 a las cabras se les ofreció "Redberry juniper" (*Juniper pinchotii* Sudw.), en el experimento 2 se les ofreció "Ashe juniper" (*Juniperus ashei* Buch.) y en un tercer experimento se les ofreció a libre elección "Redberry juniper" y "Ashe juniper". En cada experimento el "Juniper" se les ofreció a todas las cabras 2 horas después de administrarles el carbón activado. En el experimento 1, durante los primeros 5 días, las cabras que recibieron carbón activado consumieron más ( $P < 0.05$ ) "Redberry juniper". En el experimento 2, el carbón activado no afectó el consumo de "Ashe juniper". En el experimento 3, la administración de carbón activado no afectó el consumo de "Juniper". Todas las cabras prefirieron "Ashe juniper" que "Redberry juniper". En los experimentos 1 y 2 el consumo de "Juniper" aumentó a través de los días de exposición, aparentemente porque las cabras se adaptaron a los terpenoides del "Juniper" por la exposición repetida a la que estuvieron sometidas. Parece que el carbón activado solo incrementará el consumo de "Redberry juniper" durante el inicio de exposición a él.

(Provenza 1995, 1996). When herbivores encounter and consume chemically defended plants for the first time, 2 responses typically occur. Most toxins cause aversive postingestive feedback and the formation of conditioned taste aversions (Provenza et al. 1992). Thus, herbivores usually avoid toxic plants after the initial consumption. If alternative forage is limited, herbivores may continue to consume the toxic plant but limit intake below toxic levels (Launchbaugh et al. 1993). Both responses limit the effectiveness of using livestock herbivory to control chemically defended plants such as redberry and ashe juniper.

Both redberry and ashe juniper contain terpenoids, but composition of specific terpenes in the essential fraction differs among the 2 species (Riddle et al. 1996). Terpenoids in redberry juniper cause more digestive distress than those in ashe juniper, and goats prefer ashe to redberry juniper (Straka 1993).

Activated charcoal attenuates toxicosis from several toxic forages; activated charcoal reduced aflatoxicosis in chickens

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(Ademoyero and Dalvi 1983, Dalvi and Ademoyero 1984, Dalvi and McGowan 1984), toxicosis from tannins in 2 shrubs from Zanzibar (Cooney and Struhsaker 1997, Struhsaker et al. 1997), and toxicosis from the sesquiterpene lactone in bitterweed (*Hymenoxys odorata* DC) (Poage et al. 2000). Given the effectiveness of activated charcoal with several other toxins, we hypothesized that dosing with activated charcoal would improve acceptance and increase intake of both redberry and ashe juniper.

## Methods

### Animals and Feeding

Three trials were conducted at the Texas Agricultural Experiment Station, Sonora, Tex (Lat. 31°N, Long 100°W). Twenty freshly-weaned male and female Boer-cross goats, weighing about 25 kg (range 15 to 29 kg), were placed in individual pens for the duration of the study. Goats were reared on juniper-free rangelands and were naive to juniper before initiation of the study. Each goat was fed 1.5% of their body weight (BW) of alfalfa pellets (15% CP, 2.22 Mcal kg<sup>-1</sup> DE) daily to meet maintenance requirements (NRC 1981). All goats had ad libitum access to fresh water and a calcium/phosphorus mineral with trace elements. Alfalfa was fed from 1000 hours to 1700 hours each day. At 1700 hours, alfalfa residuals were weighed to estimate intake. Goats only received water and access to mineral supplement overnight.

### Trial 1

Trial 1 assessed the effect of dosing with activated charcoal on consumption of redberry juniper. The duration of the trial was 10 days. Twenty goats were randomly assigned to 1 of 2 treatments with an equal number of males and females in each treatment. Each morning (0800 hours), 10 goats were dosed (by gavage) with 1 g kg<sup>-1</sup> BW of activated charcoal mixed in solution with 500 ml of distilled water at room temperature. This dosage agrees with the recommended dose for alleviating toxicosis (Buck and Bratich 1986) and the level shown to attenuate toxicosis with the toxic plant bitterweed (Poage et al. 2000). The 10 remaining goats were not dosed. In other studies, dosing with water alone did not affect intake (Provenza et al. 1994, Poage et al. 2000).

Immediately after dosing, all goats were offered 200 g of redberry juniper for 2 hours. If an individual consumed all 200 g,

an additional 100 g was fed. Juniper was collected near the research facilities 1 hour before feeding. Branches were clipped from mature trees, and leaves were stripped from the stems before feeding. Refusals were collected and weighed to determine intake. Four additional samples were placed out of reach of goats in similar feeding troughs to account for moisture change.

Blood samples were collected by jugular venipuncture on the day before initiation of Trial 1, midway through the trial, and the day after the trial to measure serum metabolite levels. Serum metabolite levels can provide additional evidence of toxicosis or that liver damage has occurred from toxicosis (Radostits et al. 1994). For instance, elevated aminotransferase (AST) is indicative of soft tissue damage from toxicosis, while elevated levels of blood urea nitrogen (BUN), gamma glutamyltransferase (GGT), and creatinine are indicative of liver dysfunction from tissue damage (Cornelius 1989, Kramer 1989, Cheeke 1998). Nevertheless, changes in serum metabolite levels do not provide conclusive evidence that toxicosis has occurred. Serum metabolite levels vary among healthy individuals, and levels can be affected by disease or tissue damage unrelated to toxicosis (Cornelius 1989, Kramer 1989). A decrease in intake may be a more accurate measure of toxicity when dealing with plants that contain compounds that cause aversive post-ingestive feedback (Calhoun et al. 1981, Pfister et al. 1992).

Blood samples were centrifuged, serum harvested, frozen, and transported to the Texas Medical Diagnostic Laboratory, College Station, Tex. for analysis.

Samples were analyzed for BUN, creatinine, AST, and GGT levels as indications of toxicosis and liver damage.

### Trial 2

Trial 2 began 2 weeks after the completion of Trial 1 and lasted for 10 days. Trial 2 assessed the effect of dosing with activated charcoal on consumption of ashe juniper. The same protocol used in Trial 1 was used in Trial 2. The same goats were used in Trial 2 but were re-assigned to treatments. A systematic method of allocation was used to minimize the effect of previous experiences with juniper. Goats were assigned to treatments so that the dosed (control) treatment consisted of 5 goats dosed with activated charcoal in Trial 1 and 5 that were not dosed.

### Trial 3

Trial 3 began 2 weeks after the completion of Trial 2 and lasted for 10 days. Goats were randomly re-assigned to treatments (dosing with activated charcoal or not dosed) and offered a choice of redberry and ashe juniper. We fed 200 g of each type of juniper for 2 hours to each individual goat. If an individual consumed all of either type of juniper, 100 g were added. Serum metabolite levels were not measured during Trial 3, because simultaneous feeding both types of juniper would confound metabolite levels.

### Statistical analysis

Intake data from Trials 1 and 2 were analyzed using repeated measures analysis of variance with day of feeding as the repeated measure (Hicks 1993). Dosing with or without charcoal served as the

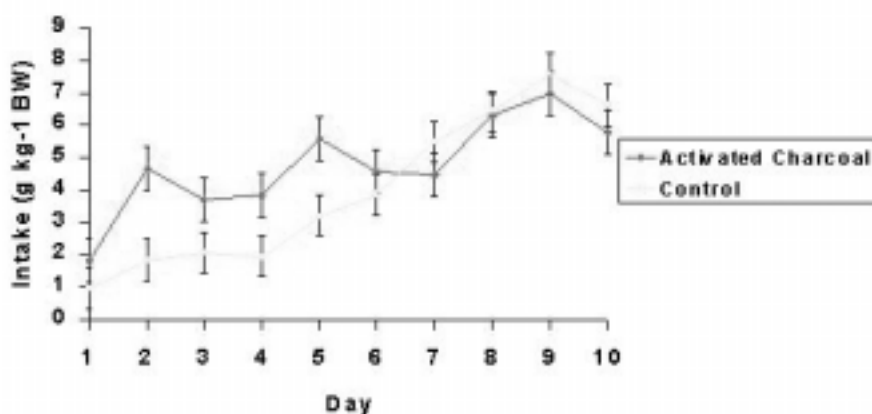


Fig. 1. Intake (g kg<sup>-1</sup> BW) of redberry juniper by goats that were dosed with either activated charcoal in aqueous solution or not dosed (control) in Trial 1.

**Table 1.** Serum metabolite levels when goats were fed redberry (Trial 1) or ashe juniper (Trial 2) immediately after dosing with activated charcoal (1 g kg<sup>-1</sup> BW). Serum was collected before, during, and after each trial. Levels before each trial were used as a covariate to account for initial variations among goats. Values presented are averaged across samples taken during and after each study.

Serum Metabolite	Treatment		SEM
	Activated Charcoal	Control	
<b>Feeding redberry juniper</b>			
BUN <sup>1</sup> (mg/dL)	18.1 <sup>b</sup>	20.3 <sup>a</sup>	0.92
creatinine (mg/dL)	0.81 <sup>b</sup>	1.12 <sup>a</sup>	0.08
AST <sup>2</sup> (U/L)	48.2 <sup>b</sup>	65.9 <sup>a</sup>	0.03
GGT <sup>3</sup> (U/L)	18.0	39.0	4.55
<b>Feeding ashe juniper</b>			
BUN (mg/dL)	16.1	17.5	0.95
creatinine (mg/dL)	0.72	0.74	0.12
AST (U/L)	44.9	44.4	3.24
GGT (U/L)	30.1	34.0	2.14

<sup>a,b</sup> Means within rows with different superscripts differ ( $P < 0.05$ ).

<sup>1</sup> blood urea nitrogen

<sup>2</sup> aminotransferase

<sup>3</sup> gamma glutamyltransferase

whole plot and sex of goat served as a subplot. Serum metabolite levels were analyzed using the same model but with the initial metabolite level as a covariate. For Trial 3, dosing with or without charcoal served as the whole plot and species of juniper as the subplot. We did not analyze for a sex effect in Trial 3 because of the lack of difference in Trials 1 and 2. Means were separated using least significant difference (LSD) when  $P \leq 0.05$  (Gomez and Gomez 1984). The statistical package JMP was used for all analyses (SAS 1994).

## Results

### Trial 1

Goats dosed with activated charcoal consumed more redberry juniper on days 1 through 5, while intake was similar among treatments thereafter (Fig. 1; treatment X day interaction,  $P < 0.05$ ). Alfalfa intake was similar among treatments (196 and 206 g day<sup>-1</sup>) and across the 10 days of the study.

Dosing with activated charcoal affected serum metabolite concentrations (Table 1). Goats dosed with activated charcoal had lower concentrations of BUN, creatinine, and AST. Concentrations of GGT also tended to be lower for goats dosed with activated charcoal ( $P = 0.14$ ).

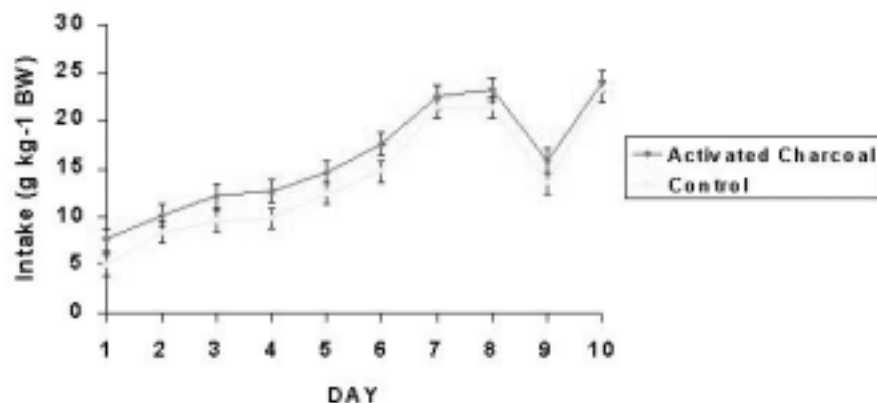
### Trial 2

Dosing with activated charcoal did not affect ashe juniper intake throughout the 10-day trial (Fig. 2). Intake increased daily for all goats until day 7. Intake decreased on day 9; intake on day 10 was similar to

intake on days 7 and 8. Alfalfa intake was similar among treatments (194 and 194 g day<sup>-1</sup>) and across the 10 days of the study. Serum metabolite levels were similar among goats dosed with activated charcoal or not dosed (Table 1).

### Trial 3

All goats preferred ashe to redberry juniper irrespective of dosing with activated charcoal (Fig. 3). Goats consumed about 20 g kg<sup>-1</sup> BW of ashe juniper and 3 g kg<sup>-1</sup> BW of redberry juniper each day. Intake of redberry juniper, ashe juniper, and alfalfa were similar among treatments. The treatment X day interaction was similar for goats offered the 2 species of juniper.



**Fig. 2.** Intake (g kg<sup>-1</sup> BW) of ashe juniper by goats that were dosed with either activated charcoal in aqueous solution or not dosed (control) in Trial 2.

## Discussion

Activated charcoal apparently attenuated aversive feedback from redberry juniper during the first few days of feeding; goats dosed with activated charcoal ate more redberry juniper on days 1 through 5 and serum metabolite levels varied among treatments. After day 5, all goats consumed similar amounts of redberry juniper and intake increased daily across treatments until day 6. The effectiveness of activated charcoal depends on the dosage of charcoal and the amount of toxin present in the digestive tract (Edwards and McCredie 1967, Decker et al. 1968, Hayden and Comstock 1975, Levy 1982). The dosage used in this study was based on general recommendations for treating toxicity (Buck and Bratich 1986) and levels effective in reducing plant-induced toxicosis in another study (Poage et al. 2000).

The amount of water used for dosing may have affected intake for goats dosed with activated charcoal. However, other studies have illustrated that dosing with water alone does not affect intake (Provenza et al. 1994, Poage et al. 2000). Evidently, the amount of fill from 500 ml of water in the rumen is not sufficient to induce satiety.

Dosing with 500 ml of water may have diluted terpenoid levels or increased urination and excretion of toxins. If toxin dilution and excretion affected the results of Trial 1 with redberry juniper, a similar response should have been observed in Trial 2 when goats were fed ashe juniper. Ashe juniper also contains terpenoids that have aversive postingestive properties. Intake of ashe juniper was similar across both treatments in Trial 2 regardless of dosing.

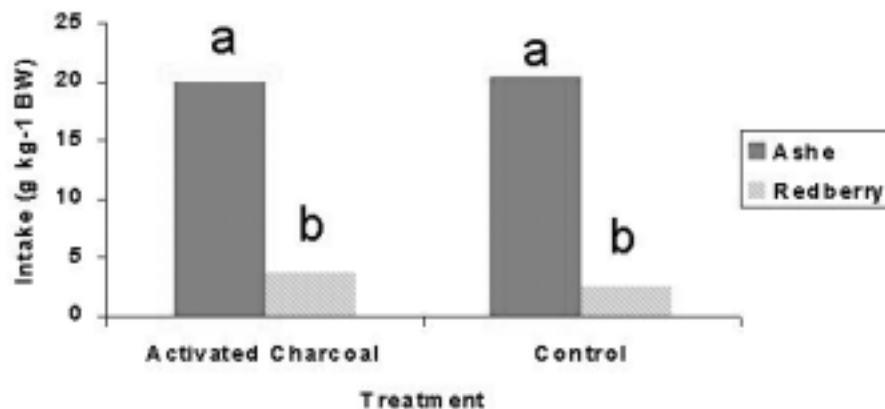


Fig. 3. Intake ( $\text{g kg}^{-1}$  BW) of ashe and redberry juniper when goats were offered a choice of the 2 species for 2 hours. Goats were dosed with either activated charcoal in aqueous solution or not dosed (control) in Trial 3.

Protein and/or energy supplementation can increase intake of juniper. In another study, feeding a cottonseed meal/alfalfa supplement increased redberry juniper intake by 40% over goats supplemented with corn and 30% over goats fed no supplement (Taylor et al. 1997). Similarly, Banner et al. (2000) showed that supplementing lambs with barley immediately before feeding sagebrush increased sagebrush intake. In this study, goats were fed a nutritious basal ration (i.e., alfalfa pellets) to meet maintenance requirements from 1000 to 1700 hours followed by fasting overnight. Goats did not receive alfalfa again until after feeding juniper for 2 hours. Thus, it seems unlikely that the effect of supplementation observed in other studies would affect the results of this study because of differences in type of supplement and time of feeding.

Daily increases in juniper consumption were probably caused by physiological changes that increased the liver's ability to metabolize the terpenoids in juniper (Launchbaugh et al. 1997). Intake increased until goats ate  $7.5 \text{ g kg}^{-1}$  BW of redberry juniper (Trial 1) and  $23 \text{ g kg}^{-1}$  BW of ashe juniper (Trial 2), thereafter intake stabilized (Fig. 1 and 2). We contend that goats increased intake of juniper until a toxic threshold was reached. The toxic threshold represents the point at which toxin intake surpasses the liver's ability to oxidize and excrete the terpenoids. When the threshold was reached, goats probably experienced aversive postingestive feedback and decreased intake accordingly.

Dosing with activated charcoal did not affect intake of ashe juniper. This is not surprising considering that goats prefer ashe to redberry juniper because of differ-

ent toxin compositions (Straka 1993). Goats apparently do not experience aversive postingestive feedback from ashe juniper to the same degree, and feeding activated charcoal did not provide any additional reduction in aversive feedback.

Analysis of serum metabolite levels supports the idea that activated charcoal reduces the toxicity of redberry juniper. As intake of terpenoids increase, AST serum levels increase apparently because of soft tissue damage (Cornelius 1989, Kramer 1989). In this study, AST levels were lower ( $P < 0.05$ ) for goats that were dosed with activated charcoal. Other serum metabolites, which are indicative of toxicosis, were also lower (BUN, creatinine). Exposure to the terpenoids in juniper early in life causes liver damage which reduces subsequent juniper consumption and animal productivity (Pritz et al. 1997). Dosing with activated charcoal during initial exposures to redberry juniper may reduce the toxicological effects of juniper consumption and lead to greater consumption of juniper later in life.

In Trial 3, goats were given a choice of redberry or ashe juniper. Goats preferred ashe juniper regardless of dosing with activated charcoal. Trial 3 was conducted after goats were exposed to both redberry (Trial 1) and ashe (Trial 2) juniper. Previous experiences with both species may have affected intake in Trial 3; goats may have selected ashe over redberry juniper because of the degree of aversive feedback experienced with each species in Trials 1 and 2. Some goats were fed redberry juniper only after dosing with activated charcoal in Trial 1 while others were fed redberry juniper alone. Activated charcoal apparently reduced aversive feedback for goats dosed with activated charcoal in

Trial 1, yet all goats preferred ashe to redberry. Thus, previous foraging experiences (avoiding or experiencing aversive feedback) cannot completely account for higher intake of ashe juniper.

Differences in nutrient quality among ashe and redberry juniper could explain differences in preference. In general, junipers contain a crude protein content of 6-9% and digestibility ranging from 57 to 66% (Launchbaugh et al. 1997), but aversive postingestive feedback from terpenoids limit intake below maintenance levels (Riddle et al. 1999). As a result, it seems unlikely that goats would consume one juniper species over another to meet energy and protein needs.

Preference for ashe over redberry juniper also suggests that activated charcoal did not alleviate all potential toxic affects, and goats probably received some aversive postingestive feedback from consuming redberry juniper. Thus, activated charcoal may reduce some of the toxic effects from redberry juniper, but goats may still choose to consume ashe juniper when given a choice of the 2 species.

## Implications

Results of this study suggest that dosing goats with  $1 \text{ g kg}^{-1}$  BW of activated charcoal will improve the acceptance of redberry juniper during initial exposures. However, after initial exposures, activated charcoal appears to have little affect on intake. Thus, continued dosing or feeding activated charcoal to maintain juniper intake is not feasible. This study also offers further evidence that goats prefer ashe to redberry juniper. If goats were used as a biological control method in mixed stands of ashe and redberry juniper, goat browsing would result in a greater decrease in ashe juniper cover. To circumvent this problem, Taylor et al. (1997) suggested prescribed burning followed by goat browsing to control mixed stands of juniper. Prescribed burning can kill ashe juniper trees (Ueckert 1997). Unlike ashe juniper, redberry resprouts from basal buds after topkill. Goat browsing can then be implemented to suppress the resprouts because resprouts have lower terpenoid levels (Straka and Taylor unpubl. data).

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# Canadian bluejoint response to heavy grazing

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## Abstract

A disclimax stand of Canadian bluejoint (*Calamagrostis canadensis* (Michx.) Beauv.) was heavily grazed by cattle and horses for 4 years to weaken the grass's competition with hardwoods important as browse and cover to wildlife. Stocking at 0.084 ha AUM<sup>-1</sup> resulted in uniform utilization of bluejoint and maintenance of early phenology through the growing season. Etiolated bluejoint declined about 90%, but grass production increased 10 to 15%, as fireweed (*Epilobium angustifolium* L.), a principal herbaceous component of the stand, decreased in response to trampling. Rhizomes of heavily grazed bluejoint had lower total nonstructural carbohydrates (TNC) ( $p = 0.0127$ ), lower weight ( $\text{g cm}^{-1}$  length) ( $p = 0.05$ ), and reduced biomass ( $\text{g cm}^{-3}$  of soil) ( $p = 0.05$ ). Shoots of grazed bluejoint maintained higher nitrogen ( $p = 0.0001$ ) and higher digestibility (IVDMD) ( $p = 0.0017$ ) than bluejoint that was never grazed. This enabled heavily grazed bluejoint to retain good forage quality through the entire growing season, as opposed to ungrazed bluejoint, which became poor forage at the time of flowering during early July. Following one season of rest, rhizome TNC, shoot nitrogen, and IVDMD returned to levels of never grazed bluejoint. Seedhead production, seed production, seed weights, and seed viability of rested bluejoint were about the same as in ungrazed stands. On wet sites, heavy grazing does not adequately reduce the vigor of this grass.

**Key Words:** *Calamagrostis canadensis*, overstocking, forage quality, boreal forest.

Canadian bluejoint (*Calamagrostis canadensis* (Michx.) Beauv.), hereafter referred to as bluejoint, is the most common of over 100 species and subspecies of the genus *Calamagrostis*, ranging throughout Alaska and most northern latitudes (Tolmochev 1964). It is a winter-hardy perennial that naturally propagates from seeds or rhizomes during mid May (Mitchell 1968, McKendrick 1984). It reaches heights of 1 to 2 m and begins forming seedheads by early July, after which its nutritional value rapidly declines (McKendrick 1983). Bluejoint readily monopolizes cutover or burned areas of boreal forest (Bliss 1973, Lieffers and Stadt 1993, MacDonald and Lieffers 1993, Mitchell and Evans 1966), preferring fine textured, moist soils (Mueller-Dombois and Sims 1966). It quickly develops a periodically dry,

## Resumen

Una posición de anticlimax de "Canadian bluejoint" (*Calamagrostis canadensis* (Michx.) Beauv.) (en gran cantidad) fue pasteado pesadamente por ganado y caballos por 4 años para debilitar la competencia de pasto con maderas duras, importantes como llanura de pasteo y cobertura de vida salvaje. Surtido a 0.084ha UAM<sup>-1</sup> resultó en una utilización de "bluejoint" uniforme y un mantenimiento de fenología temprana a través de la estación de crecimiento. Cultivado en obscuridad "bluejoint" declinó alrededor de 90%, pero la producción de pasto creció 10 a 15%, como "fireweed" (*Epilobium angustifolium*) un componente principal de el puesto, declinó en respuesta al pistoteo. Los rhizomes de pasto "bluejoint" muy pastoreados tenían un total de carbohidratos no-estructurales (TNC) ( $p = 0.0127$ ) más bajos, menos peso ( $\text{g cm}^{-1}$ ) ( $p = 0.05$ ), y biomasa más reducido ( $\text{g/cm}^{-3}$ ) ( $p = 0.05$ ). Tallos de "bluejoint" pastoreados mantuvieron nitrógeno más alto ( $p = 0.0001$ ) y digestión más alta (DIVMS) ( $p = 0.0017$ ) que "bluejoint" que no fué pastoreado. Esto facilitó al pasto "bluejoint" pastoreado retener buena calidad de forraje a través de la estación de crecimiento, contrario al "bluejoint" no pastoreado, que resultó en un forraje de mala calidad al tiempo de florecimiento durante el principio de Julio. Siguiendo la temporada de descanso, rhizome CNT nitrógeno tallos y DIVMS retorno a niveles de pasto no pastoreado "bluejoint". Producción de seedhead, producción de semilla, peso de semilla, y variabilidad de semilla de "bluejoint" descansado, fueron lo mismo que puestos no pastoreados. En lugares mojados mucho pastoreo, n reduce adecuadamente el vigor de éste pasto.

decomposing mulch layer, 10–20 cm deep, that often prevents successful establishment of hardwood and spruce seedlings (Mitchell and Evans 1966). A bluejoint disclimax may last for 25 to 200 years (Collins and Schwartz 1998, Simonson and Rieger 1967, Lutz 1963).

In wet sites, rhizome mats, thick mulch and dense cover of bluejoint frequently inhibit hardwood and conifer regeneration efforts, including soil scarification, slash burning, herbicide treatment, and planting (Lieffers et al. 1993, Collins and Schwartz 1998). McKendrick (1984) found that bluejoint status within plant communities is favored by moderate levels of uniform grazing, but Klebesadel and Laughlin (1964) reported it to be intolerant of intensive cropping, particularly if grazing begins during spring and the grass is completely cropped 3 or more times during the growing season.

Our objective was to heavily graze bluejoint grass to reduce its

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carbohydrate reserves and competitive vigor, to break down its associated mulch layer, and to expose mineral soil, thereby enhancing germination and survival of competing hardwoods important as browse and cover for wildlife (Collins 2001). Reforestation treatments of burning and scarification have been unsuccessful in wet sites, and successful planting of hardwoods has required seedlings of 1 m or greater height to escape overtopping by bluejoint. It is illegal to use herbicides on Alaska's public lands for release of forest regeneration or for any other purpose. Heavy grazing, as an alternative site preparation, would require that grazed bluejoint retain quality sufficient to support uniform utilization through the growing season.

## Methods

We studied 2 disclimax bluejoint stands that had been formed 4 years previously by clearcutting of paper birch (*Betula papyrifera* Marsh.)—white spruce (*Picea glauca* (Moench.) Voss) forest. Both stands were in the Little Susitna River drainage in the Matanuska Valley, south-central Alaska and were dominated by bluejoint and fireweed. The stands were 18 km apart (61° 43' N, 149° 08' W and 61° 40' N, 149° 26' W) on gently sloping uplands characterized by poorly drained, moderately deep silt overlying glacial till (Schoephorster 1968). The study area is important moose wintering range, is desirable livestock summer range, and receives high interest from the timber industry.

We constructed 3 ha experimental paddocks with adjacent 3 ha controls in both clearcuts. For 4 years paddocks were grazed 3 to 4 times each growing season to impose 90% utilization of bluejoint spring greenup and subsequent regrowth during periods of about 7 days each. Grazing was initiated during spring as soon as most tussocks were producing shoots in the 3 to 4-leaf stage, and it was repeated throughout the growing season whenever the grass reached about 20 cm height. The paddocks were grazed by heifers during the first year of study. The livestock owner then switched to a fall breeding strategy that prevented use of his cattle after the first year. All subsequent grazing was by horses. Paddocks and controls had no history of livestock grazing, and prior to initiation of the study, treatments and controls received identical unsuccessful reforestation treatments—burning, scarification, and planting of

white spruce, balsam poplar (*Populus balsamifera* L.), and Bebb willow (*Salix bebbiana* Sarg.).

After 4 years heavy grazing and 1 summer's rest, bluejoint seedheads were counted from clipped 1/4 m<sup>2</sup> plots, and number of seeds per head, seed weight and viability were determined from a subsample of seedheads from each plot. Seedheads were collected 20 August and stored in an unheated shelter for 1 winter prior to germination tests. Seeds were then manually cleaned by rubbing between 2 rough surfaces, and good seed was separated from empty seed and fuzz by use of a large column seed blower. Three replicates of 100 seeds each were randomly selected from each treatment. Seeds were soaked in Chlorox for 5 minutes, rinsed in water, imbibed in Captan solution (0.5 g liter<sup>-1</sup> of water), and placed on blotter paper in covered petri dishes. The seeds were chilled in dark at 4.3° C for 6 days, and placed in a growth chamber set for 16 hours of light at 15° C and 8 hours darkness at 5° C. The blotter paper was kept moist with Captan solution for duration of the trial. Seeds were checked for germination on a daily basis, and germinated seeds were removed from the petri dishes.

Rhizomes and shoots of bluejoint plants were collected from each of 3 treatments—never grazed, summer grazed 4 years, and summer grazed 3 years/rested in year 4—on a biweekly basis during the fourth grazing season. Rhizomes were analyzed for TNC, and shoots were analyzed for N and IVDMD. Paddocks were treated as a blocking variable.

Rhizomes were collected by cutting 8 x 8-cm squares of soil from the rhizome layer, then washing in cold water to remove soil. Rhizomes were then oven-dried at 60° C, total combined length per sample measured, and total sample weighed. Total nonstructural carbohydrates were extracted from ground samples with 0.2 N H<sub>2</sub>SO<sub>4</sub> and measured by the idometric method (Smith 1969). Percent nitrogen (N) of shoots was measured by combustion using a LECO CHN-1000 analyzer, and in vitro dry matter digestibility (IVDMD) (Tilley and Terry 1963) was determined.

We used a repeated measures mixed linear model (Little et al. 1996) to analyze nutrient and digestibility data from mid July through freeze up. This period was selected for analysis because it represents the growing season following the flowering stage, when digestibility of ungrazed bluejoint falls to 50% or less and its crude protein drops from 10% to 5% or less

(McKendrick et al. 1977). Paddocks (blocks) and paddock-by-period interactions were treated as random effects, while treatment, period and treatment-by-period interactions were treated as fixed effects (Winer et al. 1991). An arcsine transformation (Snedecor and Cochran 1980) was used on the response variables. The following covariance structures were considered for modeling the repeated measures portion of the data: variance components, compound symmetry, heterogenous compound symmetry, first-order ante-dependence, first-order auto-regressive, and heterogenous first-order auto-regressive.

A 3-step process was used to select the best model. First, we specified a model, including block-by-period interactions as possible random effects, and treatment, period, and treatment-by-period interaction as possible fixed effects. Second, 6 sub-models were fit, one for each of the covariance structures. An average of Akaike's and Schwarz's criteria was used to determine the best fitting variance-covariance structure for that model (Little et al. 1996). Third, higher order interactions starting with block-by-period interaction was tested with a Z-statistic, when practical, or by examining Akaike's and Schwarz's criteria for the best fitting covariance model without the random effects interaction. The process was repeated until all non-significant, non-blocking effects were removed from the model. Model testing of fixed effects was done using an F-statistic using the best fitting covariance sub-model. All tests were performed with an alpha of 0.05. A protected LSD (Winer et al. 1991) was used to control the experiment-wise error rate of the appropriate t-statistic. Differences in TNC and N by treatment were tested at the end of the season (period 14). Differences in shoot N and IVDMD by treatment were of interest. We used equal variance t-test to detect differences (0.05 level of significance) in rhizome weights and total rhizome biomass between ungrazed and grazed paddocks.

## Results and Discussion

Prior to greenup at first grazing, paddocks were completely covered by bluejoint and other plant litter or large woody debris. After 1 season of grazing, cover by litter decreased about 40%, exposing primarily humus and large woody debris. Mineral soil was exposed on about 1.5% of the area. Reduction of litter and breakdown/compaction of mulch exposed

**Table 1. Forage production (dry weight, kg/ha) in wet birch-spruce sites that had been clearcut logged then heavily grazed by livestock for 4 years. Means are followed by standard deviations in parenthesis.**

species	Paddock 1		Paddock 2	
	Control	Grazed	Control	Grazed
	----- (kg ha <sup>-1</sup> ) -----			
<i>Calamagrostis canadensis</i>	1344(1003)	1580(644)	2084(1204)	2327(662)
<i>Epilobium angustifolium</i>	1580(1187)	134(106)	1334(1111)	200(159)
<i>Equisetum pratense</i>	274(208)	958(388)	179(274)	154(97)
<i>Rosa acicularis</i>	109(130)	30(78)	21(77)	53(105)
<i>Gymnocarpium dryopteris</i>	50(94)	14(24)	2(5)	43(101)
<i>Streptopus amplexifolius</i>	0	5(16)	137(208)	0

**Table 2. Seed production and viability in heavily grazed and ungrazed bluejoint grass.**

	(heads/m <sup>2</sup> )	(seeds/head)	seeds/m <sup>2</sup>	(seeds/g <sup>a</sup> )	(% germination)
heavily grazed	107 ± 122 <sup>b</sup>	376 ± 228	40,307	11,034 ± 386	88 ± 2.9
ungrazed	88 ± 88	486 ± 213	42,525	12,308 ± 517	83 ± 5.0

<sup>a</sup>Seeds/m<sup>2</sup> = heads/m<sup>2</sup> x seeds/head.

<sup>b</sup>Mean ± SD.

ephemeral surface water on 7% and 9% of the 2 paddocks, further indicating their wetness. After the initial year of grazing, spring greenup inside grazed paddocks preceded that outside by 6 to 8 days, presumably because the insulative effects of cover were reduced, allowing earlier thawing of soil (Hogg and Liefers 1991).

After 4 years heavy grazing, grazed paddocks produced 1,580 and 2,327 kg ha<sup>-1</sup> of bluejoint, versus the 1,334 and 2,084 kg ha<sup>-1</sup>, respectively, in ungrazed stands (Table 1). Mitchell and Evans (1966) reported bluejoint production at 1,643 kg ha<sup>-1</sup> for ungrazed disclimax stands in vicinity of our paddocks.

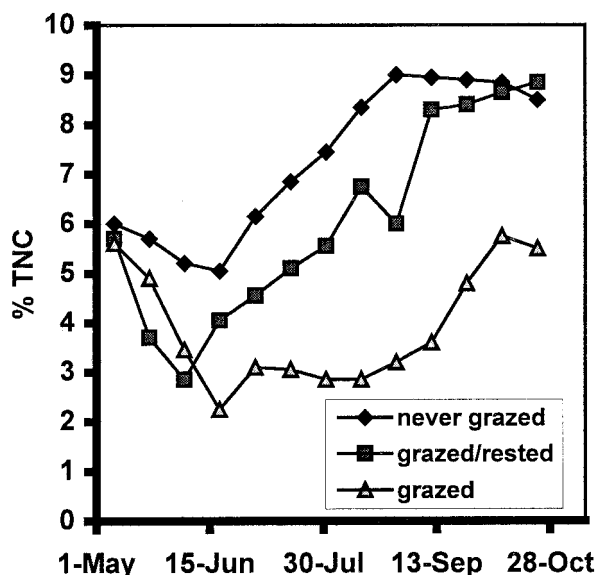
Fireweed decreased during the study, reducing total herbaceous production 19 to 26%. Cattle normally do not forage on fireweed (Mitchell and Evans 1966), and we did not observe cattle or horses selecting it. Most impact on fireweed appeared to have been caused by trampling. In the absence of grazing, especially in wet sites, fireweed does not persist in competition with bluejoint (Landhauser and Liefers 1994). Trampling simply accelerated the decrease.

Stocking at 0.084 ha/AUM resulted in uniform utilization of bluejoint to about 2 to 4 cm height within 5 to 8 days. Under this grazing regime, etiolated growth of

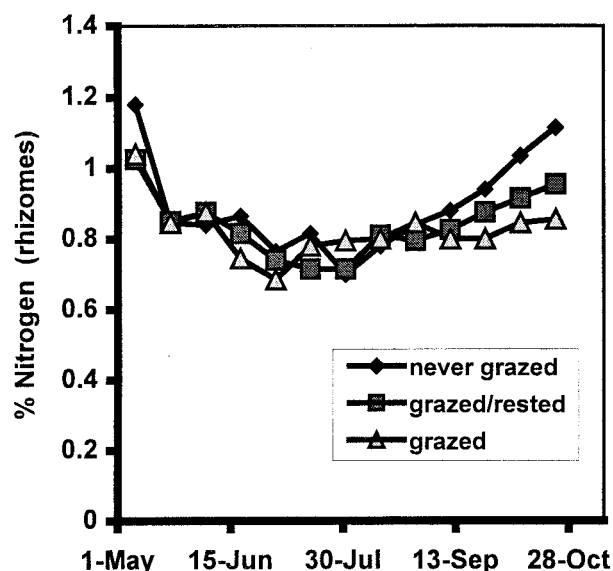
bluejoint declined 90% and 93% in the 2 paddocks by year 2, but did not decrease after that. At this stocking rate, beef heifers only maintained weight, and the total of spring growth and subsequent regrowth provided grazing for an average of 20 days per season. Locally, this range is grazed continuously at a light rate for about 90 days during the growing season, a practice resulting in serious spot grazing of bluejoint (McKendrick 1983).

During the first growing season following 3 years heavy grazing, the number of viable bluejoint seeds m<sup>-2</sup> was about the same as in stands that were never grazed (Table 2). Grazed stands produced slightly more seedheads m<sup>-2</sup> with fewer seeds per head. By contrast, Mitchell (1968) observed that bluejoint seedhead production increased 700% following single-event disturbances. We have observed increases of similar magnitude following single events such as logging or fire. Bluejoint may not have increased seed production in grazed paddocks, because the plants were weakened after 3 years of heavy utilization.

Bluejoint from the grazed treatment had significantly lower percent TNC than bluejoint from either grazed/rested or never grazed treatments, although the difference in TNC was smallest at the end of the growing season. Rhizome TNC remained lower in grazed bluejoint than in never grazed or grazed/rested plants (Fig. 1). By late winter, TNC in grazed rhizomes was about the same as in never grazed and grazed/rested plants, suggest-



**Fig. 1. Mean % TNC of bluejoint grass when never grazed, when grazed 3 years and then rested, and when grazed 4 years.**



**Fig. 2. Mean % nitrogen of bluejoint rhizomes when never grazed, when grazed 3 years and then rested, and when grazed 4 years.**

**Table 3. Differences of least squares means for shoot nitrogen in never grazed (NG), grazed (G), and grazed/rested (G/R) Canadian bluejoint stand.**

Effect	Trt	Trt	Difference	Std Error	DF	t	Pr > t	Adj. p
Trt	NG	G	-0.0639916	0.00064404	27	-99.36	0.0001	0.0000
Trt	NG	G/R	0.01412222	0.00064404	27	21.93	0.0001	0.0000
Trt	G	G/R	0.07811388	0.00064404	27	121.29	0.0001	0.0000

ing a relocation of some nonstructural carbohydrates during dormancy.

There were no differences in percent TNC between never grazed and grazed/rested treatments 11 September through the end of the growing season, indicating restoration of TNC within 1 growing season. Based on an average of Akaike's and Schwarz's values, the block-by-period term was dropped from the model representing TNC post flowering. The best fitting model used a compound symmetry sub-model for the covariance structure and displayed a significant period by treatment interaction.

After 4 years heavy grazing, rhizome weight of grazed bluejoint was 0.00040 g cm<sup>-1</sup> versus 0.00082 g cm<sup>-1</sup> in never grazed plants. During the same period, rhizome biomass decreased from 0.00066 to 0.00047 g cm<sup>-3</sup> of soil, decreasing the total pool of nonstructural carbohydrates proportionately. Rhizome death caused by relocation of TNC from weakened rhizomes to healthier rhizomes likely caused the overall decrease in rhizome biomass we observed (Christiansen and Svejar 1987).

Mean nitrogen levels in rhizomes were similar through the growing season (Fig. 2). Based on an average of Akaike's and Schwarz's values, the block-by-period term was dropped from the rhizome nitrogen model representing the period following flowering. The best fitting model for the period used a compound symmetry sub-model for the covariance structure and displayed a significant linear period-by-treatment interaction. Because of interaction we had to examine treatment differences for given periods, none of which were significant.

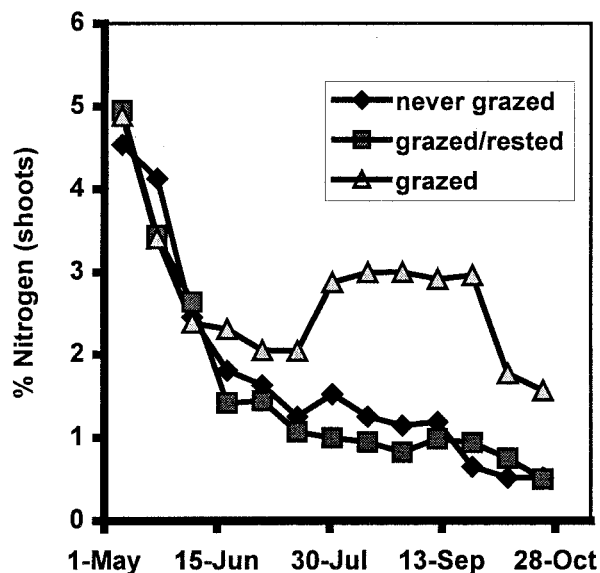
Nitrogen declined rapidly with shoot development in early summer, regardless of treatment. The grazed treatment maintained higher shoot nitrogen after mid July, because regrowth was phenologically young and not affected by the precipitous decline in nitrogen associated with flowering (Fig. 3). Shoot nitrogen in late summer was significantly higher in grazed than in grazed/rested or ungrazed treatments (Table 3). Based on an average of Akaike's and Schwarz's values, the block-by-period term was dropped from the model. The best fitting model used an

ante-dependence (1) sub-model for the covariance structure with the treatment and period effects being significant.

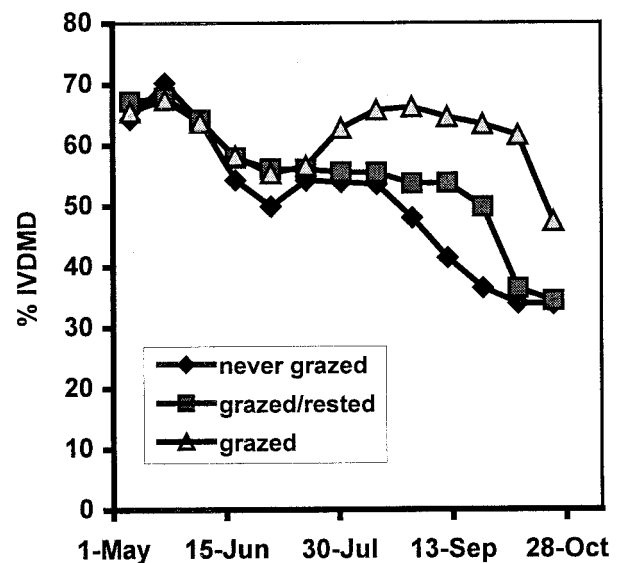
Digestibility declined similarly between treatments during shoot development in early summer (Fig. 4). After flowering, IVDMD in grazed and grazed/rested bluejoint declined at significantly lower rates than never grazed bluejoint. Based on an average of Akaike's and Schwarz's values, the block-by-period term was dropped from the IVDMD model. The best fitting model used a heterogenous auto-regressive (1) sub-model for the covariance structure and displayed a significant linear period-by-treatment interaction. Rates of decline for grazed and grazed/rested bluejoint were not significantly different. Grazed bluejoint maintained higher IVDMD than never grazed plants, even at freeze up, because regrowth had not reached phenologic senescence.

## Conclusions

In wet, disclimax bluejoint stands, heavy grazing maintained bluejoint in an early phenologic condition, causing it to retain good nutritional quality. Maintenance of forage quality supported uniform utilization of bluejoint through the entire growing season. This treatment reduced the total pool of TNC and N in bluejoint rhizomes, but it did not prevent the grass from increasing at the expense of fireweed weakened by trampling. The competitive



**Fig. 3. Mean % nitrogen of bluejoint shoots when never grazed, when grazed 3 years and then rested, and when grazed 4 years.**



**Fig. 4. Mean % IVDMD of bluejoint shoots when never grazed, when grazed 3 years and then rested, and when grazed 4 years.**

**Table 4. Differences in least squares means for IVDMD in never grazed (NG), grazed (G), and grazed/rested (G/R) Canadian bluejoint stand.**

Effect	Trt	Trt	Period	Difference	Std Error	DF	t	Pr > t
Trt	NG	G		0.09683616	0.01716124	1.84	5.64	0.0359
Trt	NG	G	7/17	-0.12289720	0.01923782	2.2	-6.39	0.0185
Trt	NG	G/R	7/17	-0.03086577	0.02462084	4.14	-1.25	0.2760
Trt	NG	G	7/31	-0.15301646	0.01723021	2.09	-8.88	0.0109
Trt	NG	G/R	7/31	-0.05906314	0.02050876	3.08	-2.88	0.0615
Trt	NG	G	8/14	-0.18313573	0.01813389	2.63	-10.10	0.0035
Trt	NG	G/R	8/14	-0.08726051	0.01916718	2.99	-4.55	0.0200
Trt	NG	G	8/28	-0.21325499	0.02158626	3.66	-9.88	0.0009
Trt	NG	G/R	8/28	-0.11545789	0.02113057	3.82	-5.46	0.0062
Trt	NG	G	9/11	-0.24337425	0.02661328	4.82	-9.14	0.0003
Trt	NG	G/R	9/11	-0.14365526	0.02565091	5.17	-5.60	0.0023
Trt	NG	G	9/25	-0.27349351	0.03249212	5.91	-8.42	0.0002
Trt	NG	G/R	9/25	-0.17185263	0.03165100	6.65	-5.43	0.0012

vigor of heavily grazed bluejoint in wet, logged sites further indicates its adaptation to disturbance and its competitive nature in absence of forest overstory. Temporary reduction of bluejoint and associated organic covers and extension of good forage quality through the growing season indicate that heavy grazing is a reforestation tool deserving investigation for drier sites.

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# Restoring degraded riparian meadows: Biomass and species responses

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## Abstract

Riparian meadows in central Nevada are highly productive and have been extensively utilized for livestock grazing. Consequently, many have been severely degraded resulting in changes in species composition and decreases in productivity. During a 3 year study, we examined the responses of mesic meadow systems to yearly nitrogen addition ( $100 \text{ kg ha}^{-1}$ ) and clipping (8–10 cm stubble height) to increase our understanding of grazing effects. We also examined the effects of a one-time, fall aeration (10 cm deep by 2 cm wide holes spaced 20 cm apart) and revegetation (removal of existing vegetation and reseeding) to evaluate the restoration potential of these sites. Changes in total biomass, species aerial cover and frequency, and surface basal cover were used to evaluate treatment responses. Clipping had no effect on total biomass, possibly because it was conducted late in the growing season. In contrast, nitrogen addition plus clipping increased biomass in all 3 years when treatments were compared across sites and for 1 out of 3 years when treatments were compared across a single site. Aeration had no effect on above ground biomass, but has been shown to increase rooting activity in these same meadows. Due to a dry, hot spring, early seral and weedy species had higher establishment than the seeded natives in the revegetation plots, and biomass was low the first year after treatment. Individual species varied in their treatment responses. The cover of low-growing forb species (western aster (*Aster occidentalis* [Nutt.] Torrey and A. Gray), long-stalk starwort (*Stellaria longipes* Goldie), and common dandelion (*Taraxacum officinale* Wigg.) declined through time for all treatments, presumably due to increased grass cover and shading following release from grazing and above average precipitation and water table levels in 1998. Examination of the key graminoids showed that Kentucky bluegrass (*Poa pratensis* ssp. *pratensis* L.), an increaser species, did not increase in response to release from grazing, but increased in response to clipping and nitrogen addition. Nebraska sedge (*Carex nebrascensis* Dewey), a desirable native, increased in response to both release from grazing and nitrogen addition. The results were influenced by high spatial and temporal variability in water table elevations within these systems.

**Key Words:** Nitrogen addition, clipping, aeration, revegetation, species composition, water tables

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## Resumen

Las praderas ribereñas de la parte central de Nevada son altamente productivas y han sido utilizadas extensivamente para el apacentamiento de ganado. Consecuentemente, muchas de ellas han sido severamente degradadas resultando en cambios de la composición de especies y la disminución de su productividad. En un estudio de 3 años examinamos las respuestas de los sistemas de praderas mésicas a la adición anual de nitrógeno ( $100 \text{ kg ha}^{-1}$ ) y el corte (8–10 cm de altura del rastrojo remanente) para aumentar nuestro entendimiento de los efectos del apacentamiento. También examinamos los efectos de la areación por única vez en otoño (hoyos de 10 cm de profundidad y 2 cm de ancho espaciados a 20 cm) y la revegetación (remoción de la vegetación existente y resiembra) para evaluar el potencial de rehabilitación de estos sitios. Para evaluar la respuesta a los tratamientos se utilizó los cambios de la biomasa total, cobertura aérea y frecuencia de las especies y la cobertura basal. El corte no tuvo efecto sobre la biomasa total, posiblemente porque se realizó al finales de la estación de crecimiento. En contraste, la adición de nitrógeno mas el corte incrementaron la biomasa en los tres años, esto se observó cuando los tratamientos se compararon entre sitios y en 1 de los 3 años cuando la comparación se realizó en un solo sitio. La aeración no tuvo efecto en la biomasa aérea, pero ha sido demostrado que incrementa la actividad de las raíces de estas praderas. Debido a la primavera seca y caliente, las especies de maleza herbácea y las de etapas serales iniciales tuvieron un mayor establecimiento que las especies nativas sembradas en las parcelas de revegetación y la biomasa fue baja en el primer año después del tratamiento. La respuesta a los tratamientos varió entre especies individuales. La cobertura de especies herbáceas de porte bajo (“Western aster”, “Long -stalk starwort” y “Common dandelion”) disminuyó a través del tiempo en todos los tratamientos, presumiblemente por el incremento de la cobertura de zacates, el sombreado por la suspensión del apacentamiento y la precipitación arriba del promedio y la elevación del manto frático ocurridos en 1998. El examen de las especies clave de gramíneas mostró que el “Kentucky bluegrass” (*Poa pratensis* ssp. *pratensis* L.), una especie increadora, no aumento en respuesta a la suspensión del apacentamiento, pero se incrementó en respuesta al corte y la adición de nitrógeno. La especie “Nebraska sedge” (*Carex nebrascensis* Dewey), una especie nativa deseable, se incrementó en repuesta tanto a la suspensión del apacentamiento como a la adición de nitrógeno. Los resultados fueron influenciados por la alta variabilidad espacial y temporal de la elevación del manto frático dentro de estos sistemas.

Riparian areas include highly productive, mesic plant communities that serve as the interface between terrestrial and aquatic environments and that are characterized by high levels of biodiversity (Knopf et al. 1988, Schulz and Leininger 1990, Goodwin et al. 1997). Meadow communities are among the most productive components of the riparian corridor (Kauffman and Krueger 1984, Knopf et al. 1988, Chambers 1994, Chambers et al. 1999) and, consequently, often have been degraded by livestock grazing (Kauffman and Krueger 1984, Abel 1989, Clary and Webster 1989, Belsky et al. 1999). Livestock trampling decreases soil macropore spaces resulting in soil compaction, reduced root growth, and lowered plant production (Orr 1960, Laycock and Conrad 1967, Bohn and Buckhouse 1985). Trampling also affects the aerial portions of plants resulting in reduced vegetation height and cover and, thus, altering the microenvironment of the remaining plants (Kobayashi and Nomoto 1997). Nitrogen is deposited in the excreta of the grazing animals, but much of this nitrogen is likely lost through volatilization and leaching (Watson and Lapins 1969, Floate 1970, Woodmansee 1978). In addition, removal of vegetation through grazing may result in a net export of nitrogen from grazed systems. Altered nutrient dynamics can lead to changes in both production and species diversity (Berendse et al. 1992). Thus, livestock grazing can act as a disturbance that alters resource availability and species interactions within riparian meadow systems. This disturbance can have a significant role in restructuring plant communities (Carson and Pickett 1990, Wilson and Tilman 1991).

Little is known about the linkages between severity of degradation and changes in hydrologic regime, soil properties, and vegetation in riparian meadows (Chambers 1994), or about the effects of various land uses or land management activities on these linkages (Richter 1992, Van Haveren et al. 1997). The overall objectives of this study were to increase our understanding of the effects of nitrogen addition and herbage removal on mesic meadows and to evaluate aeration and revegetation as restoration techniques for these ecosystems. The questions addressed were: (1) how do nitrogen addition and herbage removal affect biomass production and dominant species composition within these meadow systems, and (2) can aeration and revegetation be used to increase biomass production and modify species composition?

## Methods

### Study area and study sites

The study area is in the Toiyabe and Toquima Mountain Ranges in central Nevada. Watershed elevations range from about 1,850 to 3,200 m. The nearby town of Austin, Nev. has the only long-term weather data in the region and has mean annual precipitation of 310 mm. Approximately 60% of the precipitation arrives as winter snow. Peak runoff is during snowmelt in early June, but convective thunderstorms during summer months can contribute significant precipitation. The stream systems are typically located within confined valleys, exhibit steep gradients and are incised (Weixelman et al. 1996). Riparian vegetation consists of quaking aspen (*Populus tremuloides* Michaux), narrow leaf cottonwood (*Populus angustifolia* James), river birch (*Betula occidentalis* Hook), willows (*Salix* spp.) and meadow communities. Meadow ecosystem types occur along a continuum from high to low water tables. Nebraska sedge (*Carex nebrascensis* Dewey), a native sedge species, dominates sites that have high water tables (0 to 5 cm from the surface) and Kentucky bluegrass (*Poa pratensis* ssp. *pratensis* L.), an increaser species, dominates sites with relatively low water tables (60 cm). Sites with intermediate water tables (40 to 50 cm) are co-dominated by Nebraska sedge and Kentucky bluegrass (Chambers et al. 1999). Other grass and grasslike species that occur along the water table gradient include Baltic rush (*Juncus balticus* Willd.) and blackcreeper sedge (*Carex praegracilis* W. Boott), while forbs include western aster (*Aster occidentalis* [Nutt.] Torrey & A. Gray), cinquefoil (*Potentilla gracilis* [Nutt.] S. Watson), and common dandelion (*Taraxacum officinale* Wigg.) (Weixelman et al. 1996, Castelli et al. 2000). These ecosystems have been grazed by livestock since European settlers colonized the area.

During the summer of 1995, suitable meadow sites ( $n = 3$ ) were identified in the Austin Ranger District of the Humboldt-Toiyabe National Forest, Nev. Meadows were selected with dominant species composition (approximately 10% Nebraska sedge and 40% Kentucky bluegrass) and water table depths (40 to 60 cm) typical of the mesic meadow ecosystem type in central Nevada (Weixelman et al. 1996). The selected sites include Corral Canyon (39°7'13.5" N, 116°48'38.6" W) in the Toquima Mountain Range, and Cahill Canyon (39°27'57.6" N, 117°2'0.4" W)

and Emigrant Canyon (39°30'35.4" N, 117°1'5.9" W) in the Toiyabe Mountain Range. All 3 sites are located in trough drainageways. Soil characteristics are typical of these ecosystems (Chambers et al. 1999). Cahill Canyon (elevation 2,325 m) and Emigrant Canyon (elevation 2,174 m) have soils that are aquic cryoborolls. Corral Canyon (elevation 2,358 m) has soils that range from aquic cryoborolls to cryaquolls.

### Study design

The study design was a completely randomized block. One block (replicate) was located within each of the 3 study sites (Corral, Emigrant, and Cahill) to examine treatment differences across sites. Three additional blocks (replicates) were placed at 1 site (Corral) to evaluate differences across a single site. Study treatments consisted of a control, nitrogen addition, clipping, aeration, and revegetation. Clipping was imposed over the nitrogen, aeration, and revegetation treatments bringing the total number of treatments to 8. At each site, blocks were located in areas that appeared homogeneous in terms of vegetation, soils, and depth to water table. Block sizes were not uniform due to the small size and heterogeneity of these meadows and ranged from 16 x 16 to 25 x 25 m and treatment plots from 4 x 4 to 5 x 5 m. Fences designed to exclude livestock were constructed around the blocks at each site. A standard 30 cm diameter rain gage was placed near the blocks. A series of wells (7 to 9) were located within each block using perforated PVC pipe (10 cm in diameter) that extended into the water table.

### Treatments

Aeration was done in the fall of 1995 using an electric drill equipped with a 2 cm diameter, power ship auger to drill into the soil. Holes were uniformly spaced at 20 cm intervals to a depth of 30 cm. Aeration has been shown to eliminate the effects of subsurface compaction in forested systems (Nambiar and Sands 1992). The aeration treatment should have penetrated the compacted layer of the soil allowing water to infiltrate and through natural freeze/thaw processes to break up the compacted soil layer.

Nitrogen addition consisted of a hand application of sulfur coated urea (36-0-0), a slow release nitrogen fertilizer, at a rate of 100 kg ha<sup>-1</sup> repeated in fall 1995, 1996, and 1997. This type of fertilizer and application rate have been shown to increase both above and below ground production and disease resistance in both Nebraska



sedge and Kentucky bluegrass (Davis and Doenoe 1991, Thompson and Clark 1993, Reece et al. 1994).

The revegetation treatment started with killing all existing vegetation using a short-lived herbicide (Round-up®). The soil was then tilled with a commercial grade roto-tiller to break up the sod, and allow for removal of dead plant material. Six species native to central Nevada riparian meadows, slenderbeaked sedge (*Carex athrostachya* Olney), Nebraska sedge, blackcreep sedge, tufted hairgrass (*Deschampsia cespitosa* [L.] Beauv.), carpet clover (*Trifolium monanthum* A. Gray), and cow clover (*T. wormsjoldii* Lehm.) were selected for seeding based on their abundance in similar meadows with higher water tables. Seeds were collected adjacent to the study areas, cleaned and tested for viability. Seeding was conducted in the fall of 1995 at a rate of 150 viable seeds m<sup>-2</sup> for all species except cow clover, which was seeded at a rate of 125 seed m<sup>-2</sup> due to the limited number of seeds collected. Straw mulch blankets (5 cm thick, Granite Seed Co.) were placed over the seeded areas to aid seed germination, improve soil moisture retention, and insure that the seeds and topsoil were not blown away.

The clipping treatment, applied alone as a treatment and in combination with each of the other treatments, consisted of trimming the above ground vegetation biomass with a power trimmer to a stubble height of between 8 and 10 cm. This removed approximately 50 to 75% of the above-ground biomass of both Nebraska sedge and Kentucky bluegrass. Clipping was conducted once a year in late July and the clippings were subsequently removed from the plot. This timing and level were used to simulate the grazing activity that is normally prescribed for these sites.

### Vegetative response

Five, 0.1 m<sup>2</sup> quadrats were randomly located within each treatment plot. Ten quadrats were also randomly placed outside the exclosures at each site. At peak production (late July), and immediately prior to the clipping treatment, frequency and percent aerial cover by species, were recorded for the vegetation in each quadrat. Frequency was assessed with a nested frequency frame and percent aerial cover was visually assessed in 12 classes: <1; 1 to 5; 6 to 15; 16 to 25; 26 to 35; 36 to 45; 46 to 55; 56 to 65; 66 to 75; 76 to 85; 86 to 95; 96 to 100%. Prior to sampling, basal cover by category was determined using a point frame. Cover cate-

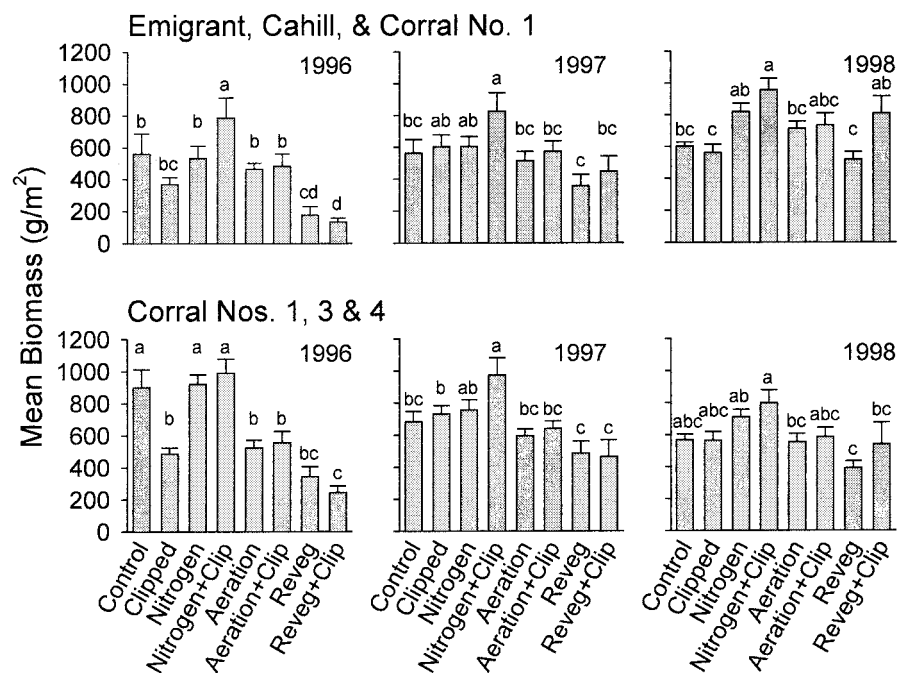


Fig. 1. Mean biomass (+ S.E.) during the study period for both the across site comparison (Emigrant, Cahill and Corral #1) and the single site comparison (Corral #1, #3, and #4). Unlike letters indicate differences among treatments within individual years ( $P \leq 0.05$ ).

gories included bare ground, litter, and vegetation by species. Standing crop biomass was determined by clipping the quadrats to ground level. Samples were oven dried at 60°C for 72 hours for dry weight determination.

### Statistical analysis

Two factor (treatment and year) repeated measures analysis of variance with repeated measures on year were used to examine differences in biomass, aerial cover, and basal cover. The sites served as blocks to examine treatment differences across sites. The 3 blocks in Corral (Corral #1, Corral #3, and Corral #4) were used to evaluate differences within a single site. Aerial cover data were pooled from the main effect treatment plots (control, clipped, nitrogen and aeration) at Corral Canyon for 6 of the dominant species for 1996 and 1998. Pooled data were analyzed with a 2 factor (treatment and year) repeated measures analysis of variance. Mean comparisons were performed using Fisher's Protected LSD (Steel and Torrie 1980). Site similarity was determined with the Bray-Curtis Similarity Index on both the species frequency and aerial cover data. Comparisons were also conducted using Spearman's Rank Order Correlation analysis of both species frequency and aerial cover (Zar 1999). The Spearman's rank

order correlation coefficient provides a non-parametric statistical measure of the similarity of 2 areas as reflected by the relative importance of the various species within the sampled areas (Chambers 1983).

## Results

### Biomass response

Significant differences in biomass existed among treatments for the across site comparison ( $F_{7,14} = 4.54$ ,  $P = 0.0078$ ) and for the single site comparison ( $F_{7,14} = 5.77$ ,  $P = 0.0027$ ). For the across site comparison, the nitrogen plus clipping treatment had greater biomass than the control for all 3 years (Fig. 1). This treatment also had greater biomass in the single site comparison in 1997. Nitrogen alone was marginally significant during 1998 for the across site comparison ( $P = 0.0579$ ) and for the single site comparison ( $P = 0.0603$ ). In 1996, biomass in the revegetation treatments was lower than in the controls for both sets of replicates (Fig. 1). These differences did not persist beyond the first year. There were no differences between the controls and either the clipped or aeration treatments for either comparison.

There was a year by site interaction for the across site comparison ( $F_{4,28} = 4.95$ ,  $P = 0.0038$ ) and for the single site comparison

son ( $F_{4,28} = 3.40$ ,  $P = 0.0219$ ). In general, biomass at all sites was lowest in 1996 and highest in 1998. Emigrant had lower biomass than the other sites in all 3 years, and Cahill had lower biomass than Corral in 1996.

### Aerial and basal cover

Total aerial cover consistently ranged from 70 to 80% across these meadows. Consequently, aerial cover did not differ among either sites or treatments. Also, there were few significant differences in total basal cover between sites or treatments.

### Revegetation success

Establishment of the seeded species in the revegetation treatment plots was very limited. Both blackcreeper sedge and Nebraska sedge occurred in the revegetation plots at Cahill Canyon in 1996, but they did not occur in either 1997 or 1998 or on the Emigrant revegetation plots. Nebraska sedge and blackcreeper sedge were present also in the Corral blocks in 1996, but only Nebraska sedge was found in 1998. Meadow barley (*Hordeum brachyantherum* Nevski) dominated the revegetation plots at all sites. Cover values were between 30 and 50% at all sites by 1998. Other species that were abundant on the revegetation plots were curly dock (*Rumex crispus* L.), elk thistle (*Cirsium drummondii* Torrey & A. Gray), common dandelion, desert goosefoot (*Chenopodium denticatum* Nelson), and water montia (*Montia chamissoi* [Ledeb.] Robins & Fern.). Because of the differences in

species composition, the revegetation treatment plots were not included in analyses of changes in species composition.

### Species composition

The 20 most common species were determined from the pooled aerial cover data from the treatment blocks. Nebraska sedge and Kentucky bluegrass were among the top 6 species for all blocks. Meadow barley, baltic sedge, and blackcreeper sedge were also common to all blocks. Forb species that occurred on all blocks included western aster, cinquefoil, western yarrow (*Achillea millefolium* L.), long-stalk starwort (*Stellaria longipes* Goldie), and common dandelion. Grasses that occurred on 4 of the 5 blocks included tufted hairgrass and creeping wildrye (*Leymus triticoides* [Buckl.] Pilger); forbs included cow clover and Rocky Mountain iris (*Iris missouriensis* Nutt.). The Bray-Curtis analysis and Spearman's Rank Sum Correlations of species frequency and aerial cover on the control plots indicated that the replicate blocks at the different sites had similar species composition (Table 1). For the comparison of Corral #1, Cahill and Emigrant, the Bray-Curtis Similarity Index ranged from 35 to 61 for species frequency and from 23 to 27 for species cover in 1996. The index ranged from 43 to 59 for species frequency and from 27 to 70 for species cover in 1998. Spearman's Rank Sum Correlations indicated significant positive correlations between blocks at the different sites for both frequency and cover. The replicate blocks at Corral Canyon also had similar species composition (Table 1).

The Bray-Curtis Similarity Index ranged from 50 to 64 for species frequency and between 24 and 48 for species cover in 1996. In 1998, the range was between 40 and 72 for species frequency and 25 to 59 for species cover. Further, the Spearman's Rank Sum Correlations indicated that there were significant positive correlations between the blocks for both species frequency and cover.

To examine potential treatment effects on cover of individual species, data from the Corral Canyon blocks were pooled. The clipping plus aeration and clipping plus nitrogen treatments were dropped from the comparisons because previous analysis indicated there were very few differences between these plots and the main effect plots. Cover of the forb species tended to decrease between 1996 and 1998 in all treatment plots, although the differences were not always significant (Table 2). Western aster decreased significantly in both the clipped and nitrogen plots. Longstalk starwort decreased significantly in the control, nitrogen and grazed plots, while dandelion decreased significantly in the control, clipped, aerated, and grazed plots. The responses of the grass and grasslike species to the different treatment were largely opposite to those of the forbs (Table 2). Nebraska sedge nearly doubled its cover in the control and in the nitrogen addition plots. Cover of meadow barley also doubled with nitrogen addition. Kentucky bluegrass increased in response to all treatments but did not increase in the control plots. With clipping, Kentucky bluegrass exhibited a 4-fold increase in cover, while its cover doubled in the unexclosed area. Increases with nitrogen and aeration were not as dramatic, but cover values still increased by 50%.

**Table 1.** Bray-Curtis similarity indices of frequency (B-C freq) and cover (B-C cov) and Spearman's rank sum correlation of frequency (Sper freq) and cover (Sper cov) for the control plots at Corral #1, Cahill and Emigrant and at Corral #1, Corral #3, and Corral #4 in 1996 and 1998. An (\*) indicates a significant positive correlation at the 0.05 level. An (+) indicates significance at 0.10.

	Corral #1				CaHill			
	B-C Freq	Sper Freq.	B-C Cov	Sper Cov	B-C Freq	Sper Freq	B-C Cov	Sper Cov
1996								
Cahill 42	0.27	27	0.59					
Emigrant	61	0.53*	25	0.44*	35	0.25	23	0.35
1998								
Cahill	44	0.47*	27	0.41*				
Emigrant	43	0.28	30	0.28	59	0.51*	70	0.48*
	Corral #1				CaHill			
	B-C Freq	Sper Freq.	B-C Cov	Sper Cov	B-C Freq	Sper Freq	B-C Cov	Sper Cov
1996								
Corral #3	50	0.60*	24	0.69*				
Corral #4	54	0.55*	48	0.59*	64	0.19	30	0.37+
1998								
Corral #3	40	0.64*	25	0.17				
Corral #4	60	0.73*	59	0.46*	72	0.84*	36	0.57*

### Environmental variables

Precipitation amounts varied between sites, seasons, and years (Table 3). As expected for Great Basin ecosystems, most precipitation fell during the winter months. The Corral Canyon site received the least precipitation and the Emigrant site the most. Precipitation amounts in 1997 were much lower than 1998 while 1996 was intermediate for all sites. Precipitation data for 1997 at Cahill Canyon was questionable and therefore not reported. It was likely similar to that of Emigrant Canyon.

Depth to water table was spatially and temporally variable as illustrated by the Corral Canyon and Cahill blocks (Fig. 2). There were seasonal declines in water table depth for all blocks with the degree

**Table 2. Mean cover (SE) for 1996 and 1998 and the ratio of the 1998/1996 cover values for 6 of the dominant species. Data for the Corral Canyon blocks (#1, #3, and #4) were pooled for the analysis. Significant differences for each treatment through time are indicated by a (+) for an increase and a (-) for a decrease.**

Treatment Year	<i>Aster occidentalis</i>	<i>Carex nebrascensis</i>	<i>Hordeum brachyantherum</i>	<i>Poa pratensis</i>	<i>Stellaria longipes</i>	<i>Taraxacum officinale</i>
Control						
1996	3.9(1.4)	14.5(4.0)	3.3(2.4)	16.4(3.2)	13.9(1.6)	6.9(1.7)
1998	3.5(1.3)	29.8(3.8)+	8.2(2.4)+	18.5(3.2)	1.0(1.6)-	1.2(1.8)-
1996/1998	0.9	2.1	2.5	1.1	0.1	0.2
Clipped						
1996	9.4(1.3)	8.9(3.5)	1.1(2.9)	4.9(3.2)	2.0(1.4)	8.8(1.4)
1998	4.5(1.3)-	9.3(3.6)	6.5(2.4)+	21.4(3.2)+	0.9(1.4)	2.9(1.6)-
1996/1998	0.5	1	5.9	4.4	0.5	0.3
Nitrogen						
1996	8.9(1.3)	20.0(3.5)	5.2(1.6)	9.8(3.2)	7.7(1.3)	9.3(1.5)
1998	3.2(1.4)-	39.9(3.8)+	10.1(1.7)+	15.8(3.8)+	3.3(1.5)-	8.2(1.9)
1996/1998	0.4	2	1.9	1.6	0.4	0.9
Aeration						
1996	7.5(1.3)	10.5(3.7)	5.2(1.6)	8.1(3.3)	3.6(1.4)	9.5(1.6)
1998	5.3(1.3)	13.5(3.5)	6.3(1.7)	18.0(3.2)+	3.3(1.4)	2.5(1.9)-
1996/1998	0.7	1.3	1.2	2.2	0.9	0.3
Unexclosed						
1996	5.5(1.9)	5.9(6.6)	4.0(2.0)	13.8(4.6)	7.0(2.4)	12.6(2.5)
1998	3.1(1.8)	7.5(7.0)	6.3(2.2)	28.5(4.6)+	0.1(0.6)-	4.5(2.3)-
1996/1998	0.6	1.3	1.6	2.1	0	0.4

of spring recharge depending on the amount of overwinter precipitation. In 1998, the year with the most overwinter precipitation, spring recharge was greater than in either 1996 or 1997, with water table levels at or near the surface of all blocks for a large portion of the growing season. Seasonal differences varied among blocks. For example, during the 1996 growing season, the water table decline for both the Cahill and Emigrant Canyon blocks was greater than 1 m, and by the end of the 1997 growing season, the water table depth at Emigrant Canyon was nearly 2 m. However, throughout the 1998 growing season there was running water flowing at depths up to 10 cm over most of the Emigrant block. In contrast, the Corral #3 block exhibited only a 22 cm difference in average water table between May and August 1996, and a 34 cm difference between May and August 1998 (Fig. 2).

The factor that likely had the greatest impact on the study was the range in water table depths found across each block for a particular sampling period. The greatest range in water table depth was observed at Cahill Canyon with a difference of over 1 m being common across the 16 x 16 m block. Corral #1 also exhibited high levels of variability with differences as great as 60 cm found between wells only 10 m apart. The least variable blocks were Corral #3, Corral #4 and Emigrant. This high level of spatial variability was not apparent at the time of site selection in August of 1995. However, the 3 years of

data collected during this period suggest that it is typical of these types of systems.

## Discussion and Conclusions

Our results provide insights into the recovery processes of riparian meadows in central Nevada and increase our understanding of functional processes within these same systems. They also increase our knowledge of potential restoration techniques.

Depth to water table has been shown to be the most important variable in structuring riparian plant communities (Wood 1975, Heady and Zinke 1978, Allen-Diaz 1991, Stromberg et al. 1996, Chambers et

al. 1999, Castelli et al. 2000), and water table depth undoubtedly influenced the study results. Despite an attempt to select study sites with similar water tables and species composition, high levels of spatial and temporal variability were observed during the 3-yr study. The confounding effects of temporal and spatial variability in the water table are illustrated by the biomass response at Emigrant and Corral Canyons. At Emigrant, biomass in 1998, the wettest year, was nearly double that of the 1996 biomass for all treatment plots. At Corral #1, the control plot consistently had the highest water table and, during both 1996 and 1997 which were dry years, it had the greatest biomass. In contrast, during 1998 there was standing water on this plot throughout the growing season and biomass was significantly lower than in 1996.

The high spatial and temporal variability of the water table provides important lessons for designing studies to evaluate structural and functional processes in similar types of meadows. In most cases, water table depth should be treated as a covariate when evaluating treatment effects on plant response variables such as biomass. Also, depending on study design, a high number of blocks or larger blocks with multiple randomly located treatment plots should be used to adequately account for the high spatial variability. Finally, sampling should be conducted over relatively long time periods (3–5 yr) to account for the temporal variability.

Few treatment effects on biomass were observed in our central Nevada meadows. Clipping had little or no effect on biomass in comparison to the control. These results are consistent with those of a similar study that indicated defoliation to a 10 cm stubble height did not significantly affect biomass production (Clary 1995). Also, the

**Table 3. Precipitation amounts at each study location for the 3 years of the study. Overwinter is from October to May and growing season is from June to September.**

Site	Period	Year		
		1996	1997	1998
		(mm)		
Corral	Overwinter	200	60	280
	Growing season	110	30	110
	Total	310	90	390
Cahill	Overwinter	290	—	460
	Growing season	60	—	20
	Total	350	—	480
Emigrant	Overwinter	260	180	590
	Growing season	80	240	50
	Total	340	420	640

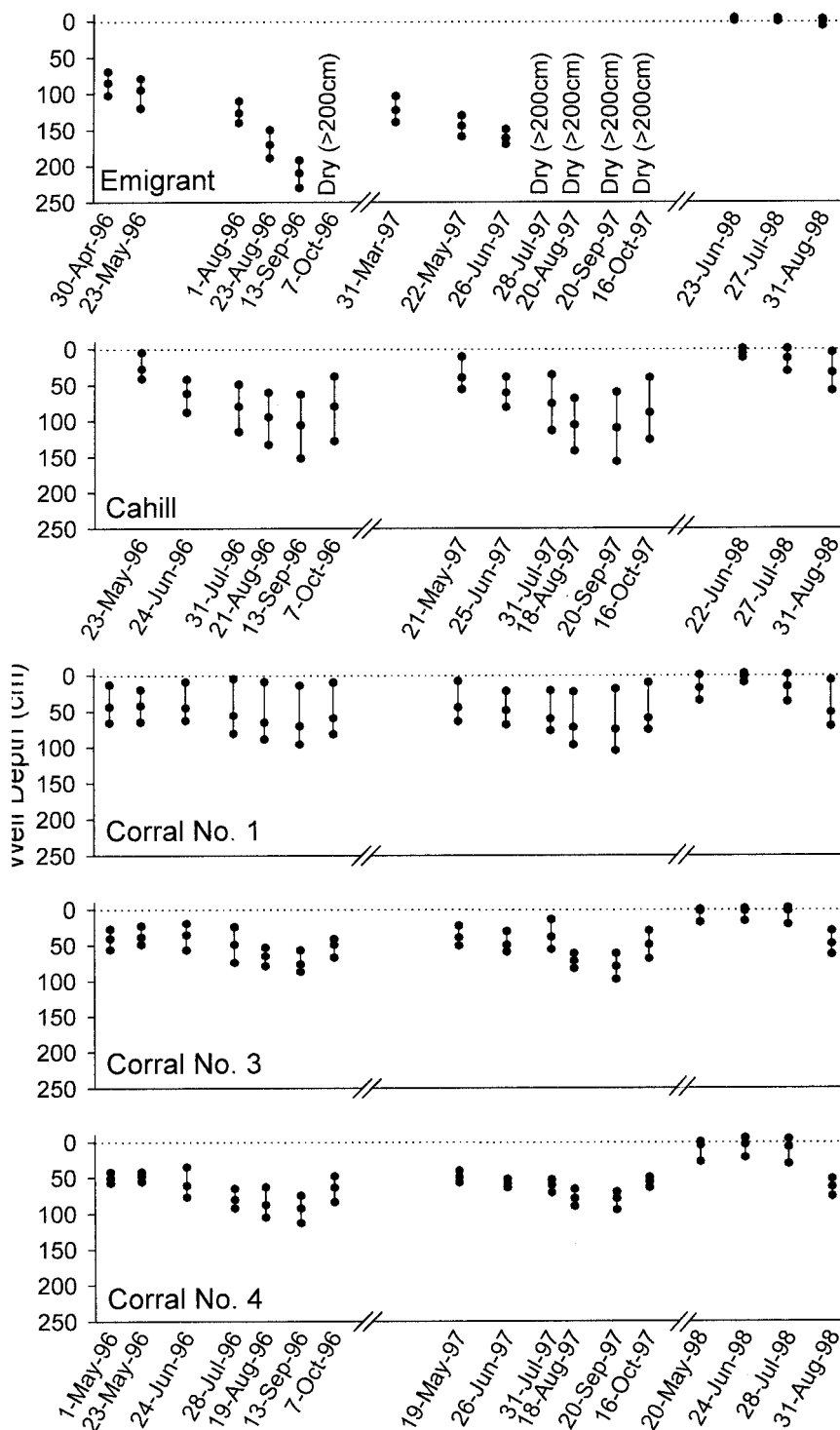


Fig. 2. Water table depths for Emigrant, Cahill and Corral for 1996, 1997, and 1998. Mean water table depth for each sampling period is indicated by the circle at the center of the line. The top of each line indicates the minimum depth to the water table within a study plot at a particular sampling time; the bottom indicates the maximum depth.

lack of a significant effect may have been related to the timing of the treatment. In the current study, clipping did not occur until late in the growing season after

plants had already begun to senesce.

Nitrogen addition was the only treatment that resulted in an increase in above ground biomass relative to the control.

Nitrogen plus clipping had a significant effect during all 3 years for the across site comparison and during 1997 for the within site comparison. Nitrogen alone was marginally significant during 1998 for both comparisons. The greater response on clipped plots was likely the result of higher contact of the fertilizer granules with the exposed soils, warmer soil temperatures and, thus, higher and more rapid nitrogen uptake. In general, phenological development of the plants on the nitrogen addition plots was accelerated. At the Corral Canyon plots, plants matured and began to senesce 2 to 4 weeks earlier on the nitrogen addition plots than on the other treatment plots. This type of accelerated development may reduce the efficiency of biomass or fruit production as a result of seasonal growth reduction (Lambers et al. 1998). Further, nitrogen addition can decrease root:shoot ratios in wetlands (Shaver and Melillo 1984) and was observed to decrease rooting activity in these central Nevada meadows (Martin 1999). Thus, the effect of added nitrogen, either as a fertilizer or as cow urine and dung, may be detrimental.

Although there was not a large effect on above ground biomass in response to aeration, the lack of an above ground response may be misleading. There was an increase in rooting activity in aerated plots, especially at Emigrant Canyon (Martin 1999), and total biomass may have increased with aeration. Aeration can reverse the negative effects of livestock trampling, including reduced root growth and lower plant production, when subsurface compaction is reduced or eliminated (Orr 1960, Laycock and Conrad 1967, Bohn and Buckhouse 1985).

Success of the revegetation treatment was limited due to constraints on the establishment of the seeded native species and competition with early seral and weedy species. The lack of significant establishment of the seeded species was likely due to the adverse conditions that existed on the revegetation plots during the dry spring of 1996. The surfaces of these dark meadow soils dried rapidly and were warmer than vegetated surfaces. Establishment of early seral or weedy species probably further decreased emergence and survival of the seeded species.

Individual species responses were related to life form. Between 1996 and 1998, there was a decrease in the aerial cover of all 3 forb species in all plots. This may be related to the differences in environmental variables between the 2 sampling years and to an increase in competition from grasses and grass-like species following

release from grazing. There was considerably more precipitation in 1998 than in 1996 and 1997. Consequently, the water table was much higher during the 1998 growing season and there was standing water on most of the Corral Canyon plots throughout the summer. Lower growth forms would have been submerged for extended periods. Also, the increased height of grasses and grasslike species within the exclosed plots may have reduced light to underlying forbs resulting in lower forb cover and decreased richness (Carson and Pickett 1990, Wilson and Tilman 1991, Kobayashi and Nomoto 1997).

Kentucky bluegrass, an increaser grass, exhibited an increase in cover in the clipped, aerated, nitrogen addition, and grazed treatments between 1996 and 1998. Its cover did not change on the control plots. These results are consistent with field observations indicating that Kentucky bluegrass significantly increases in cover in grazed riparian meadows, while no cover increases and even decreases occur in sites excluded from grazing (Schultz and Leininger 1990, Green and Kaufmann 1995).

Nebraska sedge exhibited an increase in cover in both the nitrogen addition and control plots. These results contrast with findings that grazing had no effect on shoot frequency and density (Ratliff and Westfall 1987) or cover (Schulz and Leininger 1990) of Nebraska sedge. Our data indicate that Nebraska sedge may exhibit significant increases in aerial cover when released from grazing. However, it is important to note that the relative abundance of both Kentucky bluegrass and Nebraska sedge also depends on seasonal and temporal variability in water table depth. Tiller number and above ground biomass of Nebraska sedge increase in response to locally or seasonally higher water tables, while tiller number and biomass of Kentucky bluegrass decrease under the same conditions (Martin 1999).

These results illustrate the complexity of the factors structuring riparian meadow communities and influencing their restoration. Water table plays a critical role in the functional processes within riparian meadow systems and in determining their recovery potentials. In the absence of grazing, portions of meadows with higher water tables may exhibit a shift in dominance from Kentucky bluegrass to Nebraska sedge. Also, the number or abundance of forb species in these meadows may decline in the absence of grazing regardless of water table (but see Stohlgren et al. 1999). Late season

herbage removal may not have a significant effect on biomass, because many species have already begun to senesce. Other aspects of grazing, such as nitrogen deposition, may significantly increase biomass production, but decrease rooting activity, and alter plant phenology and species composition. These effects may actually decrease system resilience to disturbance and reduce longer-term productivity.

The study indicates that aeration may be an effective restoration treatment for decreasing or eliminating compaction due to livestock trampling. Aeration does not affect species composition or above ground biomass within these meadows in the short-term, but increases in rooting activity (Martin 1999) may ultimately influence both species composition and aboveground productivity. Similar to other ecosystem types, revegetation of meadows with desirable native species requires favorable weather conditions for seed germination and seedling survival. Thus, the potential for restoring entire communities using revegetation may be limited due to constraints on establishment especially during dry years.

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# Drought and grazing III: Root dynamics and germinable seed bank

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## Abstract

Drought and herbivory frequently influence North American rangelands. While these influences may temporarily reduce vegetative cover, their mutual influence on the available seedbanks which might occupy new safe sites is unclear. We examine effects of drought and grazing upon pre- and post-drought plant root distribution and germinable seed bank to determine 1) if the response of root distributions to drought depends upon grazing use and 2) if the presence of germinable seeds is altered significantly by drought and grazing. Using twelve, 5 X 10 m non-weighing lysimeters with an automated rainout shelter, we documented root intercepts in situ using a minirhizotron from 1993-1996. Seed bank samples were incubated in a greenhouse to determine seedling emergence. Roots were fewer in shallow soil layers in grazed plots than ungrazed plots by the end of the study, irrespective of drought. Roots in deeper (Bw horizon) soil layers were fewer during drought, but were not influenced by grazing. Seed bank composition results suggest that perennial grasses were a small portion of the seed bank. Cool-season annual grass seeds accumulated after drought. Without drought, forb seed banks increased with grazing. Thus while shallow roots may decrease during drought, in the year following drought grazing may decrease aboveground net primary production, and allow large accumulations of cool-season annual grass seed in a northern mixed grass prairie.

**Key Words:** minirhizotron, northern mixed grass prairie, seed banks

Drought and herbivory commonly affect the structure and function of grasslands. Historically, studies evaluating the effects of drought and grazing have focused on in situ post-drought recovery patterns, such as those after droughts in the 1930s and 1980s (e.g. Albertson and Weaver 1944, 1946). Controlled in situ drought experiments are uncommon although notable exceptions

## Resumen

La sequía y herbívora frecuentemente influyen en los pastizales de Norteamérica. Mientras esta influencia puede reducir temporalmente la cobertura vegetativa, su influencia muta en los bancos de semillas disponibles, los cuales pudieran ocupar nuevos sitios seguros, aun no es clara. Examinamos los efectos de la sequía y el apacentamiento en la distribución de raíces y el banco de semillas germinables antes y después de la sequía para determinar: 1) si la respuesta de la distribución de las raíces a la sequía depende del grado de apacentamiento y 2) si la presencia de semillas germinables es alterada significativamente por la sequía y el apacentamiento. De 1993 a 1996 documentamos la intercepción de raíces mediante un mini-rizotron, la determinación se realizó en 12 lisímetros no pesables de 5 x 12 m equipados con un protector automático contra la lluvia. Las muestras del banco de semilla se incubaron en un invernadero para determinar la emergencia de las plántulas. Al término del estudio, independientemente de la sequía, el número de raíces en las capas superficiales de suelo fue menor en las parcelas con apacentamiento que las en las parcelas sin apacentamiento. El número de raíces en las zonas profundas del suelo (horizonte Bw) fue menor durante la sequía, pero no fueron influenciadas por el apacentamiento. Los resultados de la composición del banco de semilla sugieren que los zacates perennes fueron una pequeña proporción del banco de semilla. Las semillas de los zacates anuales de estación fría se acumularon después de la sequía. Sin sequía los bancos de semillas de hierbas aumentaron con el apacentamiento. Así, mientras que las raíces superficiales pueden disminuir durante la sequía, en el año siguiente a la sequía el apacentamiento puede disminuir la producción primaria neta aérea y permitir grandes acumulaciones de semilla de zacates anuales de estación fría en las praderas de zacates mixtos del norte.

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have occurred (e.g. Ansley et al. 1992). We hypothesized that combined effects of drought and grazing may reduce root presence and vegetative cover while simultaneously favoring portions of the seed bank. Such combined impacts could precede a transition to increased presence of particular seed bank dominants.

Removal of above-ground biomass from perennial graminoids generally decreases root growth and root biomass (Robertson 1933, Carter and Law 1948, Crider 1955, Schuster 1964, Bartos and Jameson 1974) although exceptions have occurred (Bartos and Sims 1974). While most root response studies have used either potted plant or destructive excavation techniques (Cook



and Stubbendieck 1986), optic in situ techniques (Waddington 1971, Richards 1984) were refined and have provided researchers with new opportunities to evaluate root response to an array of imposed treatments.

Seed banks provide a glimpse of both past conditions and vegetation potentials, and drought and herbivory are but 2 elements of an "environmental sieve" (Harper 1977) that affect seed bank composition. Although seed bank and overstory vegetation composition are seldom identical (Rice 1989, Major and Pyott 1966), seed banks do provide insight into shifts in plant species composition during recovery from stressful events.

Objectives of this study were to examine concurrent impacts of drought and grazing on root and seed bank dynamics in a Northern mixed grass rangeland to assess potential creation of open sites (reduced root presence) concurrent with changes in the seed bank. This research compliments previous work which addressed primary production (Heitschmidt et al. 1999), and tiller growth dynamics (Enboe 1996). In situ minirhizotron technology was used to examine impacts of drought and grazing on root dynamics. Seedling emergence in a controlled environment was used as an estimate of the propagules available for post-drought recovery (Simpson et al. 1989).

## Materials and Methods

Research was conducted at the Fort Keogh Livestock and Range Research Laboratory near Miles City, Mont. (46°, 22' N 105°, 5' W) from 1993 through 1996. Regional topography ranges from rolling hills to broken badlands with small intersecting streams which flow into rivers in broad nearly level valleys. Potential natural vegetation is a grama-needle grass-wheatgrass (*Bouteloua-Stipa-Agropyron*) mixed grass community (Kuchler 1964). Precipitation averages 34 cm with 60% received between mid-April and mid-September. Average daily temperatures range from -10°C in January to 24°C in July with maximum temperatures occasionally exceeding 37°C in summer and minimums below -40°C in winter. The frost-free growing period is about 150 days. Soils of the study area are Kobase silty clay loam, fine, montmorillonitic, frigid, Aridic Ustochrepts (USDA 1996). The typical profile description for the Kobase silty clay loam includes an A horizon from 0-22 cm, a Bw horizon from 20-46 cm, a Bk horizon 46-66 cm, and

C1 and C2 horizons to 90 and 150 cm depths respectively.

Twelve, 5 X 10 m non-weighing lysimeters were constructed in 1992 on a gently sloping (4%) clayey range site (Heitschmidt et al. 1999). An automatic rainout shelter was constructed over 6 of the 12 lysimeters to impose drought (Larsen et al. 1993). Drought was imposed on 6 lysimeters from late May to mid-October 1994. Within each water treatment (drought or non-drought), 1 of 3 grazing treatments was applied to 2 replicate lysimeter plots: 1) graze the year of and the year after simulated drought, hereafter referred to as the G 94&95 treatment; 2) graze during the year of drought and rest the year after, hereafter referred to as the G 94 treatment; and 3) rest the year of and the year after drought, hereafter referred to as the ungrazed treatment. Grazed plots were grazed intensively by 6 ewes and their twin lambs for a few hours in early June and early July 1994 and 1995. Defoliation in grazed plots reduced standing crop an average of 980 kg ha<sup>-1</sup> relative to ungrazed plots (Heitschmidt et al. 1999).

Precipitation, soil water patterns, and aboveground herbaceous production have been reported previously (Heitschmidt et al. 1999). In general, 1993 precipitation immediately before initiation of treatments was 38% above long-term means, while precipitation in 1994, the first year of the drought and grazing treatments, was 24% below the 115 year average (NOAA 1996). Precipitation in 1995 and 1996 was near normal (95 and 86% of the 115 average), although rainfall in May 1996 was 200% above the month's norm (Fig. 1).

## Root counts

Root intercepts were counted in situ using a minirhizotron (Richards 1984, Taylor 1987). Minirhizotron observation tubes (38 mm inside diameter X 122 cm long) were installed at a 30° angle from vertical in each plot at initiation of the study in 1992. These small diameter tubes offer the least disturbance to roots, which is especially important for perennial species (Richards 1984). Roots were counted if they intersected a line circumscribed on the tube at each depth (Taylor 1987, Upchurch 1987). Root counts were separated into 3 functional categories by color: white, new roots; tan, suberized roots; and black, dead or dying roots. Roots were observed in 2 minirhizotron tubes per lysimeter at 10 depths per minirhizotron (marks were inscribed 5, 15, 25, 35, 45, 55, 65, 75, 85, and 95 cm along the tube length). Beginning at the soil surface, the first mark inscribed upon the tube was located at 5 cm below the soil surface, and since the tube was placed at 30° from vertical, the 95 cm mark corresponds to a 77 cm soil depth. Root intersections were recorded on 42 sample dates beginning in April 1993 and ending in November 1996.

## Seed bank sampling procedures

Within each lysimeter, samples of surface litter and underlying soils were extracted. Litter samples were extracted using a hand vacuum, from 6 randomly located 100-cm<sup>2</sup> circular subplots within each lysimeter. Soil core samples were removed from each of the 6 subplots with a 100-cm<sup>2</sup> core sampler to a depth of 3 cm. Litter and soil core samples were bagged separately, and transported to the laboratory for incubation. Sample dates were the

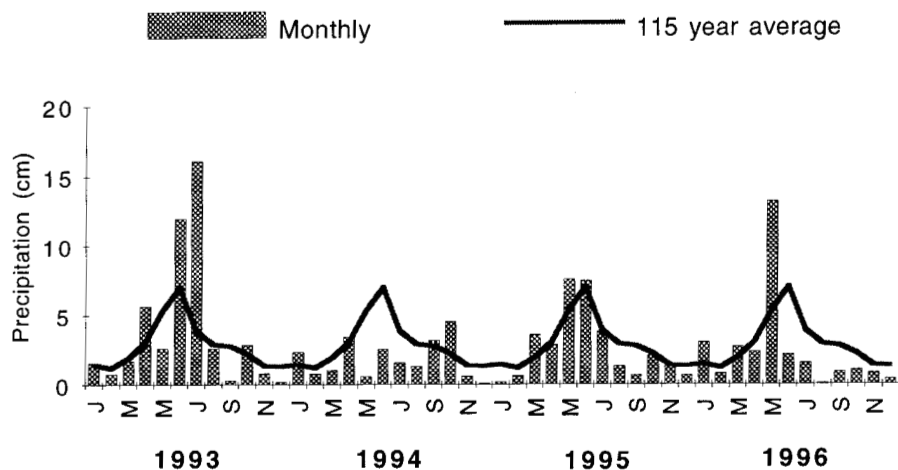


Fig. 1. Monthly precipitation (cm) from Jan. 1993– Dec. 1996, and long-term (115 year) average at Miles City, Mont. (NOAA 1996).

**Table 1. Emerged seedling species within 4 functional groups. Nomenclature follows Dorn 1984.**

Functional group	Species	Common name
Annual grasses (cool-season)	<i>Bromus tectorum</i> L.	downy brome
	<i>Bromus japonicus</i> Thunb. ex Murr.	Japanese brome
	<i>Hordeum pusillum</i> Nutt.	foxtail barley
	<i>Vulpia octoflora</i> Walt. Rydb.	sixweeks fescue
Perennial grasses (cool-season)	<i>Pascopyron smithii</i> Rydb. (Love)	western wheatgrass
	<i>Poa secunda</i> Vasey	Sandberg bluegrass
	<i>Stipa comata</i> Trin. & Rupr.	needle-and-thread
(warm-season)	<i>Bouteloua gracilis</i> (H. B. K.) Lag. ex Griffiths	blue grama
	<i>Buchloe dactyloides</i> (Nutt.) Engelm.	buffalograss
	<i>Schedonnardus paniculatus</i> (Nutt.) Trel.	Texas tumblegrass
	<i>Sporobolus crypandrus</i> (Torr.)	sand dropseed
Forbs	<i>Androsace occidentalis</i> Pursh.	fairly candleabra
	<i>Camelina microcarpa</i> Andr. ex D. C.	little falseflax
	<i>Conyza canadensis</i> (L.) Cronq.	horseweed
	<i>Convolvulus arvensis</i> L.	bindweed
	<i>Descurainia pinnata</i> (Walt.) Britt.	pinnate tansymustard
	<i>Descurainia sophia</i> (L.) Webb ex Prant	flixweed tansymustard
	<i>Draba reptans</i> var. <i>mirantha</i> (Lam.) Fern.	Carolina whitlowgrass
	<i>Euphorbia glyptosperma</i> Engelm.	ridgeseed spurge
	<i>Euphorbia spathulata</i> Lam.	spatulate-leaved spurge
	<i>Filago arvensis</i> (L.) L.	fluffweed
	<i>Hedeoma hispidum</i> Pursh.	rough falsepennyroyal
	<i>Kocia scoparia</i> (L.) Schrad.	summer cypress
	<i>Lactuca serriola</i> L.	prickly lettuce
	<i>Lepidium densiflorum</i> Schrad.	prairie pepperweed
	<i>Linum rigidum</i> Pursh.	stiffstem flax
	<i>Melilotus officinalis</i> (L.) Pallas	yellow sweetclover
	<i>Plantago patagonica</i> Jacq.	wooly Indian wheat
	<i>Salsoa iberica</i> Sennen & Pau	Russian thistle
	<i>Sisymbrium altissimum</i> L.	tumble mustard
	<i>Sisymbrium irio</i> L.	ironweed mustard
	<i>Sphaeralcea coccinea</i> (Nutt.) Rydb.	scarlet globemallow
	<i>Taraxacum officinale</i> Weber	dandelion
	<i>Triodanis leptocarpa</i> (Nutt.) Nieuwl.	Venus' looking glass
	<i>Tragopogon dubius</i> Scop.	salsify

weeks of 4 October 1993; 23 September 1994; 27 September 1995; and 23 September 1996.

### Greenhouse seedling emergence

At the lab, soil and litter samples were separately placed into prepared pots (18 cm diameter X 16.5 cm deep) within 2 days of sample collection. Within each sterilized pot, we placed a round filter paper in the bottom and then filled pots with sterilized sand to within 2.5 cm of the top edge. Another filter paper was placed on the sand surface to prevent seeds from becoming buried too deeply. Next, litter samples mixed with 200 cm<sup>3</sup> of additional sterilized sand were placed on top of the filter paper. Soil core samples were hand crushed and placed into different pots in the same manner as litter samples. Exposed seeds were buried, and pots were placed in a greenhouse maintained at temperatures ranging from 21-13°C. Pots were watered daily in the first week and

periodically thereafter to keep surface soil moist. Lighting was supplied to mimic 12-hour days.

Samples were incubated for 12 weeks each year, and emerged seedlings were counted by species at 2 week intervals and then removed by hand pulling or clipping. Unidentified seedlings were not removed until they could be identified. Individual pot counts (subsamples were 6 litter and 6

soil core pots per lysimeter) were totaled within year, and seedlings were divided into 4 functional plant type groups for analyses: forbs, warm-season perennial grasses, cool-season perennial grasses, and cool-season annual grasses. Species encountered (nomenclature follows Dorn 1984) within each functional group are listed in Table 1. Our results reflect germinable seed counts based upon successful emergence in a greenhouse setting. Viable dormant seed was not estimated.

### Root count data summary and analysis

Counts of black roots were omitted from analyses because they were observed only in 4 instances (< 0.1% of observations) in 1993 before initiation of treatments. Likewise, tan roots were observed <1% of the time, and so they were combined with white root counts to provide an estimate of total live root intersections. Root counts were summed within each minirhizotron tube within 4 soil horizons and averaged by number of soil depths contained within each of the 4 soil horizons (A, Bw, Bk, and C). Thus, although roots were observed at each 10-cm mark, root counts reported as number of roots within a soil horizon provide a more meaningful representation of soil profile conditions. The A horizon included 5 and 15-cm tube depths; Bw horizon 25-, 35-, and 45-cm; and Bk horizon 55- and 65-cm. Three tube depths (75-, 85-, and 95-cm) were combined into the C horizon, where very few roots were observed.

Root count data were analyzed within each soil horizon (A, Bw, Bk, and C) using repeated measures analysis of variance procedures (Table 2). Each of 3 grazing treatments were replicated twice within drought and non-drought treatments; replicates were plots (i.e. lysimeter). The error term for testing simple effects of drought, grazing and their interaction was plot within drought and grazing treatment.

**Table 2. Root count ANOVA model and P values by soil horizon on 42 sampling dates from April 1993 to November 1996, at Fort Koehg LARRL, Miles City, Mont.**

Source	df	A horizon	Bw horizon	Bk horizon
Drought	1	0.29	0.27	0.10
Graze	2	0.17	0.23	0.42
Drought*Graze	2	0.21	0.09	0.08
Error	6			
Date	41	<0.01	<0.01	<0.01
Date*Drought	41	0.18	<0.01	0.89
Date*Graze	82	<0.01	0.58	0.82
Date*Drought*Graze	82	0.98	0.49	0.16
Error	246			
Total	504			

**Table 3.** Seed bank ANOVA model and P values by plant functional group, 1993–1996, at Fort Koehg LARRL, Miles City, Mont.

Source	df	TOTAL <sup>1</sup>	CSAG	CSPF	WSPG	FORB
Drought	1	0.33	0.87	0.13	0.08	<b>0.01</b>
Graze	2	0.70	0.67	0.99	0.35	0.05
Drought*graze	2	0.23	0.33	0.53	0.93	<b>0.04</b>
Error	6					
Year	3	<b>0.01</b>	0.05	<b>&lt;0.01</b>	<b>&lt;0.01</b>	<b>&lt;0.01</b>
Year*Drought	3	<b>&lt;0.01</b>	<b>&lt;0.01</b>	0.13	0.65	<b>0.04</b>
Year*Graze	6	0.28	0.18	0.48	0.17	0.67
Year*Drought*Graze	6	0.32	0.24	0.92	0.94	0.28
Error	18					
Total	47					

<sup>1</sup>Columns are: total number of seedlings, cool-season annual grasses (CSAG), cool-season perennial grasses (CSPG), warm-season perennial grasses (WSPG), and forbs.

The 42 sampling dates constituted repeated measures. Full model residuals served as the error term for testing sampling date effect and its interaction with treatment effects. When analysis of variance revealed treatment differences, mean separation was completed using Fishers L.S.D. at a 0.05 alpha level, and error terms specific to the contrast (Carmer and Swanson 1971). Data were tested for conformance to assumptions of normality (Shapiro and Wilk 1965).

### Seed bank data summary and analysis

Seedling data were analyzed within functional group (cool-season annual grasses, cool-season perennial grasses, warm-season perennial grasses, or forbs) using repeated measures analysis of variance procedures (Table 3). Seedlings emerging from litter and core samples (pots) within a plot were summed for analysis. In addition to the species listed (Table 1), 1 seedling of the shrub *Ceratoides lanata* (Pursh.) Howell and succulent *Opuntia polycantha* Haw. were encountered but excluded from analysis. Each of 3 grazing treatments were replicated twice within drought and non-drought treatments; replicates were plots (i.e., lysimeter). The error term for testing simple effects of drought, grazing, and their interaction was plot within drought and grazing treatment. The 4 years of the study were included as repeated measures. Full model residual error was used to test the simple effect of year and its interactions with treatment effects. When analysis of variance revealed treatment differences, mean separation was completed using L.S.D. at a 0.05 alpha level, using error terms specific to the contrast. All data were tested for conformance to assumptions of normality (Shapiro and Wilk 1965).

### Greenhouse seedling emergence

Two-way interactions between drought and year effects occurred only for seedlings of cool-season annual grasses and total seedlings (Table 3). In general, emerged seedlings from combined soil and litter samples were dominated by forb and cool-season annual grasses, with few perennial grass seeds present (Fig. 4). Total seedling emergence differed between drought treatments in 1994–1996, but not in 1993 (Table 3, and Fig. 4). Seedling totals were greater in non-drought than drought treatments in 1994 and 1996, but were less than in the drought treatment in 1995.

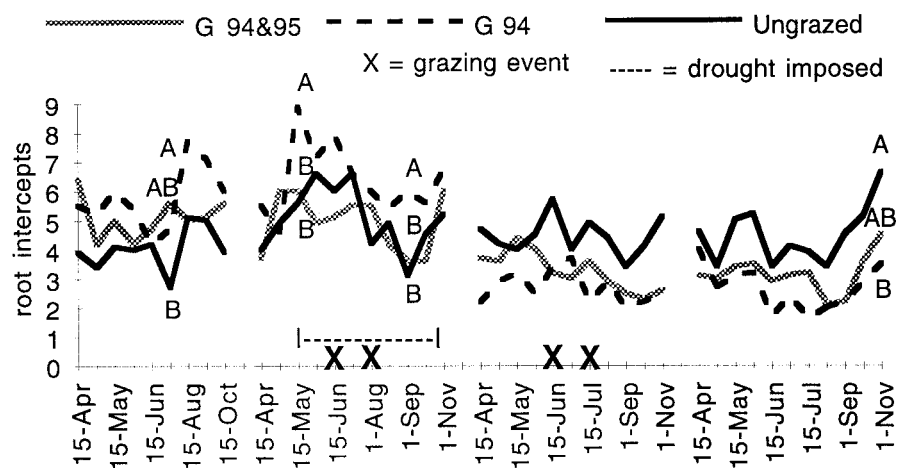
Cool- and warm-season perennial grasses (analyzed separately) were not affected by drought or grazing, but differed among years (Table 3). Averaged across drought and grazing treatments, more cool-season perennial grass seedlings emerged ( $23 \text{ m}^{-2}$ ) in 1996 than the 2–10 seedlings  $\text{m}^{-2}$  that emerged 1993–1995. Warm-season perennial grass seedlings were more numerous in 1994 and 1996 ( $23$  and  $35 \text{ m}^{-2}$ ) than in 1993 and 1995 ( $7$  and  $8 \text{ m}^{-2}$ ).

Cool-season annual grass seedlings were similar among grazing treatments, but differed between drought treatments, depending upon year (drought by year interaction, Table 2, Fig. 4). Emerged seedlings were similar between treatments in 1993 and 1996, the year prior to the imposed drought and 2 years after drought. In 1994, cool-season annual grass seedlings were fewer in drought than non-drought plots (Fig. 4). Conversely, in 1995, the year immediately following drought, cool-season annual grass seedlings were greater in drought plots than non-drought plots.

## Results

### Root counts

Analysis of A, Bw, and Bk root counts revealed no significance of simple drought and grazing effects or their interaction (Table 2). The A and Bw horizon roots differed among sampling dates (simple effect) and by drought and grazing (two-way interactions with sampling date). Within the A soil horizon root counts differed among grazing treatments on 4 of 42 sampling dates (Fig. 2). On the remaining dates, counts did not differ significantly, although root counts appear to decline in grazed plots in 1995 and 1996 relative to ungrazed plots. Root counts in the Bw horizon were fewer in the drought than non-drought plots on 4 dates in 1994 when the drought was imposed (Fig. 3). Root counts in the A and Bk soil horizons did not differ between drought treatments on any date (Table 2).



**Fig. 2.** Root intercepts in the A soil horizon by grazing treatment from April 1993–Nov. 1996. Within a date, grazing treatments with the same upper case letters do not differ  $P > 0.05$ , L.S.D.

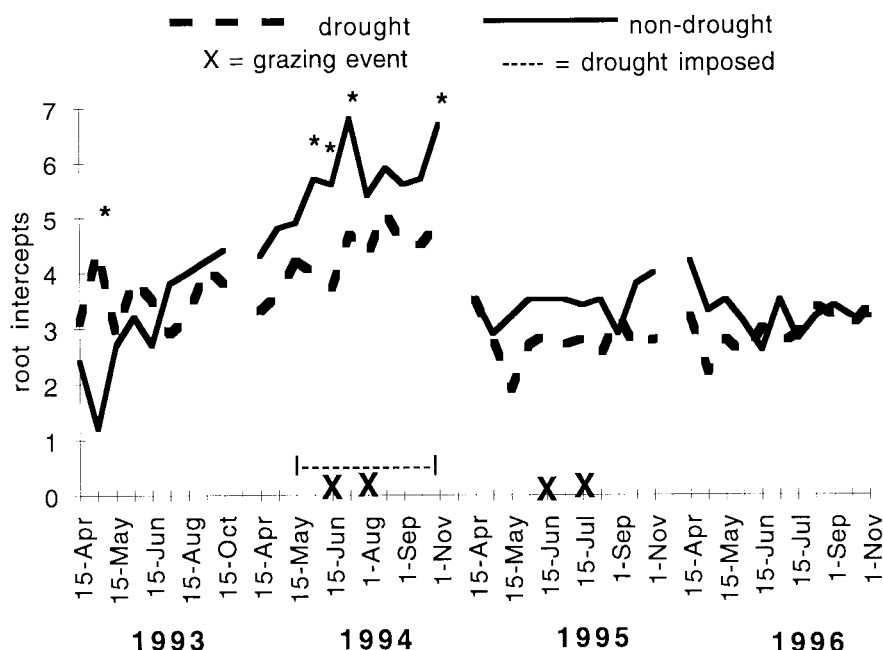


Fig. 3. Root intercepts in the Bw soil horizon by drought treatment, April 1993–Nov. 1996. Within a date, drought treatments with an asterisk differ  $P < 0.05$ , L.S.D.

Forb seedlings were affected by drought, depending upon grazing treatment and year (Table 3). Irrespective of grazing treatments, more forb seedlings were present in 1994 and 1995 than in 1993, in drought and non-drought treatments (Fig. 4). Forb seedlings in non-drought plots increased from 1993 to 1996 and were more numerous than in drought plots in 1996. Forb seedlings in drought plots were similar from 1994–1996. Irrespective of year, forb seedlings were similar in ungrazed drought and non-drought plots (131 and 115  $m^2$ ). In both G94&95 and G94 treatments, fewer forb seedlings were present in drought (133 and 114  $m^2$ ) than in non-drought plots (260 and 242  $m^2$ ).

## Discussion

Early moisture, followed by a relatively dry summer may have limited the impacts of our drought treatment (Heitschmidt et al. 1999). Even so, both root and seedbank differences in drought and non-drought plots were observed. We conclude that; 1) drought tended to limit subsoil (Bw) roots regardless of grazing treatment; 2) shallow roots in the A horizon were least in ungrazed plots initially, and were greatest in ungrazed plots at the end of the study, regardless of drought treatment; 3) forb seedlings increased in grazing treatments

only in the absence of drought; 4) germinable seed bank species composition was dominated by annual cool-season grasses that decreased during drought and increased following drought; and 5) warm- and cool-season perennial grasses were a minor portion of the seed bank and did not differ among grazing or drought treatments.

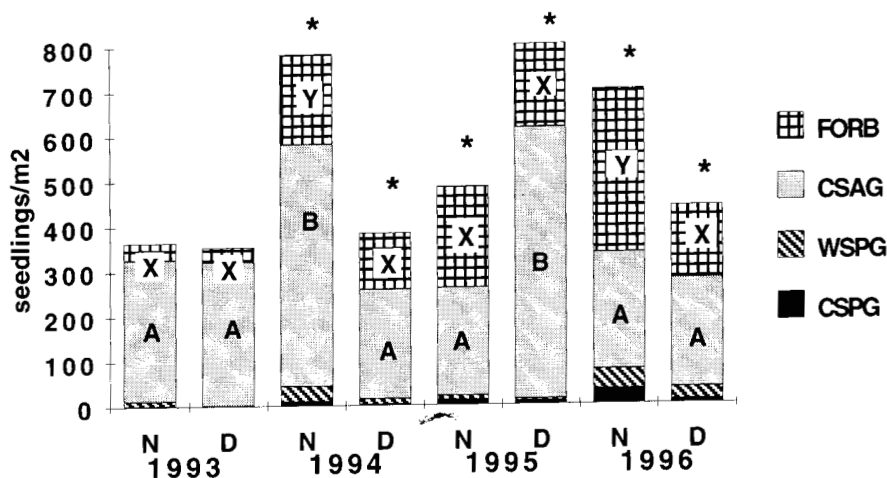


Fig. 4. Emerged seedling composition in drought (D) and non-drought (N) treatments 1993–1996, within 4 plant functional groups: forbs (FORB), cool-season annual grasses (CSAG), warm-season perennial grasses (WSPG), and cool-season perennial grasses (CSPG). Within a year, drought treatment totals with asterisks differ ( $P < 0.05$ , LSD). Within a plant type and a year, drought treatments with the same upper-case letter do not differ ( $P > 0.05$ , L.S.D.).

## Root dynamics

Differences in root counts in the Bw soil horizon suggest that the 2 moisture treatments differed prior to imposing drought treatments. There is no obvious explanation for differences observed in root counts in the Bw horizon in the first week of May 1993. However, 2 factors might help to explain this pre-treatment difference. Spring 'draw down' of root biomass in grasslands has been associated with early wet-season foliage growth (McNaughton et al. 1998); early season draw down of root biomass is followed by increased root biomass at the end of the wet season. Our results also demonstrate root declines with early spring growth and maximum root presence at the end of the growing season. We suggest that Figure 3 demonstrates a lag in the draw down in drought versus non-drought plots in April and May (excepting 1994 when very dry conditions in all plots may have limited the draw down effect). Since, our non-drought plots contained more cool-season grasses than drought plots (Heitschmidt et al. 1999), the draw down effect in drought plots may have been delayed by later growth of warm-season grasses, and thus lagged behind root declines in non-drought plots. The lag in timing of spring root declines in 1993 may explain the significant difference between the 2 treatments in May.

Lack of shallow root (A horizon) response to drought treatment is informative. We suggest that sufficient soil water was present before imposing drought treat-

ment for continued root growth of drought treatments until late into the 1994 growing season (Heitschmidt et al. 1999). Phenotypic plasticity of roots can allow plants to shift their root biomass to more favorable microsites (Mordenchai et al. 1997, Rethman et al. 1997). In the Bw horizon, root counts in the 2 drought treatments were similar prior to the imposed drought, but differed during drought. Compensatory root growth in soil layers which offer more favorable environments for roots is well documented (Hamblin 1985, Voorhees 1989, Huck and Hoogenboom 1990, Zobel 1991, Jesko et al. 1997). For example, compensatory root growth can occur at deeper soil depths when surface soils have dried (Schuster 1964, Fernandez and Caldwell 1975, Allmaras and Logsdon 1990). Thus Bw horizon roots may reflect drought treatment even though drought influence is not apparent in the A horizon roots.

Grazing treatment effects on root counts appear only in roots in the A horizon on 4 sampling dates. The general trend of fewer shallow roots in grazed plots than ungrazed plots over the entire time of the study, may be the consequence of greater allocation to above-ground growth, removal of annual plant roots by animals, and/or a compensatory shift in root distributions. Shallow roots did not decline immediately after grazing (1994), yet roots in grazed plots did not appear to over-winter well (April 1995). With return of growing season conditions early in 1995, ungrazed plants may have had greater winter root survival than grazed plants. Other explanations for decreased shallow roots with grazing are greater allocation to above-ground production (tillering) of perennials without subsequent root production (Briske and Richards 1995, Heitschmidt et al. 1999) or compensatory shift to deeper roots. Trends in rooting patterns may have been more apparent had we been able to identify roots to species.

### Seedbank dynamics

Grassland seedbanks seldom have a large perennial grass component (Rice 1989, Simpson et al. 1989, Kinucan and Smeins 1992); our results were similar. Combined evidence from production records (Heitschmidt et al. 1999) and our seed bank data indicates that summer defoliation may enhance forb presence when sufficient water is available. Decline in forb seedlings with drought could indicate reduced seed production, induced seed dormancy, or lack of seed viability.

Emerged seedlings of cool-season annual grasses (in this study primarily Japanese brome and sixweeks fescue) were affected little by grazing, but were reduced during and increased following drought treatment. Increases after drought may reflect induction of secondary dormancy in cool-season annual grasses in fall 1994 due to combined imbibition and temperature effects (Baskin and Baskin 1981, Haferkamp et al. 1994, 1995) and subsequent accumulation of seed in 1995. Similar seedling numbers were found in drought and non-drought plots in 1993. The imposed drought in 1994 clearly reduced germinable seed that year. Drought plots were denied rainfall until mid October and seed was collected on 23 September in 1994. Consequently, many of the seeds produced in 1994 on drought plots may not have had an opportunity to develop completely or germinate before sample collection. We did not measure and must assume seed production in 1995 was similar on drought and non-drought plots. In 1995 however, seedlings were greater on drought than on non-drought plots. A 6-day rainy period in mid-September 1994, was probably sufficient to allow some seeds to germinate on non-drought plots. Since August and September 1995 rainfall was not conducive to germination of annual brome seeds, drought plots retained the accumulated seeds from the prior fall. Consequently, we documented nearly twice as many germinable annual cool-season grass seeds in late September 1995 than non-drought plots. In the following year, September rains (> 25 mm) should have allowed germination of annual brome seeds and reduced seed banks on both drought and non-drought plots. Simultaneous study to document seed production and germination events versus accumulation of seed banks would have greatly enhanced our potential to evaluate secondary dormancy.

Successful establishment of perennial grass seedlings is unlikely and is much more common for annual grasses (Kinucan and Smeins 1992, Major and Pyott 1966, Rice 1989). Cool-season annual grasses could maintain their prevalence during subsequent recovery after drought. Consequently, one might speculate that overall trends in the seedbank the year after drought (decreased shallow roots with grazing, and decreased germinable forb seed with drought), suggest a potential transition favoring cool-season annual grasses. Other work suggests that combined clipping and presence of Japanese brome can decrease standing

crop of perennial cool-season grasses (Haferkamp et al. 1998). However, given the flexible composition of seed banks (Thompson and Grime 1979), dominance shifts between forbs, cool season annual grasses, and perennial grasses may be short-lived and greatly influenced by abiotic factors. Our results relative to drought effects probably would have been much different without early spring precipitation in 1994. Community dominance shifts in species composition are unlikely with normal seasonal precipitation patterns, but may occur during years containing this particular sequence of climatic conditions.

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# Forage kochia seed germination response to storage time and temperature

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## Abstract

The Eurasian low-shrub, forage kochia [*Kochia prostrata* (L.) Shad.], was introduced into western North America for use in restoration of severely disturbed landscapes in arid and semi-arid environments. Seed mature in late fall and are short-lived in typical warehouse conditions. In a preliminary, cold-temperature experiment (2° C) using 3-month-old seed from 16 forage kochia accessions, mean germination time, expressed as days to 50% germination, varied from 4 to 88 days. Follow up experiments using seed of 5 accessions tested the effects of storage time and temperature on seed viability and mean germination time and related this to field planting success. Sub-samples were air-dried and stored in plastic bags in a freezer, cold room, and lab (–15, 2, and 20° C respectively). A fourth set of subsamples was stored in a shed with no temperature control (simulated warehouse storage). Seed were tested fresh and retested after 4, 8, 12, 24, and 36 months of storage. Mean viability decreased from 77% (range 66 to 93%) for recently harvested seed, to 24 and 8% for lab- and shed-stored seed, after 36 months of storage. No significant change in viability was observed for cold room- and freezer-stored seed. Across all accessions, cold temperature mean germination time (MGT) for recently harvested seed was 73 days (range 51 to 109 days). For each accession, germination occurred primarily over a 70 day period. Mean germination time decreased as storage time increased for lab- and shed-stored seed, varied unpredictably for cold room-stored seed, and remained unchanged for freezer-stored seed. Field germination using 1- and 2-year old lab- and shed-stored seed was significantly faster than that of same-aged cold room- and freezer-stored seed. The number of live seedlings 4 months after planting for cold room- and freezer-stored seed was 10-fold or greater than that of lab- and shed-stored seed. Thus a delayed, asynchronous cold-temperature germination pattern appears to be adaptive for forage kochia establishment. Cold, dry storage prevents loss of seed viability and preserves this desirable germination pattern.

**Key Words:** *Kochia prostrata*, prostrate summer cypress, germination rate, mean germination time, after-ripening, germination synchronization, cold-desert revegetation

## Resumen

El arbusto Euroasiático “Kochia forrajera” [*Kochia prostrata* (L.) Shad], se introdujo en oeste de Norteamérica para usarlo en la restauración de paisajes severamente degradados de ambientes áridos y semiáridos. La semilla madura a finales de otoño y bajo las condiciones típicas de almacenamiento en bodega tiene una vida corta. En un experimento preeliminar, utilizando bajas temperaturas (2° C), semilla de 3 meses de cosechada y proveniente de 16 entradas de “Kochia forrajera”, se estableció que el tiempo promedio de germinación, expresado como días al 50% de semillas germinadas, varió de 4 a 88 días. En experimentos subsecuentes, usando semilla de 5 entradas, probamos los efectos del tiempo de almacenaje y la temperatura en la viabilidad de la semilla y el promedio del tiempo de germinación, y relacionamos esto con el éxito de establecimiento de las plantas en el campo. Submuestras se secaron con aire, se guardaron en bolsas de plástico y se almacenaron en: 1) congelador, 2) cuarto frío y 3) laboratorio (–15, 2 y 20° C respectivamente). Un cuarto grupo de submuestras se almacenó en un cobertizo sin control de temperatura (simulando las condiciones de bodega). Las semillas se evaluaron recién cosechadas y se reevaluaron a los 4, 8, 12, 24, y 36 meses de almacenamiento. El promedio de viabilidad disminuyó de 77% (rango de 66 a 93%) en semillas recién cosechadas a 24 y 8% en semillas almacenadas durante 36 meses en laboratorio y cobertizo. No se observaron cambios significativos en la viabilidad de semillas almacenadas en congelador y cuarto frío. La media general de tiempo de germinación en temperaturas frías de todas de las entradas de “Kochia forrajera” fue de 73 días en semillas recién cosechadas (rango de 51 a 109 días). Para cada entrada de “Kochia forrajera” la germinación ocurrió después de 70 días. El tiempo promedio de germinación de semillas almacenadas en el laboratorio y cobertizo disminuyó conforme el tiempo de almacenamiento aumentó, varió en forma impredecible para la semilla almacenada en cuarto frío y permaneció sin cambios para la semilla almacenada en congelador. La germinación en campo de semillas almacenadas por 1 y 2 años en el laboratorio y cobertizo fue significativamente más rápida que la de semilla almacenada durante el mismo tiempo en cuarto frío o congelador. El número de plántulas vivas (4 meses después de la siembra) de semillas almacenadas en cuarto frío y congelador fue 10 veces o más que el de semillas almacenadas en laboratorio y cobertizo. Por lo tanto, un patrón de germinación retasado asincrónico de temperatura fría parece ser que se adapta para el establecimiento de “Kochia forrajera”. El almacenamiento en condiciones secas y frías previene la pérdida de viabilidad y conserva este patrón deseable de germinación.

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Many arid and semiarid rangelands of the western United States are becoming destabilized due to the interrelated effects of unsustainable grazing practices (Young 1994), introductions of old-world weeds (Peters and Bunting 1994), and changes in wildfire frequency (Whisenant 1990). Unchecked, these forces are causing the conversion of shrub and perennial grasses-dominated communities to annuals-dominated communities with reduced resource values and serious management considerations. Restoring function and desired use to degraded rangelands can be accomplished by seeding adapted perennials capable of competing with weedy species and resprouting after fire. The need to develop plant materials endowed with these traits and the capacity to coexist with and complement remnant populations of native communities, is widely recognized.

Forage kochia [*Kochia prostrata* (L.) Shrad.], also known as prostrate summer cypress, is a polymorphic low-shrub native from the Mediterranean Basin to Siberia (Shishkin 1936). Baylan (1972) recognizes 2 subspecies: sp. *virescens* (Frenzl) Prat., commonly known as green-stem forage kochia, and sp. *grisea* Prat., or gray-stem forage kochia. Several germplasm introductions have been made to evaluate the utility of forage kochia for revegetation of severely disturbed arid and semi-arid sites in the western United States (McArthur et al. 1974, Frischknecht and Ferguson 1984, Blauer et al. 1993). Introductions have been evaluated for such traits as livestock and wildlife preference (Davis and Welch 1985), nutritional quality (Davis and Welch 1983, 1985), seed germination characteristics (Young et al. 1981, Waller et al. 1983, Briede and McKell 1992, Stewart 1998), establishment and competitive attributes (Stevens and Van Epps 1984, McArthur et al. 1990, Monsen and Turnipseed 1990, Stevens and McArthur 1990, McArthur et al. 1996, Harrison et al. 2000), and salinity tolerance (Francois 1976, Romo and Haferkamp 1987). Studies demonstrate that forage kochia is well suited for a variety of soil types on cold-desert rangelands receiving 150–300 mm annual precipitation. A single cultivar, 'Immigrant', (sp. *virescens*) was released after demonstrating wide spread adaptability, forage quality, and productivity (Stevens et al. 1985). Several thousand kilograms of seed of this cultivar are planted on rangelands most years.

Forage kochia grows throughout the summer, flowering indeterminately from June through September (Shishkin 1936, Baylan 1972). Fruits usually mature by the

middle of October (Waller et al. 1983, Stewart 1998) and are commonly harvested from October through January. Subsequently, current-year seed is sometimes not available in time for fall and early winter revegetation projects. Forage kochia stand establishment from seed stored for 1 or more years in typical warehouse conditions is generally poor. This is due in part to the short shelf-life for seed of this species. Shelf-life can be extended by adequate pre-drying and by storage in sealed containers at low temperatures (Young et al. 1981, Jorgensen and Davis 1984, Stewart 1998). However, a lack of stand establishment success using high-viability, stored seeds is more difficult to explain. Low seed vigor has been proposed as one possible explanation (Haferkamp et al. 1990). In this work, we provide evidence to support an alternative explanation.

For best emergence, forage kochia seed must germinate at or near the soil surface. In the cold-desert environments to which this species is adapted, soil temperature and moisture conditions favorable for surface germination and seedling growth occur most dependably during brief periods in late winter and early spring. Seed that germinate at other times (e.g. too late or too early) have a higher risk of mortality than do seed with proper germination timing. Therefore, we attempt to test the

hypothesis that seeding failure using stored but viable seed may be caused by storage-related alteration of germination timing controls.

Our objectives were to examine in the laboratory among-accession differences in cold-temperature germination rate, or cold mean germination time, expressed as days to 50% germination (based on total viable seeds), and determine the effects of storage time and temperature on seed viability and mean germination time for forage kochia. We also relate results of field plantings using differently-stored seed to test conclusions drawn from laboratory experiments.

## Materials and Methods

A preliminary experiment was conducted to determine among-accession differences in mean germination time for forage kochia. Three-month-old seed from 15 experimental lines collected from a common garden located near Boise, Ida. (Latitude and Longitude; 43° 20' North 116° 35' West) were studied. All accessions except 1 (origin Peoples Republic of China, Table 1) were sp. *grisea*. Seed were hand-collected, dried, and cleaned in November 1989. In addition, because it

**Table 1. Forage kochia accessions by plant introduction number, location and soil type of original collection, and cold temperature (2° C) mean germination time (MGT), expressed as days to 50% germination of viable seeds. All seed was 3 months old except for accession 314929 which was 1 year old. Means followed by the same letter are not significantly different at the  $p < 0.05$  level (Tukey).**

P.I. No. <sup>a</sup>	Original Collection Information <sup>b</sup>		
	Location	Soil Type	MGT (days)
-----	Inner Mongolia, Peoples Republic of China	Unknown	3.7j
314929 <sup>c,d</sup>	Stavropol', Russia "Immigrant"	Sandy	11.2j
330708	Rashat, Iran	Unknown	41.9hi
343101 <sup>d</sup>	Kyrgyzstan	Unknown	32.1hi
356817	Akt'ubinsk, Kazakhstan	Salty	44.7gh
356818 <sup>d</sup>	Akt'ubinsk, Kazakhstan	Clay	41.5hi
356819	Akt'ubinsk, Kazakhstan	Salty	48.7efgh
356820	Akt'ubinsk, Kazakhstan	Sandy	53.1defg
356821	Akt'ubinsk, Kazakhstan	Salty	50.9efgh
356822	Akt'ubinsk, Kazakhstan	Clay	55.6cdef
356823	Akt'ubinsk, Kazakhstan	Sandy	58.5bcde
356824	Akt'ubinsk, Kazakhstan	Salty	67.0b
356825	Akt'ubinsk, Kazakhstan	Sandy	66.4bc
356826 <sup>d</sup>	Akt'ubinsk, Kazakhstan	Salty	88.3a
358941 <sup>d</sup>	Stavropol', Russia	Sandy	47.6fgh
422519	Unknown	Unknown	61.2bcd

<sup>a</sup>The PI number is the USDA plant inventory number. The first 2 accessions are sp. *virescens* and the rest belong to sp. *grisea*.

<sup>b</sup>This information came with original seed packets from the USDA ARS Western Regional Plant Introduction Station in Pullman, Washington. Locations should be taken as general areas. The collections from Akt'ubinsk are regional collections taken from the Aral Sea to the Ural Mountains. Those from Stavropol' came from a botanical garden.

<sup>c</sup>The cultivar 'Immigrant' (Stevens et al. 1985).

<sup>d</sup>Accessions selected for the storage experiments.

had not been collected at the Boise common garden, 1-year-old seed of Immigrant forage kochia (sp. *virescens*) was secured and included in the experiment. For each accession, 4 replications of 50 seeds each were placed in 15 x 100 mm plastic petri dishes on top of 2 germination blotters (Anchor Paper Company, St. Paul, Minn.) moistened to saturation with tap water. Petri dishes were arranged randomly in a cardboard box. The box was enclosed in a plastic bag to retard desiccation, and placed in a walk-in cold room at 2° C. Water was added periodically to maintain blotter water content at near saturation levels. Seed were examined and germinants were counted and removed from the petri dishes on a weekly basis for 112 days. Seed were classified as germinated when radicles had elongated at least 3 mm and demonstrated a positive gravitropic response. Most germinants were also at least partially uncoiled. At the end of 112 days, the box was moved to a germination chamber set at 15/25° C (12 hour alternating) for 3 additional days. After final germination counts were made, an embryo integrity (squish) test confirmed the absence of remaining viable (dormant) seed. Viability percentages and mean germination time values were calculated for each replication.

### Storage Experiments

Seed of 4 experimental lines were harvested from a nursery site in Spanish Fork, Utah (Latitude and Longitude; 39° 40' North 111° 5' West) during October and November 1992 (Table 1). Length of harvest period was due to variability in ripening rates among accessions. Ripened fruits were easily collected by beating fruit-bearing stems against the edge of hand-held hoppers with badminton rackets. Harvested fruits were spread on tables to a depth of 10 cm for 10+ days prior to further processing. Temperatures varied between 15 and 25° C, and though not measured, relative humidity was sufficiently low to allow drying to occur. Subsequently, inert material and a portion of unfilled fruits were removed from each lot using a 2-screen fanning mill. Cleaned seed (fruits) were stored in cloth bags for approximately 1 month (15 to 25° C) before further processing. A fifth accession, non-certified Immigrant, was acquired from a commercial source and had been collected in November 1992 from a USDI-BLM planting located 15 km northeast of Milford, Utah.

In December, seed of all 5 accessions were oven-dried at 35° C for 72 hours and

subdivided into 4 equal sublots. Each subplot was placed in a labeled plastic bag closed with a rubber band. One subplot (bag) for each accession was placed inside each of 4 larger plastic bags, also closed with a rubber band. One of each of these bags was stored for 36 months in: 1) the laboratory at room temperature (20° C); 2) the walk-in cold room (2° C); 3) a freezer (-15° C); and 4) a shed in Provo, Utah with no temperature control (to simulate warehouse storage). To determine seed water content immediately after processing and again after 8 months of storage, subsamples of approximately 20 g were weighed, oven dried for 24 hours at 65° C, and reweighed. Mean water content for dried seed before storage was 4.1%. There was no significant change in water content after 8 months of storage for all storage treatments (mean = 3.9%).

Germination procedures followed those used in the preliminary experiment with the following exceptions: 1) 25 instead of 50 seeds per replication were used and 2) final incubation temperature was 10/20° C instead of 15/25° C. These changes were intended to make the germination environment less favorable for potential seed pathogens. Each accession was tested fresh (December 1992) and each accession/storage combination was tested after 4, 8, 12, 24, and 36 months of storage.

### Field Trials

A fallowed agricultural field with uniform soil and topography was selected near American Fork, Utah (Latitude and Longitude; 40° 20' North 111° 50' West; elev. 1,380 m) as a site for field germination and seedling establishment experiments. The site was tilled each fall prior to planting dates (30 November 1993 and 2 December 1994). Litter cover was less than 5%, ensuring good seed contact with mineral soil. Results were interpreted in light of ambient temperature data for the Utah Lake Lehi weather station (NOAA 1993, 1994, 1995) located 8 km west of the planting site (same approximate elevation). When data were incomplete for any month, estimates were made using data from the Vernon and Timpanogos Cave sites, 48 and 8 km distant from the planting site.

Only Immigrant seed was used for these field studies. Seed had experienced 1 and 2 years of storage prior to planting. In preparation, each year twelve, 0.2-g and three, 2-g subsamples were weighed from each of the 4 Immigrant sublots (storage treatments). The twelve, 0.2-g subsamples of approximately 160 seeds each (150

viable seeds prior to storage) were enclosed in marked 10 x 10 cm square nylon-mesh bags. Bags were randomly sorted into 12 sets, each set including 1 bag from each storage treatment.

In 1993, each set of bags was buried under 1.0 to 1.5 cm of soil and marked with a 75-cm survey flag to facilitate detection in snow. Each group of bags was placed under a 20 cm (diameter) wire-mesh cone buried 3 cm deep to discourage rodents. Cones were arranged in a 2 by 6 grid with 10–20 cm inter-cone spacing. We used similar procedures in 1994, however, bags were not buried in soil and cones were not used. Instead, bags were firmly pressed into the soil surface and covered with 1–2 cm of straw. This change was made to simplify extraction of bags from frozen soil. This mulch was held in place by 2 criss-crossed layers of pine stakes (2 x 4 x 35 cm) placed horizontally with 12 to 15 cm spacing between stakes. No rodent predation was encountered either year.

Each year, 3 sets (replications) of 4 bags each were randomly selected and retrieved from the site 1 and 2 months following burial. Retrieved bags were packed in loose snow and taken directly to the laboratory for processing. There, soil and ice were gently washed from each bag before opening. We then opened bags and determined germination status for each seed. Average time from bag retrieval to final seed evaluation was 2 to 3 hours. Due to rapid germination associated with unseasonably warm temperatures in December and January (Fig. 1), 6 sets of bags remained unused both years.

The 2-g samples were planted on twelve, 1.0 x 0.5 m plots arranged in a randomized block design each year. Planting consisted of hand broadcasting seed onto the appropriate plot and lightly raking over the entire plot to improve soil/seed surface contact and to anchor the seeds to the plots. Planting dates were the same as burial dates for the retrieval experiments. We determined the number of forage kochia seedlings per plot approximately 4 months after planting (early April), both years. At this time, the soil surface was dry and crusted and surviving seedlings had reached or passed the 6-leaf stage.

Percentage data (seed viability in storage experiments and seed germination and seedling survival in field experiments) were arcsine transformed for statistical analysis. Results were analyzed using the GLM procedure (SAS 1998) to test for effects of storage treatment and time on

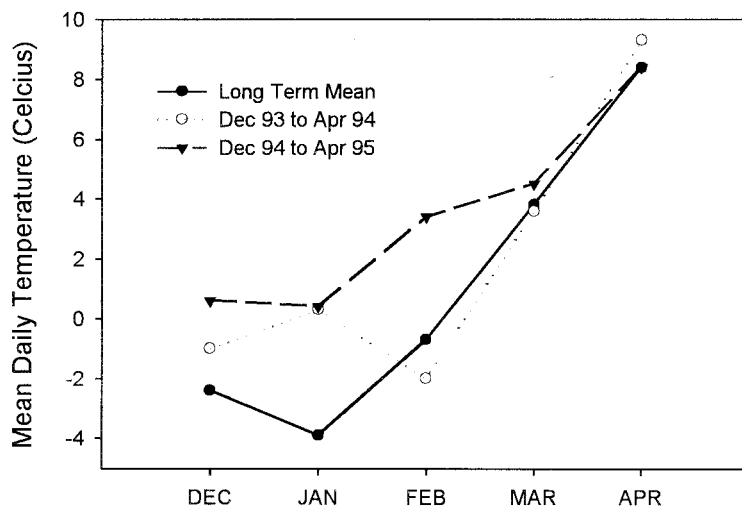


Fig. 1. Mean daily temperatures for the months of December to April for the Utah Lake Lehi weather station. Values for the winters of 1993–1994 and 1994–1995 are compared to the long-term mean (1961–1990) for the site (NOAA 1993, 1994, 1995). When data were missing, means were estimated using data from the Vernon and Timpanogos Cave stations.

viability percentage and cold mean germination time in laboratory experiments, and field germination and seedling survival in field experiments. Significant differences among accession and treatment means were determined using the Tukey-Kramer (Tukey) multiple means comparison test.

## Results

Mean germination time (MGT) for the 15 experimental lines of the preliminary experiment ranged from 3.7 to 88.3 days (Table 1). The fastest germination rates belonged to the accession originally collected in the Inner-Mongolia region of the

People's Republic of China (MGT = 3.7 days) and to 1 year-old Immigrant seed (MGT = 11.2 days). Mean germination time for the remaining accessions (all recently harvested seed) was 54.1 days. Maximum percentage of ungerminated seed after 112 days of chilling was 29% (MGT = 88.3 days). Accessions selected for the storage experiments represented nearly the full range in observed mean germination time values.

## Storage Experiments

Mean viability of recently harvested seed was 77% (range 66 to 93%). After 12 months storage, viability of lab- and shed-stored seed (71%) was significantly lower

( $p < 0.05$ ) than that of cold room- and freezer-stored seed (83%). After 36 months of storage, viability of lab- and shed-stored seed decreased to 24 and 8%, respectively (Fig. 2). Viability percentages for 36-month old cold room- and freezer-stored seed were not significantly different than those of recently harvested seed. However, viability of 24-month old cold room- and freezer-stored seed was significantly lower than that of either recently harvested or 36-month old seed for 4 of 5 accessions. Because viability can not increase through time, the observed increase is best explained as differential selection among test dates for filled fruits. This is not surprising in as much as fill for intact fruits can be difficult to detect. Only with the commercially collected and conditioned Immigrant seed were we able to consistently eliminate most empty fruits by visual inspection. Within test dates, treatment-related differences in viability estimates were similar for all accessions (including Immigrant), suggesting that within-test date seed selection was much more consistent than among-test date selection. All ungerminated, viable seed germinated within a few days after exposure to warmer germination temperatures (10/20° C) at the end of the 112-day cold treatment.

Although similar in duration (approximately 70 days), the primary period of germination for recently harvested seed varied considerably among accessions (Fig. 3). Mean germination time (MGT) was 73 days (range = 51 to 109 days). As in the preliminary experiment, significant among-accession differences in germination rate were observed (Table 2). Mean germination times for these accessions were greater for this experiment than in the preliminary experiment, suggesting differences in afterripening and/or site conditions during seed maturation. This difference was most pronounced for seed of Immigrant (MGT = 11 vs. 70 days). However, Immigrant seed in the preliminary experiment was 1-year-old, therefore, comparisons between that seed and recently harvested seed of the storage experiment would be invalid. A more appropriate inter-experimental comparison for Immigrant seed germination rate would be between results of the preliminary experiment and those derived after 12 months of lab- or shed-storage (MGT = 13 and 15 days, respectively).

After 8 months of storage, mean germination times for lab-, shed-, and cold room-stored seed (17, 19, and 22 days, respectively) was significantly shorter

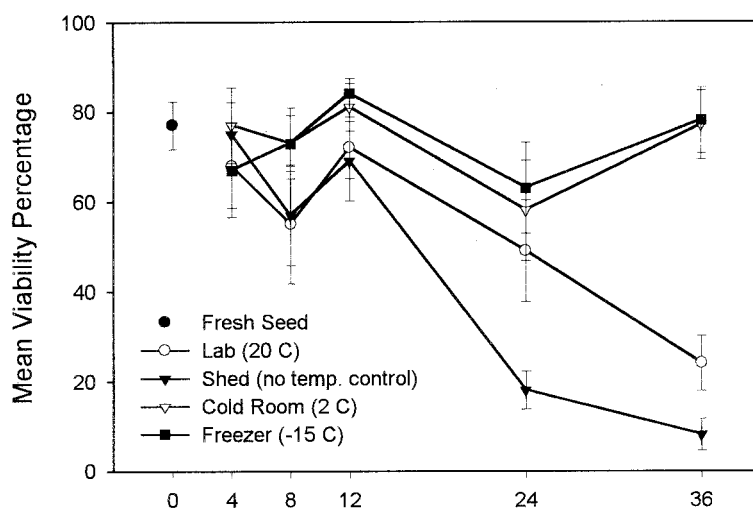


Fig. 2. Mean viability for 5 accessions of forage kochia tested fresh and in response to dry storage treatments.

**Table 2.** Cold temperature (2° C) mean germination time (days to 50% germination of viable seeds) for 5 accessions of forage kochia tested fresh and after 4-36 months dry storage in a lab (20° C), cold room (2° C), freezer (-15° C), and shed with no temperature control. Among accessions for fresh seed, and within accessions and storage period for stored seed, means followed by the same letter are not significantly different at the  $p < 0.05$  level (Tukey).

Accession No./ Storage Treatment	Fresh	Mean Germination Time (days to 50% germination)				
		Storage Period (months)				
		4	8	12	24	36
----- (days) -----						
<b>314929</b> (Immigrant)	70b					
Lab		47b	16b	13c	11b	6b
Cold Room		44b	26b	36b	58a	16b
Freezer		71a	70a	70a	67a	76a
Shed		59a	19b	15bc	21b	15b
<b>343101</b>	51c					
Lab		40a	12b	17b	12b	8b
Cold Room		21b	14b	24b	46a	28b
Freezer		54a	56a	64a	55a	59a
Shed		49a	17b	13b	12b	9b
356818	53c					
Lab		43ab	21b	23b	13b	16b
Cold Room		26b	19b	37b	51a	31b
Freezer		49a	49a	63a	58a	67a
Shed		59a	20b	16b	18b	19b
<b>356826</b>	109a					
Lab		61b	17b	7c	11b	6c
Cold Room		62b	31b	66a	86a	37b
Freezer		96a	93a	87a	90a	106a
Shed		78ab	21b	13b	10b	---
<b>358941</b>	81b					
Lab		55ab	20b	12b	12b	6b
Cold Room		40b	20b	23b	63a	8b
Freezer		69a	87a	67a	76a	75a
Shed		62a	18b	14b	12b	11b

than those observed for recently harvested seed (Fig. 4). Within-accession changes and among-accession differences in mean germination time were small and essentially insignificant for lab- and shed-stored seed in response to longer periods of storage. Mean germination time for cold room-stored seed (all 5 accessions) changed unpredictably over the duration of the experiment with values significantly higher ( $p > 0.05$ ) after 12 and 24 months (37 and 61 days, respectively), but not after 36 months (24 days) when compared to those observed after 8 months (22 days) of storage. Across all storage periods, differences in the observed mean germination time for freezer-stored seed were not significantly different than that of fresh seed. Although initial (recently harvested seed) mean germination times varied more than 2-fold among accessions, relative differences in treatment effects are similar among accessions (Table 2). For all accessions, freezer storage was the only method found effective in preserving original germination patterns through 36 months of storage.

## Field Trials

Laboratory germination results generally supported results observed for field experiments. For both years of burial, significantly higher percentages of viable seed had not yet germinated 1 month after planting for cold room- and freezer-stored seed than for lab- and shed-stored seed (Table 3). Nearly all viable seed from all 4 storage treatments had germinated by the second retrieval date. Unseasonably warm temperatures during December and January both years (1993–94 and 1994–95; Fig. 1) undoubtedly allowed germination to occur at a more rapid rate than might have been observed under

colder conditions.

Mean numbers of live seedlings counted on the 0.5 m<sup>2</sup> emergence plots for cold room- and freezer-stored seed were approximately 10-fold those counted for lab- and shed-stored seed the first year (Table 4). Differences in second-year results are greater than those of the first year. This is true whether expressed as the absolute number of seedlings counted or as a percentage of viable seed planted as estimated by retrieval experiments. Differences between cold room- and freezer-stored seed and between lab- and shed-stored seed were not significant either year.

## Discussion

Forage kochia is well adapted to the sometimes severe and generally variable weather conditions found in the cold-deserts of western North-America (McArthur et al. 1974, Pendleton et al. 1992, McArthur et al. 1996). Although successful seedling establishment may require some disturbance in perennial communities (McArthur et al. 1990, Stevens and McArthur 1990, Harrison et al. 2000) new seedlings are observed near established plants most years. Late-season seed maturation and a delayed/asynchronous germination pattern in cold temperatures result in a high probability that some fraction of seed will germinate during a time favorable for establishment success. Germination that is too early or too uniform places seedlings at risk to conditions unfavorable for survival. The timing of these late winter/early spring 'windows of opportunity' varies annually, favoring the selection of a bet-hedging germination strategy (Phillipi and Seger 1989). Asynchronous cold-temperature germination functions as a bet-hedging strategy for forage kochia. Changes in seed germinability in dry storage, also known as dry afterripening, are common and are generally expressed as loss of innate dormancy, loss of light and temperature sensi-

**Table 3.** Field germination of Immigrant forage kochia seed 1 and 2 months after planting as affected by storage treatment. Seed planted in 1993 and 1994 had been stored dry for 1 and 2 years before planting. Data are shown as mean number of viable seed ungerminated and percent ungerminated based on total viable seed (in parentheses). Within rows, means followed by the same letter are not significantly different at the  $p < 0.05$  level (Tukey).

Year of Planting	Months after Planting	Storage Treatment			
		Lab	Shed	Cold Room	Freezer
		No. (%)	No. (%)	No. (%)	No. (%)
93	1	60 (51)b	61 (49)b	138 (92)a	135 (92)a
	2	18 (15)ab	6 (8)b	26 (17)a	32 (21)a
94	1	3 (4)b	3 (22)b	113 (76)a	124 (84)a
	2	0b	0b	6 (4)ab	20 (7)a

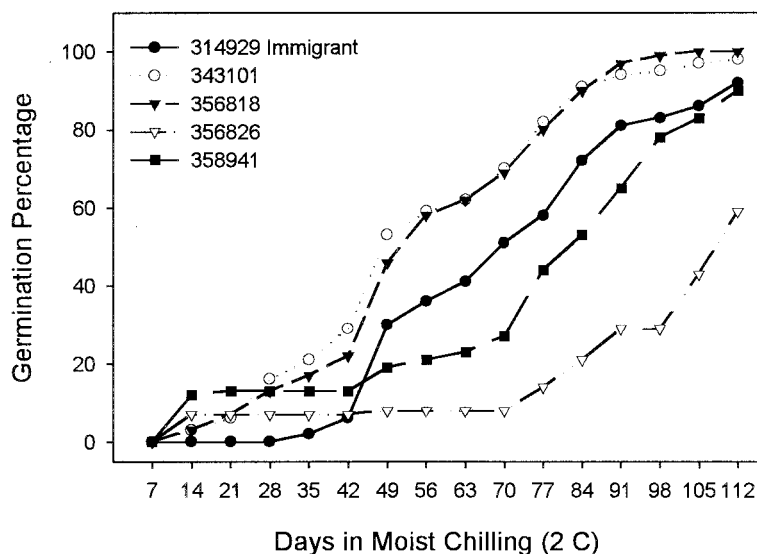


Fig. 3. Time course germination plots for 5 recently-harvested accessions of forage kochia at 2° C.

tivity, and/or changes in germination rate (Bewley and Black 1982). After-ripening is uni-directional and temperature dependent. Therefore, it can be expected that the process of after-ripening is greatly slowed, or even arrested, at freezing temperatures. Our data suggest that this is the case for forage kochia seed.

Conversely, we might expect seed stored at constant warm temperature to show a relatively rapid, continuous change in germinability, or in our case, decrease in mean germination time (MGT). Seed

stored in the lab for the first 8 months at room temperature followed just such a pattern. A leveling off of MGT after 8 months of storage suggests that warm-stored seed reached a threshold in germination rate. Temperatures for shed-stored seed were controlled by ambient temperatures which fluctuate daily and seasonally. For much of the first 4 months of storage (January–April) ambient temperatures were cold, often sub-freezing (Fig. 1), resulting in slower rates of afterripening. We might predict that 4-month MGT for

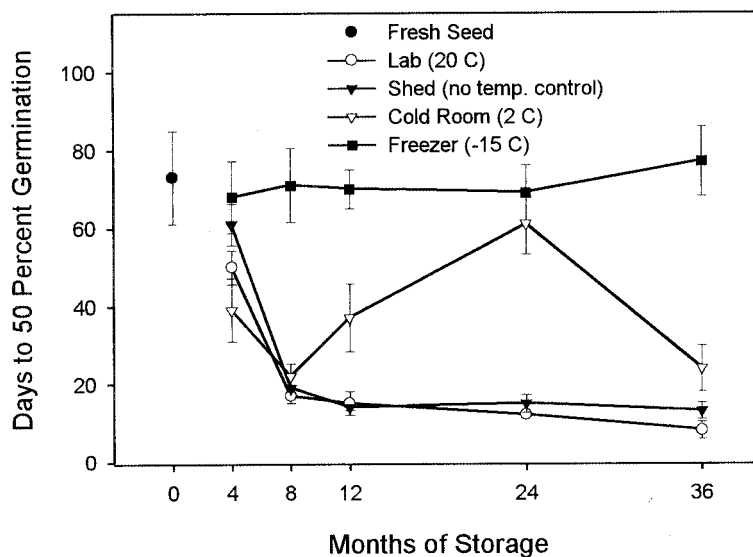


Fig. 4. Mean germination time (days to 50% germination) for 5 accessions of forage kochia as affected by storage location (temperature) and time.

this storage treatment would have to be intermediate to that of freezer- and lab-stored seed. This was indeed the case (Fig. 3). In the time period between 4 and 8 months of storage (May–August), seed in the shed storage treatment were exposed to ambient temperatures higher than in any other storage treatment. Subsequently, changes related to after-ripening should have been accelerated for this storage treatment during this time. Not surprisingly, the change in mean germination time for all accessions in the 4 to 8 month interval was greater for this storage treatment than for any other. From this point on, mean germination time for shed- and lab-stored seed did not differ significantly with length of storage.

Accounting for the changes in mean germination time (MGT) for cold room-stored seed over time is more difficult. Because after-ripening is temperature dependent, we expected changes in MGT for cold room-stored seed to be slower than those observed for lab-stored seed. This was not the case for the first 8 months of storage suggesting that another process, perhaps akin to prechill (stratification), may have been responsible. However, prechill treatments are generally effective only when seed have imbibed water. Our seed remained dry through the storage treatment. Waller et al. (1983) reported that after 3 months dry storage, forage kochia seed stored at 4° C produced germination percentages higher than seed stored at either -18 or 21° C, also suggesting an accelerated rate of after-ripening in near freezing temperatures. Increases in MGT associated with 12 and 24 months of storage and subsequent decrease observed with the 36 month treatment are puzzling and identifying a process or processes responsible for these unexpected reversals will not be easy.

Among accession differences in MGT for freshly collected seed were significant and likely adaptive, probably reflecting climatic differences in the Eurasian origins of the respective accessions. We have insufficient knowledge concerning those origins to speculate on the significance of those differences including the unusually rapid cold germination rate of 3-month old seed of the Chinese accession (Table 1). Waller et al. (1983) observed differences in germination (15/25° C) for 2 accessions of forage kochia (one of each subspecies) as affected by harvest date, drying method, and storage temperature. They concluded that, based on their data, the gray-stem variety (sp. *grisea*) had better germination characteristics than the red-

**Table 4. Number of forage kochia seedlings 5 months after planting as affected by seed storage treatment. Seed planted in 1993 and 1994 had been stored for 1 and 2 years. Numbers in parentheses are live seedlings expressed as a percent of viable seed planted. Within rows, means followed by the same letter are not significantly different at the  $p < 0.05$  level (Tukey).**

Year of Planting	Storage Treatment			
	Lab	Shed	Cold Room	Freezer
	No. (%)	No. (%)	No. (%)	No. (%)
1993	30 (2)b	22 (2)b	240 (16)a	207 (14)a
1994	10 (1)b	2 (2)b	278 (20)a	292 (21)a

stem variety (sp. *virescens*) and suggest that it would therefore be preferred for revegetation. Our study significantly expands understanding of forage kochia intra-specific variability in germination behavior both because of the quantity of germplasm tested and because of the exposure of that germplasm to treatments relevant to storage and seedbed environments. We contend that the germination patterns for recently collected seeds of all accessions that we have tested (with the likely exception of the Chinese accession) are broad enough for successful establishment in the arid/semiarid West. Further speculation concerning how adaptive the germination timing of any one accession might be for specific environments, based on our data, would be inappropriate. Changes in MGT in storage were similar for all accessions even though initially values varied 2-fold. Ultimately, MGT for all accessions dropped to between 21 and 12 days after 8 months of lab or shed storage suggesting that similar storage treatments are unsuitable for any and all accessions to preserve a germination profile suitable for wildland plantings.

Storage treatment related differences in laboratory germination trials were largely matched by field seed retrieval experiments. In addition, successful seedling establishment was significantly greater for cold room- and freezer-stored seed; those treatments with the slowest MGT in laboratory experiments after 12 and 24 months (Table 2).

## Conclusions

Data from this study support the conclusion that an altered germination timing regime may be responsible for forage kochia seeding failure using after-ripened seed of known high viability. We observed that low temperature germination is delayed and asynchronous for recently harvested seed and that germination rate increases dramatically with after-ripening. We also observed poor field performance of after-ripened seed. With this study we

provide additional evidence of why forage kochia seed need to be dried to less than 7% moisture, sealed in water tight containers, and stored at temperatures below 5° C (Jorgensen and Davis 1984, Stewart 1998) when not planted soon after harvest. Because of the unpredictable changes in germination patterns we observed for cold room-stored seeds, we believe that there may be an additional advantage to storage at temperatures below freezing. Finally, after-ripened seed with rapid germination may be suitable for spring or summer plantings where supplemental irrigation is available.

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# Species composition on reclaimed ski runs compared with unseeded areas

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## Abstract

The cover of native and non-native introduced plants was compared between seeded (reclaimed) ski runs and adjacent or nearby unseeded (control) areas at a managed ski area in northern Arizona to determine the potential effects of revegetation efforts on plant species composition of the area. Although vegetative cover was similar, plant species richness was significantly lower on reclaimed ski runs compared with control areas. At 3 of 4 sites, the number of plant species was more than 2-fold greater in control areas, although species richness was similar between control and reclaimed areas at 1 site. The proportion of native species was more than 3-fold greater in control areas compared with reclaimed ski runs. The proportion of non-native species was more than 5-fold greater on reclaimed ski runs than in control areas. Although sites differed substantially in time since seeding, no evidence was found at 3 of the 4 sites for either an invasion of non-native species into the native plant community, or significant re-establishment of native species in reclaimed areas. Relatively high biomass of native species on a reclaimed ski run at 1 site appeared to be tied to a low level of initial disturbance and favorable conditions for growth. Results suggested that minimizing initial soil disturbance, retaining topsoil, and maintaining islands or patches of natural vegetation within cleared areas promoted the re-establishment of native species on ski runs.

**Key Words:** disturbance, reclamation, ski runs, non-native species, richness

The use of native plant species in reclamation and revegetation projects has been advocated for a number of years, primarily because of concerns about potentially adverse impacts of non-indigenous species on native plant communities (Wade 1997, Baker 1995). Negative effects of non-native plant species cited include competitive exclusion of native species (Rosentreter 1992, Melgoza and Novak 1991, Aguirre and Johnson 1991, Young and Evans 1973, Harris 1967, Stewart and Hull 1949), contamination of native gene pools and loss of genetic diversity (Rosentreter 1992), increased fire frequency (Hughes et al. 1991,

## Resumen

Se comparó la cobertura de plantas nativas e introducidas no nativas entre corredores de esquiar sembrados (rehabilitados) y en áreas adyacentes o cercanos sin sembrar (control) de un área de esquiar manejada del norte de Arizona. La comparación se realizó con el objetivo de determinar los efectos potenciales de los esfuerzos de revegetación en la composición de especies vegetales del área. Aunque la cobertura vegetal fue similar, la riqueza de especies fue significativamente menor en los corredores de esquiar que en las áreas control. En 3 de 4 sitios el número de especies vegetales fue 2 veces mayor en las áreas control, aunque en el sitio 1 la riqueza de especies fue similar entre las áreas control y las rehabilitadas. La proporción de especies nativas fue 3 veces mayor en las áreas control en comparación con los corredores de esquiar rehabilitados. En los corredores de esquiar rehabilitados la proporción de especies introducidas no nativas fue mas de 5 veces mayor que la de las áreas control. Aunque los sitios difirieron substancialmente en el tiempo en que fueron sembrados, en 3 de 4 sitios no se encontraron evidencias de la invasión de especies introducidas no nativas en las comunidades vegetales nativas ni del restablecimiento significativo de especies nativas en los corredores de esquiar. La biomasa relativamente alta de especies nativas en el corredor de esquiar del sitio 1 parece estar ligada a un bajo nivel inicial de disturbio y condiciones favorables para el crecimiento vegetal. Los resultados sugieren que minimizando el disturbio inicial del suelo, reteniendo la capa superficial del suelo y manteniendo islas o parches de vegetación nativa dentro de las áreas aclareadas para esquiar se promueve el restablecimiento de las especies nativas en los corredores de esquiar.

Rogers and Steele 1980, Beatley 1966), and change in soil characteristics (Kourtev et al. 1998).

From a management standpoint, the primary objective of revegetation of disturbed areas is soil stabilization. The construction and maintenance of ski runs on steep slopes requires erosion control measures to prevent soil loss. Although physical erosion control features, like berms, are often constructed, the re-establishment of vegetative groundcover is critical in reducing runoff and soil loss as it binds soils and increases infiltration rates (Andreu et al. 1995, Williams et al. 1995, Oliver and Larson 1990, Marks and Bormann 1972). Natural re-establishment of indigenous vegetation in disturbed areas may take years (Curtin 1995, Dyrness 1973), dictating the need for artificial seeding to re-establish vegetative groundcover quickly. In many instances,

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local cultivars for herbaceous plants and shrubs are not commercially available for a particular area. The need for immediate erosion control therefore often results in the use of a variety of species for reclamation, including commercially available cultivars of native species and species that have been introduced from other geographic regions.

The objective of this study was to determine the effects of reclamation on plant species composition on reclaimed (seeded) ski runs and on adjacent or nearby unseeded control areas in a managed ski area. The specific questions of interest were: 1) did native plants become re-established on reclaimed ski runs through time and 2) did non-native species invade adjacent natural areas and competitively exclude native species? To address these questions, we compared plant species composition between reclaimed areas with known seeding histories and adjacent or nearby control areas. We also studied the effects of time since seeding on the interaction between native and non-native species by comparing areas with varying times since seeding.

## Methods

### Study Sites

The study took place at the Arizona Snowbowl Ski Area on the western slopes of the San Francisco Peaks, an extinct volcanic cone located approximately 25 km northwest of Flagstaff, Ariz. U.S.A., at 35° 19' N and 111° 41' W. Study sites were selected based on the presence of suitable unseeded control areas adjacent to or near reclaimed (seeded) areas to reduce potential within-site variability. Sites with different seeding histories were used in an attempt to examine the effects of length of time since seeding on plant species composition and cover.

Data were collected at 4 study sites, referred to as Southern Belle, Casino, Frontier, and Meadows. These study areas corresponded to the names of the existing ski runs and adjacent or nearby areas on which control plots were established. The Southern Belle site was at the lowest elevation (2,900–3,000 m) and occurred within mixed-conifer habitat dominated by Douglas fir [*Pseudotsuga menziesii* (Mirb.)], Engelmann spruce [*Picea engelmannii* (Parry)], and limber and ponderosa pine [*Pinus flexilis* (James) and *P. ponderosa* (Lawson)]. Dominant herbaceous cover in forest openings and meadows included fescue [*Festuca arizonica* (Vasey) and *F. ovina* (L.)], peavine

**Table 1. Seed mixtures used during reclamation of the Southern Belle, Casino, and Frontier ski runs in 1984, 1985, and 1987–1988, respectively.**

Common Name	Scientific Name	Cultivar/Variety
Timothy	<i>Phleum pratense</i> L.	'Climax'
Sheep fescue	<i>Festuca ovina</i> L.	ns <sup>1</sup>
Canada bluegrass	<i>Poa compressa</i> L.	ns
Mountain brome	<i>Bromus marginatus</i> Nees.	'Bromar'
Small burnet	<i>Sanquisorba minor</i> Scop.	'Delar'
Hairy vetch	<i>Vicia villosa</i> Roth	ns
Birdsfoot trefoil	<i>Lotus corniculatus</i> L.	ns
Clover	<i>Trifolium hybridum</i> L.	'Alsike'
Wooly pod vetch	<i>Vicia dasycarpa</i> Ten.	'Lana vetch'

<sup>1</sup>Cultivar/variety not specified.

[*Lathyrus arizonicus* (Britton), sedges [*Carex bella* (Bailey) and *C. wootonii* (Mackenzie)], and mountain muhly [*Muhlenbergia montana* (Nutt.)].

The 3 other study sites (Casino, Frontier, and Meadows) occurred at higher elevations (3,000–3,100 m) in spruce-fir subalpine conifer forest dominated by Engelmann spruce, corkbark fir [*Abies lasiocarpa* var. *arizonica* (Merriam)], and bristlecone pine [*Pinus aristata* (Engelm.)]. Herbaceous cover in subalpine meadows and forest openings included brome [*Bromus richardsonii* (Link.)], sedges, peavine, avens [*Geum turbinatum* (Rydb.)], bluegrass and muttongrass [*Poa pratensis* (L.) and *P. fendleriana* (Steud.)], and muhly.

Southern Belle was reclaimed and seeded in 1984, Casino in 1985, Frontier in 1987 and 1988, and Meadows in 1993. An existing ski run, Tiger, was used as a control area for Casino. To the best of our knowledge, Tiger was never seeded and was used in the study because it was the only available control area for Casino. Seed mixtures used in each of these areas are summarized in Tables 1 and 2.

### Vegetation Measurements

Four measurement plots at each site were randomly established in reclaimed ski areas and adjacent or nearby unseeded control areas. Plots in reclaimed areas were placed near the center of ski runs. Control plots were established in adjacent or nearby nat-

ural or man-made openings, including a natural meadow (Southern Belle), natural forest openings (Meadows and Frontier), and a man-made unseeded ski run (Tiger). Areas where control plots were placed were generally similar in elevation, slope, aspect, and dimension (width) to reclaimed areas where plots were established (Table 3). Plots were located by initially establishing 4 parallel lines in both reclaimed and control areas, which were then subdivided to form 4 different rectangular quadrats. The upper right corner of each of four, 2 m<sup>2</sup> plots established in the grid was determined at random using both line number and position along parallel lines within each quadrat.

Vegetation data were collected using the point-intercept method (Mueller-Dombois and Ellenberg 1974). A point-intercept frame was placed at 20 cm intervals on both sides of the 2 m<sup>2</sup> plot centerline. Five points were measured along each frame placement by lowering guided pins and recording the plant species intercepted. When more than 1 species was intercepted, the species contributing most to the intercept was recorded. This technique yielded a total of 100 measurements per plot and allowed estimation of vegetative cover, plant species richness, and the proportion of native and non-native plants. Plants were identified to species in the field or later verified with herbarium specimens. All data were collected between 16 and 30 August 1996.

Data were analyzed for differences in

**Table 2. Seed mixture used during reclamation of the Meadows ski run in 1993.**

Common Name	Scientific Name	Cultivar/Variety
Slender wheatgrass	<i>Agropyron trachycaulum</i> Link	'Revenue'
Mountain brome	<i>Bromus marginatus</i> Nees.	'Bromar'
Timothy	<i>Phleum pratense</i> L.	'Climax'
Orchard grass	<i>Dactylis glomerata</i> L.	Pauite'
Sheep fescue	<i>Festuca ovina</i> L.	'Covar'
Hard fescue	<i>Festuca ovina</i> L.	'Durar'
Creeping red fescue	<i>Festuca rubra</i> L.	ns <sup>1</sup>
Canada bluegrass	<i>Poa compressa</i> L.	'Reubens'
Hairy vetch	<i>Vicia villosa</i> Roth	ns

**Table 3. Characteristics of reclaimed (seeded) ski runs and adjacent or nearby unseeded control areas where four, 2 m<sup>2</sup> plots were established and measured.**

Area	Elevation (m)	Aspect	Slope (%)	Width <sup>1</sup> (m)
<u>Southern Belle</u>				
Reclaimed	2,970–3,030	W/SW	22	45–60
Control	2,990–3,030	SW	20	80–230
<u>Casino</u>				
Reclaimed	3,140–3,250	NW	49	30–60
Control	3,000–3,140	NW	47	20–45
<u>Frontier</u>				
Reclaimed	3,390–3,415	W/NW	33	45–60
Control	3,405–3,415	W	44	100–150
<u>Meadows</u>				
Reclaimed	3,080–3,100	SW	24	25–35
Control	3,085–3,110	SW	24	35–110

<sup>1</sup>Estimated range of width of ski runs and adjacent or nearby control areas within which plots were established and measured.

vegetative cover and plant species richness, and differences in the proportion of native and non-native plants between reclaimed ski runs and adjacent or nearby unseeded control areas. Vegetative cover was estimated as the proportion of intercepts that contacted vegetation divided by the total number of possible intercepts (100), which included vegetation as well as bare ground, rock, and litter. Species richness was the total number of species recorded in each plot. For this analysis, native species were defined as those native to the San Francisco Peaks which were not found in the seed mixes. This distinction was made because it was not possible to determine the origin of species found in the field which were both native and which also occurred in the seed mix. These species were therefore conservatively included in the “non-native category”. Two other classes of non-native species were also recognized, non-natives not found in either seed mix (origin unknown) and non-natives found in one or both of the seed mixes (origin assumed to be from seed mix). The proportion of native species was expressed as the number of intercepts that contacted native vegetation divided by the total number of intercepts contacting vegetation, either native or non-native. The proportion of vegetative cover contributed by non-native species was calculated in the same fashion.

### Statistical Analyses

A randomized block experimental design was used in this study. Two-way analysis of variance was used to determine whether vegetative cover, plant species richness, and the proportions of native and non-native plants differed consistently between reclaimed and control plots across sites. Each of the 4 sites represent-

ed a block within which site conditions (elevation, slope, aspect, soils) and time since seeding of the treatment plots were relatively constant. At each site, 4 plots (replications) were measured in both the reclaimed and control areas. Data were analyzed for differences between “treatments” (reclaimed vs control) across sites and for overall differences among sites. All statistical analyses were performed using SAS (SAS Institute 1986). A Friedman rank test was used to verify results of parametric tests when there were significant ( $p \leq 0.05$ ) departures from normality (Neter et al. 1990).

When significant ( $p \leq 0.05$ ) differences were found among sites or treatment vs control plots, a Bonferroni or T-method test for multiple comparisons among pairs of means was used to determine differences among means (Sokal and Rohlf 1995, Neter et al. 1990). Because each site was seeded at a different time, data for each site were examined for trends through time.

The proportions of each type of non-native species in reclaimed and control

areas were analyzed separately using Wilcoxon Signed Rank tests for paired samples because of non-normally distributed data (Sokal and Rohlf 1995).

## Results and Discussion

### Vegetative Cover

Total vegetative cover was not significantly different between reclaimed and control areas. More recently reclaimed runs had less vegetative cover than runs with longer durations since seeding (Table 4). Southern Belle and Casino (seeded in 1984 and 1985, respectively) had significantly greater vegetative cover than Frontier and Meadows (seeded in 1987–88 and 1993, respectively), although cover was not significantly different between Southern Belle and Casino and between Frontier and Meadows.

Although an increase in vegetative cover over time was expected, these differences were not attributable to duration since seeding only. This was apparent because reclaimed areas with high vegetative cover also had high vegetative cover in associated control areas and vice versa, implicating other factors as well. Low vegetative cover at the Frontier site (seeded 9 years prior) may have resulted from high elevation, steep slopes, and a high degree of exposure to wind and direct sun. Lower vegetative cover at the Meadows site compared with the Southern Belle site, both of which occurred at similar elevations and had similar aspects and slopes, likely resulted from less time since seeding (Meadows was seeded 3 years prior, Southern Belle 12 years prior). Casino, the site with the highest vegetative cover, was seeded 11 years earlier and faces northwest, in the lee of prevailing southwest winter winds. Coupled with indirect winter sun, this allowed snow to accumulate

**Table 4. Mean vegetative cover in reclaimed (seeded) and adjacent or nearby unseeded control areas based on four, 2 m<sup>2</sup> plots site<sup>-1</sup> treatment<sup>-1</sup> (32 plots total).**

	Site			
	Southern Belle (12)	Casino (11)	Frontier (9)	Meadows (3)
(yrs since seeding)				
Reclaimed	0.78	0.91	0.49	0.50
Control	0.89	0.83	0.69	0.64
Combined <sup>1</sup>	0.83 <sup>A</sup>	0.87 <sup>A</sup>	0.55 <sup>B</sup>	0.57 <sup>B</sup>
ANOVA	df	MS	E	p
Sites	3	0.22	17.73	<0.001
Treatments	1	0.05	3.74	0.065
Interaction	3	0.02	1.75	0.18
Error	24	0.01	—	—

<sup>1</sup>T-method for multiple comparisons among means. Combined averages with same upper case letter within a row are not significantly different ( $p \leq 0.05$ ).

**Table 5. Mean species richness in reclaimed (seeded) and adjacent or nearby unseeded control areas based on four, 2 m<sup>2</sup> plots site<sup>-1</sup> treatment<sup>-1</sup> (32 plots total).**

	Site			
(yrs since seeding)	Southern Belle (12)	Casino (11)	Frontier (9)	Meadows (3)
Reclaimed <sup>1</sup>	4.0 <sup>a</sup>	9.8 <sup>a</sup>	5.5 <sup>a</sup>	5.3 <sup>a</sup>
Control	9.0 <sup>b</sup>	9.0 <sup>a</sup>	12.0 <sup>b</sup>	12.5 <sup>a</sup>
Combined	6.5	9.4	8.8	8.9
<b>ANOVA<sup>2</sup></b>	<b>df</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Sites	3	13.08	2.05	0.13
Treatments	1	16.20	25.33	<0.001
Interaction	3	26.25	4.10	0.0174
Error	24	6.40	—	—

<sup>1</sup>Significant differences between reclaimed and control plots within sites were tested using a Bonferroni multiple comparison procedure with a family confidence coefficient of 0.95.

Averages with the same lower case letters within a column are not significantly different ( $p \leq 0.05$ ).

<sup>2</sup>Data were non-normally distributed; results of the ANOVA were verified with a non-parametric Friedman rank test.

through the winter, making the site more mesic. Furthermore, surface disturbance during construction was much less severe than at any of the other sites, preserving the topsoil, seedbank, and microsites favorable for plant establishment.

## Plant Species Richness

Plant species richness was generally greater in control areas compared with reclaimed areas (Table 5). The total number of plant species was nearly 2-fold greater for control plots than plots in reclaimed areas over all sites studied. However, a significant interaction occurred between sites and treatments within sites, indicating that greater species richness in control areas was not consistent across all sites. At the Casino site, plots in the reclaimed area had similar richness as control plots. However, at the 3 remaining sites (Southern Belle, Frontier, Meadows), species richness was more than 2-fold greater for control plots as compared with reclaimed areas. No relationship could be found between duration since seeding, represented by different sites, and species richness.

Lower plant species richness in reclaimed areas at all sites except Casino was primarily attributable to lack of re-establishment of native species. Species composition consisted primarily of non-native, seed-mix species in reclaimed areas and native species in control areas. Greater species richness in reclaimed areas at Casino likely resulted from a number of factors, including site characteristics such as slope and aspect, and favorable soil moisture conditions. Perhaps the most important factor was the minimal amount of substrate disturbance that occurred during construction of this run, which likely

preserved the native seedbank and soil profiles. Overall, no clear pattern was found in relation to time since seeding, and it appeared that natural and manipulated site factors were of primary importance in determining species richness in revegetated areas.

## Distribution and Frequency of Native and Non-native Plants

As expected, the proportion of native species was greater in control areas and the proportion of non-native species was greater in reclaimed areas (Table 6). Across all sites studied, the proportion of native species was more than 3-fold greater in control areas compared with reclaimed areas. The proportion of non-native species was more than 5-fold greater in reclaimed compared with control areas. The interaction between sites and treatments within sites was significant, which indicated that differences in the proportion of native vs non-native species varied significantly among some

of the sites. At Casino, the proportion of native plants in control plots was about 27% higher than that in reseeded plots. In contrast, the proportion of native plants in control plots was from about 5-fold to nearly 20-fold higher than that of plots in reclaimed areas at the 3 other sites.

Some differences were found between reclaimed and control areas in the frequency of occurrence for different types of non-native species. There were no differences between reclaimed and control areas in the proportion of native species that were also found in one of the seed mixes (conservatively included as a “non-native” category, Wilcoxon sign rank,  $z = -0.91$ ,  $p = 0.18$ ) or in the proportion of species not indigenous to the study area and also not found in the seed mixes (origin unknown, Wilcoxon sign rank,  $z = -0.55$ ,  $p = 0.71$ ). However, species not native to the San Francisco Peaks that were found in one or both of the seed mixes made up a significantly higher proportion of the vegetation in reclaimed areas compared with control areas (Wilcoxon sign rank,  $z = -1.64$ ,  $p = 0.05$ ). At control areas, these species were found only at the Casino site, where they made up slightly more than 2% of the vegetative cover. These species were not recorded at the 3 other sites. Of the 3 categories of non-native species analyzed, only the presence of this category of species could be reliably attributed to prior seeding.

No relationship between time since seeding and the proportion of native and non-native species was apparent. In reclaimed areas, the greatest proportion of the vegetative cover contributed by native species occurred at Casino (seeded in 1985), followed by Meadows (seeded in 1993), Southern Belle (seeded in 1984), and Frontier (seeded in 1987–88) (Table

**Table 6. Mean proportion of native species out of all intercepts contacting vegetation (native and non-native species) within plots in reclaimed (seeded) and unseeded control areas, based on four, 2 m<sup>2</sup> plots site<sup>-1</sup> treatment<sup>-1</sup> (32 plots total).**

	Site			
(yrs since seeding)	Southern Belle (12)	Casino (11)	Frontier (9)	Meadows (3)
Reclaimed <sup>1</sup>	0.09 <sup>a</sup>	0.74 <sup>a</sup>	0.06 <sup>a</sup>	0.14 <sup>a</sup>
Control	0.96 <sup>b</sup>	0.95 <sup>b</sup>	0.90 <sup>b</sup>	0.68 <sup>b</sup>
Combined <sup>2</sup>	0.52 <sup>B</sup>	0.85 <sup>A</sup>	0.48 <sup>B</sup>	0.41 <sup>B</sup>
<b>ANOVA</b>	<b>df</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Sites	3	0.30	29.18	<0.001
Treatments	1	3.038	295.38	<<0.001
Interaction	3	0.20	18.97	<<0.001
Error	24	0.0103	—	—

<sup>1</sup>Significant differences between reclaimed and control plots within sites were tested using a Bonferroni multiple comparison procedure with a family confidence coefficient of 0.95. Averages with the same lower case letters within a column (first 2 rows only) are not significant at  $p \leq 0.05$ .

<sup>2</sup>T-method for multiple comparisons among means. Combined averages with same upper case letter (within the row) are not significantly different ( $p \leq 0.05$ ).

6). The opposite relationship held for non-native species.

These data suggest neither re-establishment of native species on ski runs over time, nor invasion of adjacent unseeded areas by non-native species occurred. At Frontier, Meadows, and Southern Belle, plant species composition was very distinct between the reclaimed areas, which supported primarily non-native species, and control areas, which supported an entirely native plant community. Differences in plant species composition were less distinct between reclaimed and control plots at the Casino site. This result was likely due to minimal initial disturbance, which preserved soil conditions, microsites, and a predominantly native seedbank.

Similar results have been obtained by other researchers. An assessment of 4 ski areas in Colorado showed that ski slopes were covered with seeded species and largely devoid of indigenous species. There was also no indication that the seeded species were invading adjacent undisturbed habitats (Redner, N., unpublished monitoring report. USDA For. Serv., Silverthorne, Colo., 13 September 1994). Curtin (1995) concluded that disturbed subalpine plant communities in Colorado remained distinct in species composition, richness, and cover from surrounding undisturbed areas for hundreds of years. Disturbed sites, some abandoned over 100 years ago, were still covered with monotypic stands of exotic grasses and weedy species. In the Cascades in Oregon, Dyrness (1973) found that logged and lightly burned sites regained dominance by predisturbance native plants within 5 years, while severely burned sites continued to be dominated by invasive species. Since native plant regeneration after disturbance occurs primarily through germination of buried seeds and vegetative propagation (Whittle et al. 1997), protection of seed banks and minimized surface disturbance during construction activities should promote the conservation of native plant communities.

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## Book Reviews

**Warming the World: Economic Models of Global Warming.** By William D. Nordhaus and Joseph Boyer. 2000. MIT Press, Cambridge, MA, and London, England. 232 p. US\$35.00 hardback. ISBN 0-262-14071-3.

By means of a number of interventions such as the atmospheric emission of carbon dioxide, the use of ozone depleting chemicals, and the destruction of natural habitat, humans are having a perceptible and largely negative impact on the natural environment. Indeed, climatologists and other scientists have repeatedly warned us that “the accumulations of carbon dioxide and other greenhouse gases (GHGs) are likely to lead to global warming and other significant climatic changes over the next century” (p. 3). How serious is the problem of global warming? If it is a serious problem, what should we do about it? Finally, how does the presence of fundamental uncertainty affect what we do and when we do it? This book sheds light on these sorts of questions.

The authors are economists and this book is a culmination of their research efforts on the economics of global warming. As the authors see it, the problem of climate change is a problem of investing under uncertainty. In this way of looking at global warming, the problem is essentially this: Should we take costly steps now to slow emissions of GHGs, in the process reducing the amount of output available for consumption and productive investment now, to (hopefully) get lower damages and higher consumption in the future? The authors use a Dynamic Integrated model of Climate and the Economy (DICE) and a Regional dynamic Integrated model of Climate and the Economy (RICE) to address the many and varied facets of this question.

Chapter 2 describes the RICE model. The authors note that this model is “an extension of the Ramsey model to include climate investments in the environment” (p. 10). A key aspect of the RICE model is that except in exchange for carbon emissions permits, there is no international trade in capital or goods. Further, by way of a carbon cycle, a radiative forcing equation, and climate change equations, the RICE model explicitly accounts for salient geophysical relationships that connect the various factors affecting climate change. One question that comes up in this kind of model relates to the uncertainty about total factor productivity (TFP) in the future. Does TFP grow over time and, if so, how does it grow? As the authors helpfully explain, in the RICE model, “TFP growth is assumed to slow gradually over the next three centuries until eventually stopping” (p. 17).

Chapter 3 concentrates on the calibration of the principal sectors in the RICE model. A novel feature of the present version of the RICE model is that the production process is revised and energy use is incorporated into the model by defining an aggregate called “carbon energy.” This aggregation permits the authors to work with a single energy input and it also allows them to treat all non-carbon fuels as amalgamations of capital and labor. Although the RICE model and the description of this model are generally complete, 2 aspects of the model receive insufficient attention from the authors. First, how do we explicitly model the uncertainties associated with the future values of things like rates of return on capital and per capita output in developing and transition economies? Second, what are some of the alternatives to assuming the exogeneity of GHG gases other than CO<sub>2</sub> and aerosols?

Chapter 5 uses the RICE model to provide a nice description of

the economic impacts of climate change. With respect to the United States, a central finding of the authors is that more “than 90 percent of the economy...is not likely to be significantly affected by climate change” (p. 77). More generally, the analysis shows that “Europe, India, and many low-income regions...appear vulnerable to significant damages over the next century” (p. 96), whereas the “United States appears to be less vulnerable to climate change than many countries” (p. 96). Although these results are instructive, it should be noted that they are based on rather “rough estimates” of the ecosystem impacts of climate change.

In Chapter 7, the authors use the RICE and the DICE models to investigate the relative efficiency of alternate policies to the climate change problem. It is noted that the “major region to gain from climate policies is OECD Europe, which benefits from all the policies, even the ones that have high global costs” (p. 131). What are the net impacts of implementing a geoengineering option that offsets global warming at little or no cost? This salient and largely unexplored question receives some attention in this chapter. After showing that the major benefits from geoengineering accrue to OECD Europe, the authors rightly observe that the “difference between the geoengineering results and the results for the other policies is so dramatic that it suggests that geoengineering should be more carefully studied” (p. 132). How does a policy that delays taking action on the global warming problem compare with a policy that acts immediately? In response to this question, the authors show that “the loss from waiting and gathering more information is relatively small, assuming that action is appropriately taken in the future” (p. 127). The authors should have noted that this finding nicely complements the “value of waiting to invest” result in the theoretical investment under uncertainty literature (see the book *Investment Under Uncertainty* by A.K. Dixit and R.S. Pindyck and the paper by A.A. Batabyal in the *Journal of Environmental Management*, Vol. 59, pp. 195–203, 2000).

An insightful economic analysis of the Kyoto protocol is provided in Chapter 8. This discerning analysis leads to 2 noteworthy conclusions. First, the authors bluntly point out that “the strategy behind the Kyoto protocol has no grounding in economics or environmental policy” (p. 167). Second, it is noted that “the United States is a net loser while the rest of the world on balance benefits from the Kyoto protocol” (p. 168). Now, the efficacy of a policy is clearly related to the difficulties encountered in implementing it. Indeed, high implementation costs can “kill” an otherwise meaningful policy. As such, this chapter would have been better had the authors paid more attention to implementation issues generally and to implementation costs in particular.

Although one can quibble with specific parts of the analysis contained in it, for the most part, this is a perspicacious book. It nicely shows how the investment under uncertainty approach can shed light on a number of important and complex questions related to the phenomenon of global warming. One noteworthy feature of this book is that it is quite honest about the constraints imposed on the analysis by the presence of fundamental uncertainty about the climate change problem. Given these qualities, it seems apposite to conclude by noting that in general this book is worth your time and your money.—Amitrajeet A. Batabyal, Rochester Institute of Technology, Rochester, New York.

**Tropical Forage Plants: Development and Use.** Edited by Antonio Sotomayor-Rios and W. D. Pitman, with 23 text contributors. 2001. CRC Press, Boca Raton, Florida. 391 p. US\$129.95 hardback (US\$84.95 textbook price). ISBN 0-8493-2318-5.

The 19 chapters of this multi-authored book attempt to present the current state of knowledge about tropical forage plants, particularly in the Western Hemisphere. The flavor of *Tropical Forage Plants* is more agronomic than many range management scientists and range managers might prefer, but these individuals too will find it an interesting statement of current directions in tropical forage research.

Emphasis of the book is equally split between development and use. Section 1, consisting of Chapters 1 and 2, provides an introduction to the tropical environment. Chapter 1 is a brief, generic description of the land resources of the tropics, examining broad soil types and moisture relations. Chapter 2 revisits essentially, and just as briefly, the same tropical turf, considering the same low-latitude factors, this time as constraints to forage plant adaptation and productivity. Collectively, this introductory section is, broadly speaking, not that strong, and is not a particularly inspired sendoff into the intricacies of forage development that follow.

The 6 chapters of Section 2 focus on the development of tropical forages. Chapters 3 and 4 examine the germplasm resources of tropical grasses and legumes, respectively. In each of these chapters, the authors introduce the respective families, and summarize the important species in each, emphasizing their adaptations, values and other traits. Chapters 5 and 6 examine the breeding of tropical forage grasses and legumes, respectively, focusing on particularly important genera. Chapter 7 considers the constraints to tropical forage grass development, and includes discussions of forage quality, palatability, seed viability, and disease resistance, using examples of important species.

Chapter 8 is a lengthy chapter on biotechnology in tropical forage crops. This chapter, which those with more managerial interests may find uncomfortably technical, promises to get even longer and more technical in future books. With every university administrator in the country scrambling to foster lucrative biotechnology research, I was assured that jargon, as well as biotechnology, has a bright academic future. This chapter also assured me that the seminar announcements and poster papers that decorate the walls outside my office in our agriculture building will become even less comprehensible than they are now.

Section 3, *The Use of Tropical Forages*, is generally more managerial in flavor, and includes 8 chapters, many of which are by Latin American authors and emphasize aspects of forages in the tropical zone of the Western Hemisphere. Included are chapters on seed production technology, intensive management of forage grasses, pennisetums and sorghums in an integrated feeding system, effects of arthropods, diseases and nematodes, animal production in grass-legume pastures, conservation of forages, and symbiotic nitrogen fixation.

Chapter 16, the final chapter of Section 3, entitled *Contributions of Rangelands to Animal Production in the Tropics*, provides an interestingly agronomic view of rangelands, based mostly on examples from Australia and South America. With population pressures driving demands for more forage production in many parts of the tropics, the discussions in this chapter inevitably turn to introduced forage crops, fertilization, and other examples of intensive agriculture. Even the discussions of low-input strategies here involve introduced, productive cultivars, and these strategies are seem of interest only on the lowest value,

e.g., saline, rangelands. The author discusses the need to develop sustainable management strategies for tropical rangelands that consider water supply and soil nutrients, but introduced plant species are considered possible solutions, and the philosophy here is more intensive, integrated management for sustainable, year-long production than yearlong management of natural systems for productive conservation. The ever-increasing demands of proliferating humanity have compelled some forage scientists to seek *sustainability*, whatever its merits, as a kind of push-it-to-the-limit compromise, somewhere between old-style *conservation* and *exploitation*.

A *Global Review of the Latest Research on Tropical Forages* is the subject of the 3 chapters of Section 4. The 3 chapters examine research in Australia, Africa, and Asia and the Americas, respectively; the first 2 provide detailed coverage of their respective continents, while the third is a shorter, more philosophical closing discussion of the relevancy of general approaches, their sustainability, and their role in the stability of tropical lands.

*Tropical Forage Plants* has extensive lists of cited literature at the end of each chapter, and a detailed general index follows the final chapter. The book contains one page of black-and-white photographs, a map or 2, and some figures and tables. Overall readability for the nonspecialist is fair to good, except possibly for Chapter 8 on biotechnology. The book is, in many respects, a typical collection of specialized contributions, like many that have been published on forages over the years, only now with somewhat increased emphasis on sustainability and integrated, albeit intensified, production. I have in the past been critical of some forage books as containing the same old stuff, and even though much of *Tropical Forage Plants* seems familiar, Chapter 8 and its promise of well-funded, philosophically questionable, futuristic tinkering almost had me wishing I could see just the same old stuff, just one more time.—David L. Scarnecchia, Washington State University, Pullman, Washington.