Journal of Range Management


The Trail Boss

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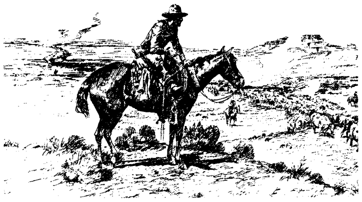

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—to develop an understanding of range ecosystems and of the principles applicable to the management of range resources;

—to assist all who work with range resources to keep abreast of new findings and techniques in the science and art of range management;

—to improve the effectiveness of range management to obtain from range resources the products and values necessary for man's welfare;

—to create a public appreciation of the economic and social benefits to be obtained from the range environment;

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Remote sensing for cover change assessment in southeast Arizona

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Abstract

Understanding landscape conversion is vital for assessing the impacts of ecological and anthropogenic disturbances at regional and global scales. Since rangelands cover nearly half of the global land surface, and because a large part of rangelands is located in semi-arid ecosystems, they serve as critical land cover types for determining regional biodiversity, global biogeochemical cycles, and energy and gas fluxes. For such vast ecosystems, satellite imagery is often used to inventory biophysical materials and man-made features on Earth's surface. The large area coverage and frequent acquisition cycle of remotely sensed satellite images make earth observation data useful for monitoring land conversion rates at different spatial scales. Remote sensing could also be used for temporal assessment of semi-arid ecosystems by providing complimentary sets of rangeland health indicators. In this paper, temporal satellite data from multiple sensors were examined to quantify land use and land cover change, and to relate spatial configuration and composition to landscape structure and pattern. The findings were correlated with the role of fire to better understand ecological functionality and human and/or natural activities that are generating environmental stressors in a rapidly developing, semi-urban census division located in southeastern Arizona. Results indicate that conversion of a fire-suppressed native grassland area has 2 spatial components; in the rural areas, grass is being eliminated by increasingly homogeneous shrub and mesquite-dominated areas, whereas in the urban and suburban areas, grass as well shrubs and mesquite are being eliminated by a fragmented and expanding built landscape.

Key Words: land conversion, landscape indices, fire suppression, rangeland maintenance, semi-arid, grasslands

Resumen

La conversión del paisaje que entiende es vital para evaluar los impactos de disturbios ecológicos y humanos en las escalas regionales y globales. Desde las praderas cubra casi la mitad de la superficie global de la pista, y porque una parte grande de praderas está situada en los ecosistemas semiáridos, sirven como tipos críticos de la cubierta de pista para determinar biodiversitad regional, ciclos biogeoquímicos globales, y flux de la energía y del gas. Para tales ecosistemas extensos, las imágenes basadas en los satélites se utilizan a menudo para inventariar los materiales biofísicos y las características artificiales en la superficie de la tierra. La cobertura grande del área y el ciclo frecuente de la adquisición de imágenes basadas en los satélites remotamente detectadas hacen datos de la observación de la tierra útiles para vigilar índices de conversión de la pista en diversas escalas espaciales. La detección alejada se podía también utilizar para el gravamen temporal de los ecosistemas semiáridos proporcionando a conjuntos elogiosos de indicadores de la salud de las praderas. En estos datos basados en los satélites de papel, temporales de los sensores múltiples fueron examinados para cuantificar el cambio de la utilización del suelo y de la cubierta de pista, y para relacionar la configuración y la composición espaciales con la estructura y el modelo del paisaje. Los resultados fueron correlacionados con el papel del fuego para entender mejor funciones ecológicas y las actividades humanas y/o naturales que están generando las tensiones ambientales en rápidamente convertirse, división semi-urbana del censo localizaron en el Arizona del sudeste. Los resultados indican que la conversión de un área nativa fuego-suprimida del prado tiene dos componentes espaciales; en las áreas rurales, la hierba está siendo eliminada por el arbusto cada vez más homogéneo y las áreas mesquite-dominadas, mientras que en las áreas urbanas y suburbanas, se chiban también arbustos y el mesquite está siendo eliminado por un paisaje construido hecho fragmentos y que se amplía.

Land cover change may be the most significant agent of global change; it has an important influence on hydrology, climate, and global biogeochemical cycles (Skole et al. 1997). Characterizing the forcing factors that drive changes in landscapes, and the resultant impacts on biogeochemical and hydrological cycles and energy and gas fluxes, is essential to understand the total Earth system and the effects of natural and human-induced changes on the global environment. Further, assessment of environmental responses to drivers of changes in land cover and land use, particularly in parts of the world that are currently undergoing the most stress, such as semi-arid rangelands, is an important function (Nemani et al. 1996). The benefits of such assessments include understanding the consequences of land cover and land use changes as they impact ecological processes, and evaluating which human activities contribute to changes occurring on the landscape.

Remotely sensed data are inherently suited to provide information on land cover characteristics related to ecological and dynamic aspects of developed regions at various spatial and temporal scales (Ridd 1995). However, few studies have looked at how remote sensing may be utilized to develop complimentary indicators for determining rangeland conditions. Recently, a con-

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sensus has been developing that environmental analysis requires a set of complementary indicators for a complete study of the causes and threats to ecological systems and for their protection and restoration (U.S. EPA 1997, 1999). Landscape indices quantify aspects of spatial pattern that can be correlated with ecological processes (O'Neill et al. 1988). In this context, numerous mathematical indices have been developed that allow the objective description of different aspects of landscape structure, function, and change. While traditionally satellite data were used to address questions concerning vegetation types and amounts, this paper asked a different question: How can satellite data be used to assess land conversion and cover change, study spatial configuration and composition of landscape elements, and, hence, assist in understanding the ecological integrity of a semi-arid grassland ecosystem?

The paper's main objective is to evaluate rangeland conditions through remotely sensed imagery in a census division that is undergoing rapid urban and suburban development. The utility of remote sensing as an ecological assessment tool will be determined by examining not only land use land cover change, but also the spatial arrangement and complexity of cover types in a semi-arid rangeland ecosystem. Finally, an assessment of changes correlates satellite findings with effects of fire suppression. The assessment is conducted for aiding in the development of sustainable land use practices, successful regional planning, and effective policy implementation.

Materials and Methods

Study Area

The formerly rural Sierra Vista (31.6 N, 110.3 W) census division is a thriving community of 55,000 that serves as the regional urban center for southeastern Arizona (Figs. 1 and 2). Located approximately 120 kilometers southeast of Tucson, Ariz., the city is surrounded by the Huachuca, Dragoon, and Mule Mountains, and is bordered on the east by the San Pedro River. Changes in land management techniques such as increased grazing intensity and frequency due to diminishing pastureland, coupled with tremendous urban growth have altered the vegetation patterns and dynamics in the San Pedro River basin (Qi et al. 2000). In the last 30 years, the Sierra Vista census division has experienced a sizable increase

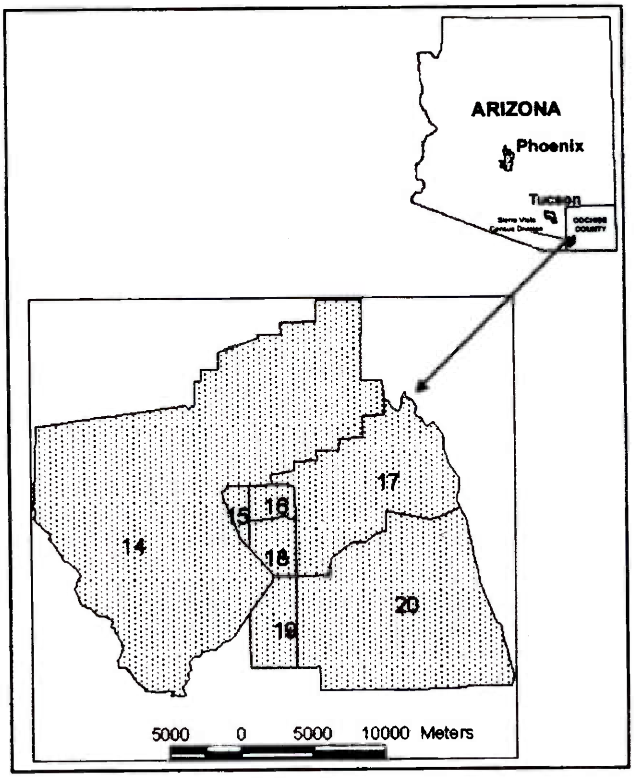


Fig. 1. Study site: Sierra Vista census division (census tracts 14–20), southeastern Arizona.

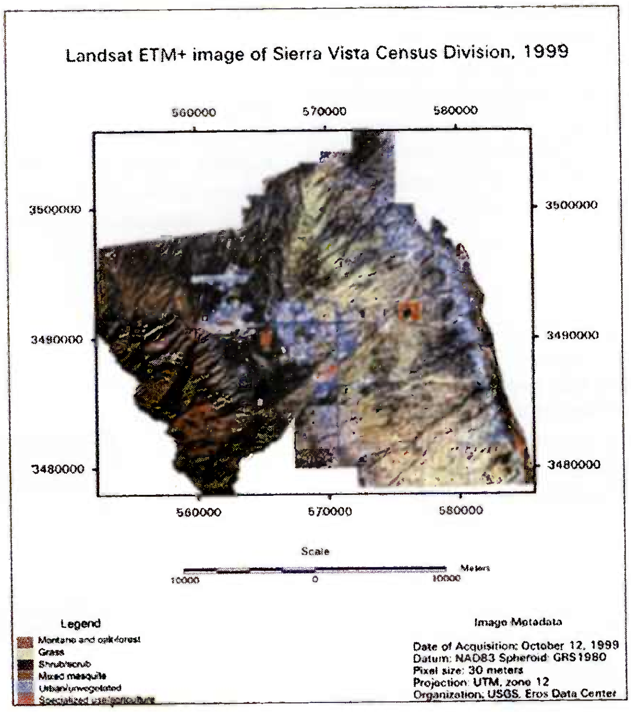


Fig. 2. Landsat ETM+ 4,3,2 composite image and metadata of Sierra Vista census division, 1999.

Table 1. Land cover area totals and temporal assessment of land cover change, selected years.

R: Rural U: Urban	Land cover area totals 1973	 1985	 1999	Temporal assessment of land cover change 1973–1985 Net Gain/ Loss	 1973–1985 Gain/Loss	 1985–1999 Net Gain/ Loss	 1985–1999 Gain/Loss	 1973–1999 Net Gain/ Loss	 1973–1999 Gain/Loss
	------------------	(ha)	------------------	(ha)	(%)	(ha)	(%)	(ha)	(%)
R: Grass	3493	2679	1882	–814	–23%	–797	–30%	–1611	–46%
R: Shrub/scrub	7765	8194	8311	429	6%	117	1%	546	7%
R: Mixed Mesquite	3040	3241	3652	201	7%	411	13%	612	20%
R: Urban/unvegetated	1377	1562	1787	185	13%	225	14%	410	30%
R: Agr./Specialized	112	114	164	2	2%	50	44%	52	46%
R: Water/Clouds	74	71	64	–3	–4%	–6	–8%	–9	–12%
U: Grass	7541	6340	6150	–1201	–16%	–190	–3%	–1391	–18%
U: Shrub/scrub	9141	8908	8714	–233	–3%	–194	–2%	–427	–5%
U: Mixed Mesquite	4709	4542	4470	–167	–4%	–72	–2%	–239	–5%
U: Urban/unvegetated	3347	4531	5146	1184	35%	615	14%	1799	54%
U: Agr./Specialized	115	484	386	369	321%	–98	–20%	271	236%
U: Water / Clouds	85	133	72	48	56%	–61	–46%	–13	–15%
Total: Grass	11034	9019	8032	–2015	–18%	–987	–11%	–3002	–27%
Total: Shrubscrub	16906	17102	17025	196	1%	–77	0%	119	1%
Total: Mixed Mesquite	7749	7783	8122	34	0%	339	4%	373	5%
Total: Urban/unveg.	4724	6093	6933	1369	29%	840	14%	2209	47%
Total: Agr./Specialized	227	598	550	371	163%	–48	–8%	323	142%
Total: Water/Clouds	159	204	137	45	28%	–67	–33%	–22	–14%

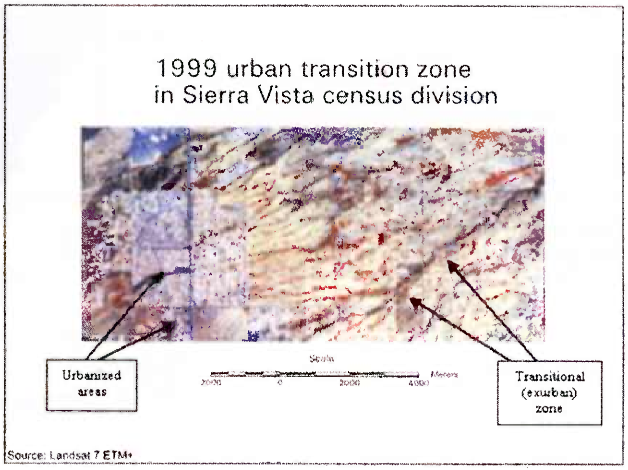
in developed land due mostly to its increasing regional importance and popularity as a retirement spot. According to satellite data, in the period between 1973 and 1999, the total area of developed land rose from 4,724 ha to 6,933 ha—a 47% increase (Table 1). Most of the new urban growth took place over areas of native, perennial grasslands in the San Pedro River basin located in the southeastern quadrant of the census division. These transitional zones are characterized by unpaved roads, new utility corridors, and substantial residential development in the southeastern quadrant of the 1999 image (Fig. 3).

Data Sources

As typically is the case with most long-term, multi-temporal land use and land cover studies, this paper utilized satellite images from different sensors (Landsat 1 Multispectral Scanner (MSS), Landsat 5 Thematic Mapper (TM), and Landsat 7 Enhanced Thematic Matter (ETM+)) at various scales and resolutions for assessing land use and land cover change. The images were acquired during the growing season and their acquisition was relatively close to the maximum green-up time in the region (usually late August through early October). The dates of acquisition were 5 Sep. 1973 (MSS), 30 Sep. 1985 (TM), and 12 Oct. 1999 (ETM+). All the imagery was acquired from the Arizona Regional Image Archive. A political boundary coverage consisting of 7 census tracts comprising the Sierra Vista census division was used as the study area mask. The coverage was obtained from the USGS National Biological Information Infrastructure.

Image Processing

To remove the effects of atmospheric scattering from the images, Chavez's improved dark object subtraction (Chavez 1988) was utilized for the 1973 MSS image. For the 1985 TM and 1999 ETM+ images, a location-specific correction method, called the refined empirical line (Moran et al. 2001), was used for atmospheric correction. To correct the inherent geometric distortion, all images were resampled to 1973 MSS ground resolution, projected to the Universal Transverse Mercator projection, and the 1973 and 1985 images were co-registered to the orthorectified 1999 image with acceptable root mean square error of less than 0.05 pixel. Resampling and image-to-image registration was necessary for temporal assessments of land cover change and landscape indices. To reduce image noise and improve visual interpretability, images were modified using a 3-by-3 low-pass local-average spatial filter before classification.



Source: Landsat 7 ETM+

Fig. 3. 1999 urban transition zone in Sierra Vista census division.

Image Classification

A multispectral classification was performed using the supervised algorithm approach with maximum likelihood parametric decision rule. Known a priori land cover types were identified by combination of previously published vegetation maps, fieldwork data, recent personal field observations (utilized for the 1999 image classification), and personal interviews with U.S. Department of Agriculture personnel with over 30 years of classification experience in the region. The selected sites in the remotely sensed data represented homogeneous examples of these known land cover types. Before the supervised classification algorithm was applied to the images, image data were merged with topographic information. A mosaicked 7.5-minute 1990 USGS digital elevation model with 30-meter contour interval was registered to the images to remove montane forest and oak woodland areas in the Huachuca Mountain region. Species that have very similar spectral characteristics (e.g., velvet mesquite (*Prosopis velutina* Woot.), oaks (*Quercus* L.), quaking aspen (*Populus tremuloides* Michx.), and evergreens) occupy quite different elevation ranges. The majority of the Upper Sonoran life zone species such as oaks, Mexican pinyon pine (*Pinus cembroide*s Zucc.), juniper (*Juniperus* L.), as well as transition life zone species such as open ponderosa pine (*Pinus ponderosa* P.& C. Lawson), characteristically found in elevations of 1,800 meters (6,000 feet) and higher, were removed since grasslands, shrubs, and mesquite do not correspond to this elevation range. Use of ancillary elevation data thus aided in delineating the habitats and various associations between land cover characteristics associated with most anthropogenic disturbances. A 3-by-3 majority filter was applied for post-classification smoothing in order to reduce the pixel-by-pixel spectral variability encountered by the classifier. Finally, the classification results were labeled based on the resource-oriented USGS Land Use/Land Cover Classification System Level I (Anderson et al. 1976).

Classification accuracy assessment of land use/land cover maps required comparison of 2 sources of information: (1) the imagery-derived classification data, and (2) reference data (ground truth). As a broad guideline, 50 ground points were selected outside of training areas using systematic random sampling and field-checked for each land cover category included in the classifications. Accuracy results for the 1973, 1985, and 1999 classifications are listed in Table 2. Producer's accuracy (measures errors of omission, e.g., 8 pixels that should have been classified as "grass" were omitted in 1973 in Table 2), users' accuracy (measures errors of commission, e.g., 10 pixels were improperly included in the "grass" category in 1973 in Table 2), overall accuracy (percent of pixels correctly classified), and the Kappa statistic (percent of how much a given classification is better than a classification resulting from chance) for the 3 images were all above 80 percent. Satellite and classified images for 1973, 1985, and 1999 are displayed in Figures 4, 5, and 6, respectively.

Table 2. Accuracy assessments for 1973, 1985, and 1999 supervised maximum likelihood classifications.

Year	Producer's Accuracy	User's Accuracy
1973		
	Grass (42/50) = 84%	Grass (42/52) = 81%
	Shrub (41/50) = 82%	Shrub (41/53)= 77%
	Mesquite (45/50) = 90%	Mesquite (45/58) = 78%
	Urban/unveg. (45/50) = 90%	Urban/unveg. (45/47) = 96%
	Agriculture (38/50) = 80%	Agriculture (38/40) = 95%
	Water (50/50) = 100%	Water (50/50) = 100%
	Overall Accuracy:	84%
	KHAT-statistic:	81%
1985		
	Grass (43/50) = 86%	Grass (43/48) = 90%
	Shrub (44/50) = 88%	Shrub (44/56)= 79%
	Mesquite (42/50) = 84%	Mesquite (42/50) = 84%
	Urban/unveg. (45/50) = 90%	Urban/unveg. (42/49) = 96%
	Agriculture (42/50) = 84%	Agriculture (42/49) = 86%
	Water (50/50) = 100%	Water (50/50) = 100%
	Overall Accuracy:	86%
	KHAT-statistic:	83%
1999		
	Grass (44/50) = 88%	Grass (44/52) = 85%
	Shrub (42/50) = 84%	Shrub (42/52) = 81%
	Mesquite (43/50) = 86%	Mesquite (43/57) = 75%
	Urban/unveg. (39/50) = 78%	Urban/unveg. (39/43) = 91%
	Agriculture (43/50) =86%	Agriculture (43/46) = 93%
	Water (50/50) = 100%	Water (50/50) = 100%
	Overall Accuracy:	84%
	KHAT-statistic:	81%

Landscape Indices

For complete ecological assessments of managed ecosystems, there is a need to quantify aspects of spatial configuration and composition that can be correlated with other ecological processes such as land use/land cover change and the role of fire. To that end, satellite images offer another unique facility for observing and documenting landscape structure, function, and change. There is a wide variety of landscape metrics and many software programs to calculate them (O'Neill et al. 1988, Turner and Gardner 1991). Many of these metrics have been shown to be highly correlated with one another (Riiters et al. 1995). In a factor analysis study, Riiters et al. (1995) analyzed 55 landscape metrics for their statistical independence. They concluded that the information contained in the 55 metrics could be narrowed down to 5 metrics. These metrics have also been proposed for implementation as watershed integrity indicators, landscape stability and resilience indicators, and biotic integrity and diversity indicators (U.S. EPA 1997). The metrics include patch density, edge density, Shannon's Diversity Index, Interspersion and Juxtaposition Index, and Contagion. These indices were derived directly from the classified images using the FRAGSTATS software (McGarigal and Marks 1995). However, because the Patch Density, Edge Density, and Shannon's Diversity Index are dependent on the size of the smallest spatial unit mapped and the number of different categories distinguished, the 1973 classified image was resampled to the spatial resolution of 1985 and 1999 images, i.e., 30 meters. Shannon's Diversity Index, a structural measure of the area distribution of classes, did not display any variation due to census division's large area extent, and was not interpreted. In addition, the census division was partitioned into rural and urban zones based on census tract population statistics before landscape metrics were calculated for improved interpretation of different land use patterns and associated spatial structures. The U.S.

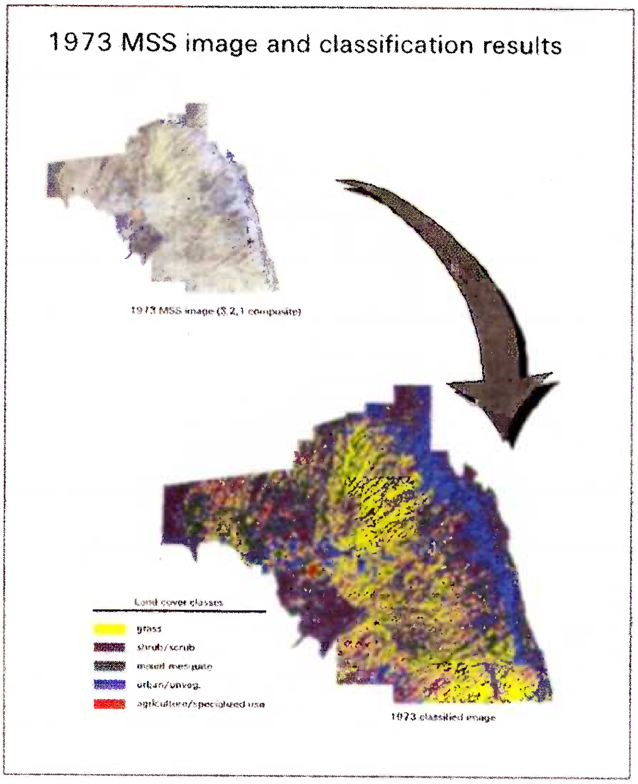


Fig. 4. 1973 MSS image and classification results.

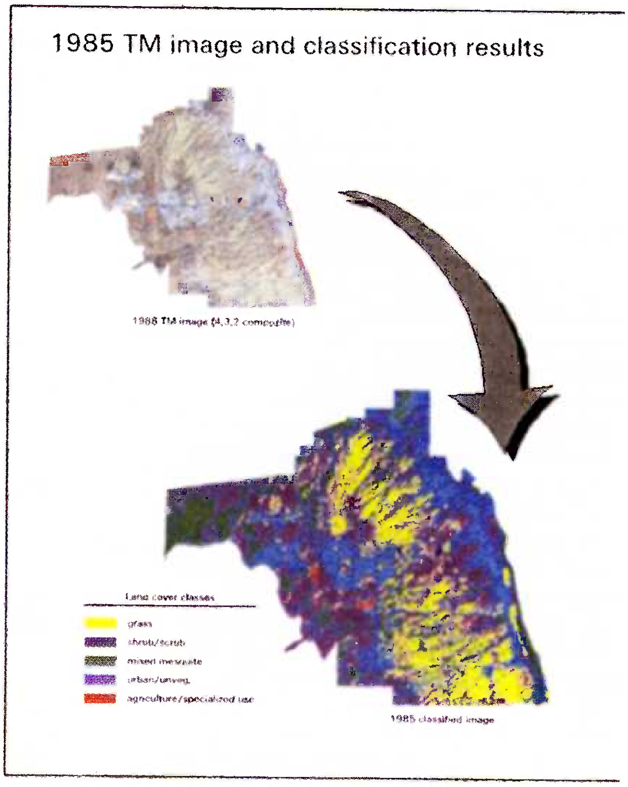


Fig. 5. 1985 TM image and classification results.

Census Bureau defines a rural area as one that is not urban (U.S. Department of Commerce 1992). "Urban" is defined as either an urbanized area or places with populations of 2,500 or more outside urbanized areas. An urbanized area includes places and their adjacent densely settled surrounding territory that together have a minimum population of 50,000 (U. S. Department of Commerce 1992). Two regions of census tracts meeting the defined criteria for urban and rural areas of the census division were selected from the imagery (Fig. 7). Descriptions of the metrics, how to interpret their value, and outputs are listed in Table 3. The reader may refer to McGrigal and Marks (1995) for a more complete assessment of landscape metrics.

Results and Discussion

Land Cover Changes

The expected general model for the land cover classes should describe a strong differentiation between each class. Specifically, urban/unvegetated cover in the urban sector should substantially increase, and shrub and mesquite covers should replace grass cover in rural areas. Land cover area totals derived from the 1973, 1985, and 1999 classified imagery clearly reveal endemic changes unique to rural and urban landscapes of the census division. Table 1 and Figure 8 reveal substantial loss of grass cover in both rural and urban sectors of the census division. Between 1973 and 1999, net loss of grass cover for rural zones was 46%, and of the 1,611 grassland ha converted in rural areas, 65% was replaced by shrub and mesquite. During the same time, urban zones experienced an 18 and 5% net loss in grass and shrub/mesquite, respectively, and 69% of this loss was converted to urban/unvegetated land cover. These results clearly suggest different land use mechanisms, and drivers of land cover change for rural and urban areas of the census division. Although loss of grass cover is significant in both sectors, shrub and mesquite invasion is apparent in the rural areas, whereas built areas in the urban sector replaced grass as well as shrub and mesquite. Both of these land use mechanisms of conversion result in habitat degradation on native grasslands.

Table 3. Outputs and descriptions of landscape metrics.

		PD	ED	IJI	Contagion
				(%)	(%)
1973 (30m)	Rural	35.3	128.6	51.2	39.8
	Urban	35.6	133.4	61.5	41.3
	Total	33.6	128.0	56.7	40.4
1985	Rural	81.7	184.5	46.9	42.1
	Urban	87.1	189.5	65.7	37.4
	Total	82.2	186.7	57.5	39.3
1999	Rural	128.3	229.3	43.0	46.0
	Urban	170.1	260.2	69.2	31.2
	Total	145.8	242.7	59.2	36.1

PD: Patch Density - expresses the number of patches within the entire reference unit on a per area basis (100 ha).
ED: Edge Density - length of all borders between different classes in a reference area divided by the total area of the reference unit (100 ha).
IJI: Interspersion and Juxtaposition Index - analyzes the adjacency of each patch with all other patch types, and measures the extent to which classes are interspersed.
Contagion: measures the extent to which classes are aggregated or clumped.

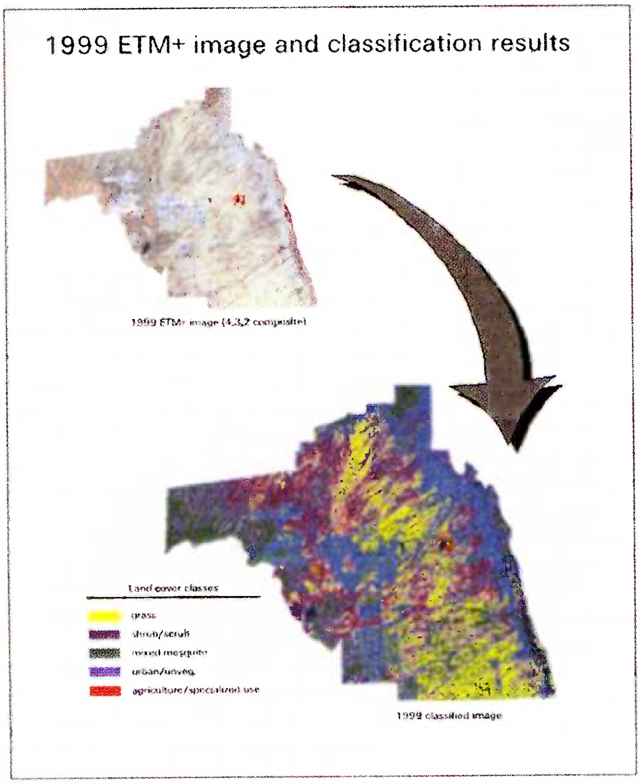


Fig. 6. 1999 ETM+ image and classification results.

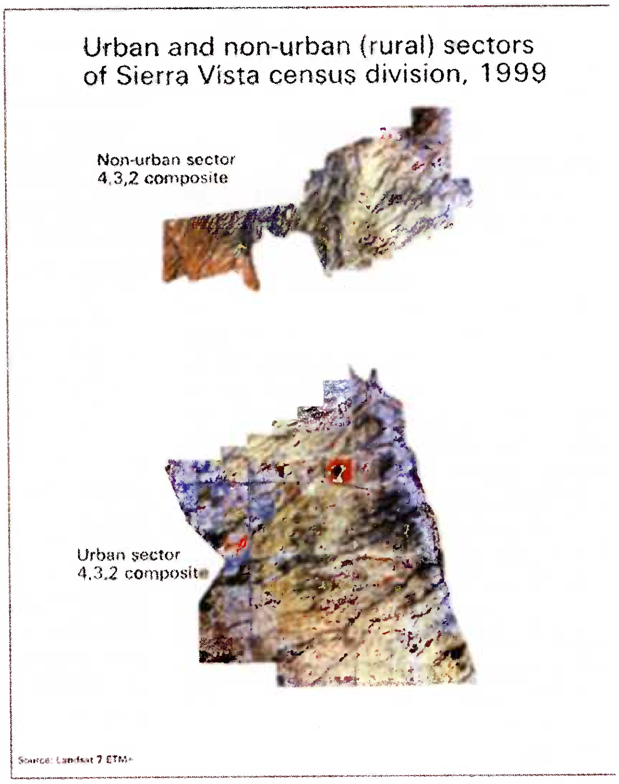
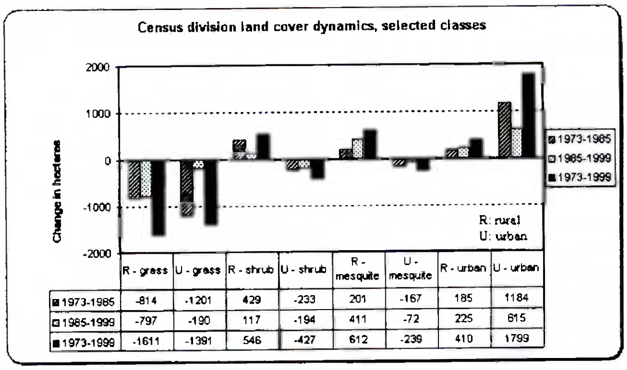


Fig. 7. Urban and non-urban (rural) sectors of Sierra Vista census division, 1999.

Landscape Changes

The first expected general model for landscape change detection was that the farther away the site from the urban center (located in center of Fig. 2), the lower the fragmentation and shape complexity. Hence, the rural sector was expected to display lower values for Edge Density, Patch Density, Interspersion and Juxtaposition Index, and higher values for Contagion as compared to the urban sector in a single scene. In a time series, rural indicators should remain constant in a healthy ecosystem. The second model states that the urban sector should have higher shape complexity since it consists of a mixture of roads, residential, business, and industrial areas. Visibly, the urban area is more fragmented than non-urban areas in the census division and should have higher fragmentation values. In a time series, urban Edge Density, Patch Density, and Interspersion and Juxtaposition Index should increase, and Contagion should decrease. Table 3 shows the results for landscape indices with respect to different sectors and years.

The output indicates substantial and increasing grassland disturbance in both rural and urban sectors between 1973 and 1999. Urban areas have higher shape complexity, or modification (Edge Density) values than rural areas in both space and time although the difference is not substantially large. Urban fragmentation values over space and time (increasing Interspersion and Juxtaposition Index, Patch Density and decreasing Contagion) indicate dissected and equally adjacent classes in an expanding urban landscape. However, significant modification is also occurring in the rural landscape. From 1973 to 1999, the northwest corner of the rural census division experienced a substantial increase in mesquite, and the northeast quadrant witnessed significant conversion of grass to shrub (Figs. 4, 5, and 6). Clumping (decreasing Interspersion and Juxtaposition and increasing contagion) and high modification (increasing Edge Density and Patch Density) in rural areas, coupled with substantial loss of grass cover identified by land cover change indicate expanding communities of homogeneous and aggregated shrub and mesquite. The increasing rural modification and urban fragmentation of grasslands indicate that the habitat



	R - grass	U - grass	R - shrub	U - shrub	R - mesquite	U - mesquite	R - urban	U - urban
▨ 1973-1985	-814	-1201	429	-233	201	-167	185	1184
▫ 1985-1999	-797	-190	117	-194	411	-72	225	615
■ 1973-1999	-1611	-1391	546	-427	612	-239	410	1799

Fig. 8. Census division land cover dynamics, selected years.

for grasslands is becoming more unsuitable for community stability and survival in the census division.

Land Cover and Landscape Assessment

A basic premise of this paper is that effects of anthropogenic and natural stressors in the census division can be interpreted by remote sensing. The introduction of urban development and invasive shrub and mesquite species raises a number of questions about impact on the native grasslands and when this is coupled with changing external forcing mechanisms such as a potentially rapid climate change, then it is necessary to examine even more carefully these introductions.

Development pressures in the Sierra Vista census division hold crucial implications for grassland sustainability. Changes in the extent and pattern of urban land cover reveal that grass as well as shrub and mesquite communities are being fragmented and converted to built landscapes. A developing urban landscape has disproportionate influence on the grassland ecosystem due directly by increased fragmentation, complexity, and conversion, and also indirectly by fire suppression policies typically enacted to protect rural and suburban subdivisions.

Declining fires in the census division reported in Table 4, coupled with findings from land cover and landscape indicators strongly suggest that a sustained, long-term program of fire suppression can produce dramatic changes in community structure and function, particularly if soils do not limit shrub establishment (Holechek et al. 1998). Many grass species common in southeastern Arizona including blue (*Bouteloua gracilis* (Willd. Ex Kunth) Lag. Ex Griffiths) and hairy grama (*Bouteloua hirsute* Lag.), plains lovegrass (*Eragrostis intermedia* A.S. Hitchc.), as well as the introduced Lehmann lovegrass (*Eragrostis lehmanniana* Nees), recover much more quickly following early growing-season fires than large, decadent scrub species because their rhizomatous roots are located below the soil surface, and thus usually escape lethal temperatures (Glendening and Paulsen 1955). In the absence of fire, desert grasslands develop dense, woody overstories and forbs that significantly reduce herbaceous grass production (Engle et al. 1998). The resulting lack of fine fuel reduces fire intensity and frequency, and the community changes from grassland to shrubland (Brown and Lowe 1980). Ideally, before this threshold between grassland and shrubland is crossed, land management strategies should be reevaluated. Once woody plants dominate a site, fire alone cannot return it to the earlier composition since fine fuel is too scarce and discontinuous to produce fires of sufficient intensity to kill woody plants. Thus, woody plants become permanent occupants of the site. Without herbicides or mechanical shrub control the change is irreversible (Dormaar and Willms 1998). The net result of the absence of periodic fires is a reduction in herbaceous grass production (Holechek et al. 1998).

Increasing demand for residential and industrial development, hobby farms, ranchettes, and land speculation are other common factors influencing the increase in built land in the census division. However, identification of these human drivers, i.e., causal factors, of land use and land cover change requires substantial in-situ ranch-level surveys, economic indicators and modeling, and land use modeling techniques that are beyond the scope of this paper. Similarly, in-situ data relating to soil conditions, grass vigor, and grazing techniques were not available on a consistent basis.

Another dramatic change in the grasslands in greater Sierra Vista between 1973 and 1999 has been the rapid increase of shrubs and mesquite. In the southwestern United States, range productivity on most sites can be greatly increased by control of velvet mesquite, and American tarwort (*Flourensia cernua* DC.) (Holechek et al. 1998). It is well known that mesquite competes vigorously with warm-season perennial grasses. The inverse relationship between density of mesquite and perennial grass production has been widely recognized (Reynolds and Martin 1968). The roots of mesquite and acacia (*Acacia* P. Mill.) are generally more extensive than those of herbaceous grass species, and allow the plants to tap soil water sources at greater depths.

The likely causes for the shrub and mesquite increase include (1) a reduction in the frequency and intensity of wildfires due largely to overgrazing following settlement and fire suppression; (2) a decline in natural perennial grasses, which, when healthy and dense, can reduce mesquite seedling establishment; (3) increased dissemination by livestock and/or Merriam kangaroo rats (*Dipodomys merriami*) of scarified mesquite seed; (4) hoof damage to ground cover and soil compaction by livestock resulting in reduced moisture in the upper layers of soil, which hinders grass establishment and growth; and (5) land clearing and cultivation (Bahre and Shelton 1993). These management-related causation factors have contributed greatly to the demise of grass cover in the Sierra Vista census division.

Conclusions

The ecological assessment of the Sierra Vista census division is an attempt to gain more scientific knowledge than we now possess of the physical and anthropogenic extent, character, and consequences of land conversion. Of the major physical processes of global change—climatic change, alteration of biogeochemical cycles, and land use—the most influential agent of future change in grasslands will be land use. If the current land use patterns remain unchanged, the most likely outcome in southwestern United States semi-arid ecosystems is an extensive transformation of the grasslands, either by degradation through the encroachment of invasive species and unsustainable use or by conversion to urban use and cover. These changes will be principally, but not exclusively, driven by the effect of a growing human population. To that end, remote sensing is vital for detecting and quantifying changes in land use and land cover, monitoring spatial composition and configuration, and quantifying the impact of grazing strategies and fire suppression and other subtle forcing factors on the land surface.

Between 1973 and 1999, rapid urbanization and land management practices contributed to significant grassland conversion in greater Sierra Vista. According to satellite data between 1973 and 1999, grasslands were reduced by 46% in rural areas, and 18% in urban areas, and 27% of the grass cover in 1973 was eradicated by 1999 in the census division (Table 1). During the same period, shrub and mesquite cover increased by 7 and 20%, respectively, and gained 1158 ha in rural areas. Landscape indices in Table 3 also indicate a large degree of conversion due to replacement of native grasses by fragmented urban development, and a substantial increase in aggregated patches of woody shrubs and trees at the expense of native grasses.

If the present rate of urban growth is sustained and current ecological trends continue, further conversion, fragmentation, and degradation of grasslands in greater Sierra Vista will be inevitable. Of local and regional significance is not just the area converted but also the area modified, or changed in ecological condition. Grasslands in the rural sector are degrading, with such consequences as soil erosion, changed floristic composition, diminished productivity, and habitat value for wildlife. In addition, population growth in the urban sector is not only leading to conversion of land cover from grass to urban, but is also an additional contributor to land fragmentation and degradation.

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Observations of cattle use of prairie dog towns

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Abstract

We investigated the use of prairie dog towns by cattle (*Bos taurus*) on the shortgrass steppe of northeastern Colorado by conducting surveys of cattle and vegetation from June to August 1999. Cattle presence and behavior were recorded 3 times a week during driving surveys of 15 black-tailed prairie dog (*Cynomys ludovicianus*) towns. A subset of 3 pastures with prairie dog towns was intensively surveyed twice weekly wherein the habitat and activity of a randomly chosen focal animal was recorded every 6 minutes for 3.5 hours. Bite and step counts of other individuals were recorded for 5-minute intervals. Vegetation height and cover data were collected monthly on each of 6 habitats. Results from driving surveys and intensively surveyed pastures were similar; cattle neither significantly preferred nor avoided prairie dog towns. Bare ground cover on prairie dog towns did not significantly differ from most other habitats, but vegetation on prairie dog towns was significantly shorter on (mean = 6.7 cm) than that off (mean = 11.9 cm) prairie dog towns. Nevertheless, foraging observations indicated that there was no significant difference between cattle foraging rates on swales (70.9 bites/min) and prairie dog towns (69.5 bites/min). Thus, cattle on the shortgrass steppe appear to use prairie dog towns in proportion to their availability and, while there, they graze as intensively as they do on habitats not inhabited by prairie dogs.

Key Words: cattle, prairie dogs, *Cynomys ludovicianus*, grazing, shortgrass steppe

Resumen

Investigamos el uso de las colonias de los perritos de la pradera por el ganado (*Bos taurus*) en la estepas de zacates cortos del nordeste de Colorado, mediante la conducción de muestreos del ganado y la vegetación de Junio a Agosto de 1999. La presencia de ganado y su comportamiento se registro 3 veces por semana durante el periodo de muestreo en el recorrido en vehículo de 15 colonias de perritos de la pradera de cola negra (*Cynomys ludovicianus*). Un subgrupo de 3 potreros con colonias de perritos de la pradera se muestreo intensivamente, 2 veces por semana, y cada 6 minutos durante 3.5 horas se registro el hábitat y las actividades de animales elegidos aleatoriamente. Los conteos de mordidas y los pasos de otros animales se registraron en intervalos de 5 minutos. Mensualmente se colectaron datos de cobertura y altura de la vegetación en cada uno de los 6 hábitats. Los resultados de los muestreos en vehículo y los de los potreros intensivamente muestreados fueron similares, el ganado ni prefirió ni evitó significativamente las colonias de los perritos de la pradera. El porcentaje de suelo desnudo en las colonias de los perritos de la pradera no difirió significativamente en la mayoría de los otros hábitats, pero la vegetación en las colonias de los perritos de la pradera fue significativamente mas corta dentro (media = 6.7 cm) de la colonia que fuera de ella (media 11.9 cm). Sin embargo, las observaciones de forrajeo indicaron que no hubo diferencia significativa entre las tasas de forrajeo del ganado fuera (70.9 mordidas/minuto) y dentro de las colonias de los perritos de la pradera (69.5 mordidas/min). Así, el ganado en las estepas de zacates cortos parece usar las colonias de los perritos de la pradera en proporción a su disponibilidad y ellos apacientan tan intensivamente en las colonias de perritos de la pradera como en los hábitats no colonizados por esta especie.

Black-tailed prairie dogs (*Cynomys ludovicianus*) greatly alter vegetation (Coppock et al. 1983a, Fahnestock and Detling 2002) and share many preferred forage species with cattle (*Bos taurus*) (Hansen and Gold 1977), leading to speculation about competition between these species for forage. On the shortgrass steppe, prairie dog activities increase the number of both forb and grass species and, through selective grazing, exert selective pressure against blue grama (*Bouteloua gracilis* [H.B.K.] Lag. ex Griffiths) and in favor of buffalograss (*Buchloe dactyloides* [Nutt.] Engelm.) (Bonham and Lerwick 1976). In mixed-grass prairie, canopy height decreases as prairie dogs clip vegetation (Archer et al. 1987, Day and Detling 1994); as taller grass species decline shorter species become relatively more abundant (Painter et al. 1993). As the colony ages, older areas become dominated by forbs and dwarf shrubs, while more recently occupied areas remain grass-dominated (Coppock et al. 1983a, Whicker and Detling 1988, Fahnestock and Detling 2002).

On both the shortgrass steppe and mixed-grass prairie there is diet overlap between cattle and prairie dogs. On the Colorado shortgrass steppe, Hansen and Gold (1977) reported a 64% annual similarity in diet. In western Oklahoma, O'Meilia et al. (1982) observed lower biomass of grass species palatable to cattle on prairie dog towns than on control pastures, and speculated that there was a high degree of competition between cattle and prairie dogs.

Despite this speculation, some studies have shown that prairie dog grazing may actually positively affect large herbivores by

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influencing forage quality. On the mixed-grass prairie of South Dakota, Coppock et al. (1983a) found greater crude protein concentrations, in vitro digestibilities, and live:dead ratios in plants from prairie dog towns than in plants of the same species from uncolonized areas. Even though prairie dog towns had 40% less forage standing crop than surrounding uncolonized areas, bison (*Bison bison*) strongly selected prairie dog colonies to graze on whenever they were in the vicinity of one (Coppock et al., 1983b). In another study, Krueger (1986) concluded that rather than a competitive relationship, bison and prairie dogs have a mutually beneficial relationship. Vanderhye (1985) quantified diet quality differences on and off prairie dog towns and used Swift's (1983) ruminant nutrition model to simulate effects on bison from feeding on prairie dog towns. Her results indicated that bison that selectively feed on prairie dog towns in the summer would significantly increase body weight relative to those feeding exclusively off prairie dog towns.

Cattle have replaced bison as the dominant herbivore on most of the Great Plains. While some studies have examined the effects of prairie dog grazing on forage preferred by cattle or diet overlap between the 2 herbivores (Hansen and Gold 1977, O'Meilia et al. 1982, Uresk 1983, 1984, 1985), little information is available regarding whether cattle actually preferentially graze on prairie dog towns.

The objectives of this study were to: (a) obtain estimates of cattle use on vs. off of prairie dog towns across the Shortgrass Steppe Long Term Ecological Research Site (SGS-LTER) through driving surveys; (b) to intensively study a subset of the pastures from the driving surveys to quantify the amount of time cattle spend on prairie dog towns compared to each of several other habitats; (c) compare foraging rates of cattle on prairie dog towns with those on other habitats in the intensive survey pastures; and (d) measure vegetation cover by species and height on and off prairie dog towns in the intensive survey pastures to determine whether vegetation differences correlated with cattle grazing activities.

Methods

Study Area

This research was conducted at the SGS-LTER in northeastern Colorado (Lat. 40° 49' N, Long 104° 46' W) and includes the Pawnee National Grassland (PNG) and the USDA-ARS Central Plains Experimental Range (CPER). The dominant plant species are blue grama and prickly pear cactus (*Opuntia polyacantha* Haw.), with blue grama making up 90% of the basal plant cover. Annual precipitation ranges from 300–550 mm, and 70% occurs between May and September as localized thunderstorms (Lauenroth and Milchunas, 1991). Most soils are well drained loams or sandy loams, and the topography consists of rolling hills at an elevation of 1,310m to 1,935m (Hazlett 1998).

Cattle are present on the pastures used for this study from mid-May until mid-October. Pasture sizes for this study range from 130 to 2,378 ha, and the black-tailed prairie dog towns range in size from 1.7 to 81.6 ha and occupy 0.3 to 10.7% of the those pastures (Table 1).

Most pastures contain stock tanks to supply cattle with water. For this study, we chose prairie dog towns that were not adjacent to or surrounding water tanks. Pastures are grazed at "moderate" stocking rates (1.74 ha/cow/month, Bob Peterson, pers. comm.). Most of these prairie dog towns are less than 10 years old because of plague-induced die outs and subsequent prairie dog recolonizations (Mark Ball, pers. comm.).

Driving Surveys

We conducted driving surveys to obtain SGS-LTER-wide estimates of cattle use of prairie dog towns approximately 3 times per week from 28 May to 15 Aug. 1999, for a total of 31 surveys of each of 15 prairie dog towns in 12 pastures (Table 1). Because cattle are most active the half hour before sunrise until approximately 3 hours after sunrise, and from 3 hours before sunset to a half hour after sunset (Arnold and Dudzinski 1978), we restricted our surveys to those times. Time (morning vs. evening), starting location,

Table 1. Characteristics of pastures and prairie dog towns surveyed during summer 1999, on the Shortgrass Steppe LTER. All allotments on the Pawnee National Grasslands had cow/calf herds. On the Central Plains Experimental Range pastures 5W, 22W, and 28N had steer herds, pasture 29–30 had yearling breeders, and pasture 27–34 had stock heifers. Age of towns were determined from U.S. Forest Service records and indicate the number of consecutive years towns have been active up until the time of this study.

allotment	pasture size	U.S. Forest Service town #	area of town	pasture occupied by town	cattle	age of town
	(ha)		(ha)	(%)	(No.)	(Yrs.)
Pawnee National Grasslands						
Roe	1468	79	5.6	0.4	175	6
Coal	1535	51	8.7	0.6	144	6
Keota	2378	17	14.3	0.6	168	2
Simmons	1948	13	5.1	0.3	252	18
Fiscus	534	30	3.3	0.6	64	5
Box	1536	35	40.5	2.6	144	6
Stoneham	1173	5	81.6	7.0		6
		8	13.8	1.2	147	6
Central Plains Experimental Range						
5W[1]	130	5W	13.9	10.7	20	3
29-30[1]	324	29	7.9	2.4		2
		30	2.4	0.7	65	3
22W[1]	130	22	4.4	3.3	17	2
27-34	332	27	3.0	0.9		3
		28NE	1.7	0.5	62	3
28N	130	28N	3.5	2.7	14	3

[1] Pastures also used for intensive surveys.

and order of visitation of the towns were changed with each survey. Prairie dog towns were either entirely visible from the road with 7 x 35 binoculars or could be seen by walking to a nearby vantage point. Pastures were only chosen for the survey if all of the prairie dog towns on the pasture could be viewed at the time of the survey. These prairie dog towns encompassed a variety of soil types and upland and lowland sites. The number of cattle on each prairie dog town and their behaviors (grazing, resting, traveling, or standing still) were recorded. Cattle were considered to be grazing if feeding while moving or standing still. Resting was defined as cattle lying down, and traveling was movement with the head up. For this general overview, we were only concerned with whether the cattle were on or off the towns. Pastures were often very large, and not all of the cattle could be seen at the time of the survey if they were off of the prairie dog town. Consequently, behavior of cattle off prairie dog towns was not recorded for the driving surveys.

Driving survey data were analyzed using resource selection functions (Manly et al. 1993). The ratio of the proportion of the cattle population occupying a habitat (o_i) to the proportion of pasture area the habitat occupies (π_i) gives a selection ratio (w_i), where i = habitat (in this case, on or off prairie dog towns):

$$w_i = o_i/\pi_i \qquad \textbf{(1)}$$

These selection ratios are standardized (B_i) to values between 0 and 1 wherein:

$$B_i = w_i/(\sum_{i=2}^{1} w_i) \qquad \textbf{(2)}$$

Standardized selection ratios can be interpreted as probabilities, such as the probability of selecting habitat i next if all the habitats were equally available. When only 2 habitats are considered (e.g. on and off towns), values above 0.5 indicate preference for a habitat, values of 0.5 indicate random use, and values below 0.5 indicate avoidance of a habitat. Chi-square values were calculated for the selection ratios to determine significant differences from random use (0.5).

Intensive Surveys

To obtain a more detailed assessment of where cattle were spending their time, a subset of 3 smaller pastures from the driving surveys, located on the CPER, were chosen for more intensive surveys conducted from 4 June to 20 Aug. 1999 (Tables 1 and 2). In each of these intensive study areas, the entire pasture could be observed from several vantage points so the entire pasture was considered the home range of the cattle and all habitat types could be observed. Plant communities on these pastures were divided into 6 habitats: prairie dog towns, swales, rocky ridgetops, uplands, planted crested wheatgrass (*Agropyron cristatum* [L.] Gaertn.) strips, and *Atriplex canescens* (Pursh) Nutt. dominated terraces (Table 2).

Table 2. Habitats of the 3 intensive survey pastures on the Central Plains Experimental Range and relative composition of the habitats within each pasture.

Habitat	22W	Pasture 5W	29-30
		(%)	
upland	86.0	0.0	75.4
Atriplex terrace	0.0	73.7	16.1
prairie dog town	3.3	10.7	3.2
swale	7.9	6.3	3.0
rocky ridgetop	2.8	4.4	2.1
crested wheatgrass	0.0	4.9	0.0

During a 3.5 hour feeding bout (morning or evening), a randomly chosen focal animal (Altmann 1974) was observed every 6 minutes. To minimize disturbance, cattle were observed from a vehicle at a distance of at least 1 km, using 7x35 binoculars or a 15 to 60 x zoom spotting scope. Habitat, instantaneous behavior (grazing, resting, traveling, or other), and number of other cattle within a 50 m radius were recorded. Frequency of behaviors was analyzed using tests of 2 percentages (Lehner 1996). In between the focal animal observations, we conducted foraging surveys to examine foraging efficiency. The number of bites and steps in a 5-minute period were recorded for randomly chosen individuals. Each jaw movement when the head was touching vegetation constituted a bite and each movement of a front leg was considered a step. Comparison of foraging data between habitats was conducted using an ANOVA and Tukey's HSD procedure.

The 3 pastures were mapped in September with a hand-held Global Positioning System (GPS) unit (Trimble Navigation Ltd., Sunnyvale, Calif. 94086) and areas of each habitat were determined using PC ARC/INFO 3.5.1 and ArcView GIS 3.2 (Environmental Systems Research Institute, Redlands, Calif. 92373). The habitat use data for these 3 pastures were divided into 2 periods (Period I = 28 May to 9 July, Period II = 12 July to 15 August) and also combined to detect changes in habitat use over the season using log-ratio compositional analysis (Aebischer et al. 1993). This method examines the proportional habitat use by animals in comparison to habitat availability. Instead of the number of locations, it uses the number of animals as the sample size; therefore, it does not require independence of sequentially collected locations. This method also accounts for the unit-sum constraint, a common problem when using compositional data, wherein habitat proportions are non-independent and must sum to 1. For example, if an animal avoids one habitat, it must spend time in another, leading to an apparent preference for that habitat type. Finally, compositional analysis accounts for the arbitrary definition of habitat preference by allowing habitats to be ranked according to relative use. This technique tests for random use on all habitats. When there is deviance from random use, the available habitats can be ranked from most preferred to least preferred. The data from this study were divided into 2 periods in an attempt to detect any seasonal difference while still having a large enough sample size for meaningful statistical analysis.

Vegetation data were collected in June, July, and August on the 3 intensive survey pastures. Twenty, 0.1 m^2 Daubenmire frames (Daubenmire 1959) were placed randomly in each habitat on each pasture to determine plant species composition and canopy cover. Average vegetation height was measured by setting a light cardboard piece over the Daubenmire frame area and measuring the height from the ground to the center of the cardboard. Data from all 3 pastures were combined for vegetation analysis due to the close proximity of the pastures (within 8 km) and the similarity in soils and vegetation types. Vegetation heights and canopy cover were analyzed using an ANOVA and Tukey's HSD procedure.

Results

Driving Surveys

Standardized resource selection ratios for each pasture across the season for all surveys displayed no clear trend in the use of prairie dog towns by cattle (Fig. 1). A Chi-square test indicated a slight preference (B_i = 0.527, p = 0.003) for the use of prairie dog towns by cattle for all pastures over the entire sampling period. Of 789 cattle observed on prairie dog towns over the season, 91.4% were grazing, 5.7% were resting, 2.9% were standing still, and none were traveling.

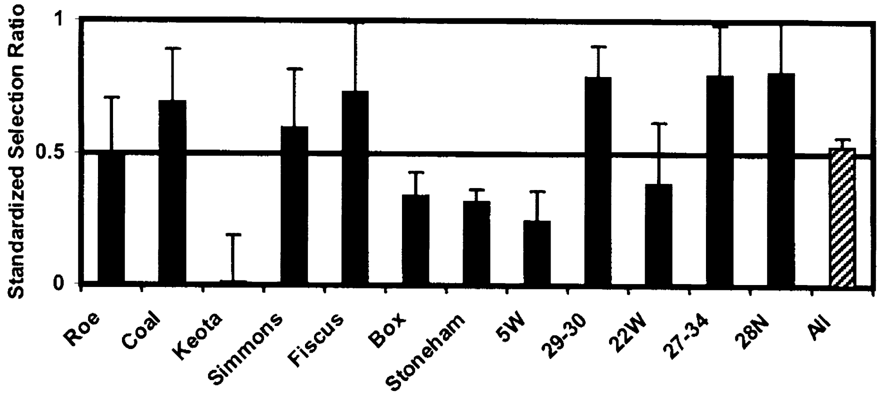

Fig. 1. Standardized resource selection ratios (B_i) and standard error bars for cattle occurring on prairie dog towns from the driving surveys for each pasture and all pastures combined from 28 May to 15 Aug. 1999. Values above 0.5 represent selection for prairie dog towns, values below 0.5 represent avoidance of prairie dog towns, and 0.5 represents random use of prairie dog towns.

Intensive Surveys

Each of the 3 pastures was surveyed 16 times for a total of 25 surveys for Period I and 23 surveys for Period II. Focal animals were within a 50 m radius of half or more of the herd 54% of the time. Cattle did not use habitats randomly on any of the 3 intensively surveyed pastures based on log-ratio compositional analysis (Table 3). The 3 pastures used for the intensive surveys were analyzed separately for habitat use due to the differing proportions of each habitat type on the pastures (Table 2). The prairie dog town was consistently ranked last (least preferred habitat) on pasture 22W, but was not used significantly differently from the rocky ridgetops. On pasture 5W, cattle used habitats almost in the direct order of availability (Table 2), with the exception of the swale being ranked higher than the prairie dog town. Again, there were no significant seasonal differences, with the town consistently ranked in the middle. Pasture 29–30 revealed the only significant seasonal difference regarding cattle use of prairie dog towns. The town was ranked last in Period I (early summer) and first in Period II (late summer), whereas the swale switched from the first rank in Period I to second to last in Period II. Combined data over the season for pasture 29–30 ranked the town as second to last.

Behavior observations (n = 1,720) of the focal animals (Table 4) indicated that cattle spent the majority of their time grazing during the 3.5 hour observation periods. While on prairie dog towns, cattle spent 60% of their time grazing, 13% resting, 15% traveling, and 12% doing other activities such as interacting with other cattle or standing still. Focal animals for the log-ratio compositional analysis spent more overall time in the swales (Table 3). However, those same animals spent a higher proportion of their time grazing while on prairie dog towns, uplands, *Atriplex* terraces, and rocky ridgetops than in the swales (Table 4).

Foraging observations of numbers of bites per step (Fig. 2) revealed few differences between cattle foraging on prairie dog towns (mean = 6.3 bites/step) and most other habitats. Cattle did have significantly fewer bites per step on the rocky ridgetops and upland habitats (4.7, and 4.8 bites/step, respectively) and consequently moved at a faster rate across those habitats. Foraging observations of the number of bites per minute indicated that there was no significant difference between cattle foraging on swales (70.9 bites/min) and prairie dog towns (69.5 bites/min). The cattle on these 2 habitats had significantly higher foraging rates than on all other habitats.

Vegetation Characterization

We compared cover for 5 plant species palatable to cattle and 2 non-palatable species, as well as cover of bare ground and litter across all 3 intensively surveyed pastures (Fig. 3). Of the palatable plants, swales had the highest cover of western wheatgrass (*Pascopyrum smithii* [Rydberg] Love). Prairie dog towns and the *Atriplex* habitat had the next highest cover of western wheatgrass and they were not significantly different from each other. Prairie dog towns contained significantly less blue grama cover than the *Atriplex* terraces and upland habitats, but more than swales and crested wheatgrass habitats. The prairie dog towns and swales had significantly more cover of buffalograss than the other habitats. Cover of needleleaf sedge (*Carex eleocharis* Bailey) and scarlet globemallow (*Sphaeralcea coccinea* [Pursh] Rydberg var. *coccinea*) was low (<5%) across all habitats.

Of the non-palatable plants (Fig. 3), red three-awn (*Aristida purpurea* Nuttall var. longiseta [Steud.] Vasey) had low cover (1.2%) on the prairie dog towns, and this was lower than on either the rocky ridgetops or upland habitats. Sixweeks fescue (*Vulpia octoflora* [Walt.] Rydb.) had low (0–2%) cover across habitats and few significant differences between habitats. Bare ground cover on prairie dog towns was not significantly different from

Table 3. Results of the log-ratio compositional analysis for the 3 intensive survey pastures including habitat rankings according to use. The designation "cw" refers to the crested wheatgrass habitat, "rocky" refers to rocky ridgetops, and "town" refers to prairie dog town. Period I refers to surveys conducted from 3 June to 8 July 1999, and Period II refers to surveys conducted from 13 July to 21 Aug. 1999. Within a row, and within a pasture, values with the same letter were not significantly different at P < 0.05.

	pasture 22W	pasture 5W	pasture 29–30
Period I	swale^a > upland^b > rocky^b > town^b	swale^a > *Atriplex*^{ab} > town^{bc} > cw^c > rocky^c	swale^a > upland^a > *Atriplex*^{a} > rocky^{ab} > town^b
Period II	swale^a > upland^a > rocky^b > town^b	*Atriplex*^{a} > swale^{ab} > town^{abc} > cw^{abc} > rocky^c	town^a > *Atriplex*^{a} > upland^a > swale^a > rocky^b
Combined	swale^a > upland^b > rocky^c > town^c	*Atriplex*^{a} > swale^a > town^b > cw^b > rocky^b	*Atriplex*^{a} > upland^a > swale^{ab} > town^b > rocky^c

Table 4. The proportion of behaviors of focal animals averaged over all 3 intensive survey pastures on the CPER, summer, 1999. Within a column, values with the same letter were not significantly different at $P < 0.05$. The designation "other" refers to behavior such as standing still, drinking water, or interacting with other cattle The designation "cw" refers to the crested wheatgrass habitat, "rocky" refers to rocky ridgetops, and "town" refers to prairie dog town.

Habitat	grazing	resting	traveling	other	n
rocky	0.82^{a}	0.00^{a}	0.14^{a}	0.04	44
Atriplex	0.75^{a}	0.04^{a}	0.14^{a}	0.07	512
upland	0.62^{b}	0.14^{b}	0.11^{a}	0.13	614
town	0.60^{b}	0.13^{b}	0.15^{a}	0.12	108
cw	0.56^{bc}	0.30^{c}	0.07^{b}	0.07	27
swale	0.42^{c}	0.20^{bc}	0.07^{b}	0.31	415

that in other habitats with the exception of the crested wheatgrass habitat and rocky ridgetops which had higher percentages of bare ground (Fig. 3).

Averaged over all 3 pastures and over July and August (Fig. 4), vegetation on prairie dog towns (mean = 6.4 cm) was significantly shorter than that in all other habitats (mean = 11.9 cm).

Discussion

Although Chi-square analysis of the 1999 driving survey data indicated that cattle significantly selected for prairie dog towns on this Colorado shortgrass steppe site, the magnitude of the effect was quite small ($B_i = 0.527$) and differed little from random use ($B_i = 0.500$). Clearly, cattle did not exhibit a strong preference for prairie dog towns as did bison on the mixed-grass prairie (Coppock et al. 1983b, Krueger 1986). However, 91% of the cattle observed on prairie dog towns during driving surveys were grazing. This may seem intuitive since we surveyed during peak grazing times; however this shows that cattle did not spend their time simply traveling across prairie dog towns to get to more preferred grazing areas. Instead, they actually spent a significant amount of time on the prairie dog towns actively using them as a foraging resource.

On the more intensively surveyed pastures, focal animals apparently represented herd movements well as more than half the herd was within 50m of them. Preference rankings derived from log-ratio compositional analysis indicated that over the season, swales and *Atriplex* terrace habitats were usually most preferred and rocky ridgetops were often least preferred. In general, prairie dog towns were ranked near the middle or below, but significance tests did not indicate differences between the prairie dog towns and anywhere from 1 to 4 other habitats. Swales were highly ranked in all 3 pastures indicating that cattle were strongly selecting for 1 habitat low in proportional area (Table 2). This is consistent with Senft's (1983) findings that swales were preferred during the growing season. While cattle do not appear to strongly prefer the prairie dog towns, they also do not avoid them.

The compositional analysis of the intensive survey data was used because of our ability to observe and sample the animal's entire home range, our ability to record an equal number of observations for each animal, and because all habitats were used in each pasture. Aebischer et al. (1993) suggest that caution is required for gregarious animals. For this study, the focal animals appear to represent the movements of the herd and therefore we cautiously extrapolate our findings to the rest of the herd.

Bison on mixed-grass prairie were found to have significantly higher bite/step ratios on prairie dog towns compared to uncolonized areas in 5 of 6 months of the May to November study, excluding November (Krueger 1986). This implied greater forage quality on those prairie dog towns compared to the uncolonized area. In our study, the number of bites/step on prairie dog towns was not significantly different than productive habitats such as swales and *Atriplex* terraces. The foraging rate (bites/minute) for cattle on prairie dog towns was also not significantly different from swales, a preferred habitat. While bite size was not measured (and could have been smaller on prairie dog towns), this nevertheless implies that the plants on prairie dog towns have forage value. A study of cattle on the shortgrass steppe found that foraging velocities (rates of walking in steps/minute) only changed if the differences in forage quantity were

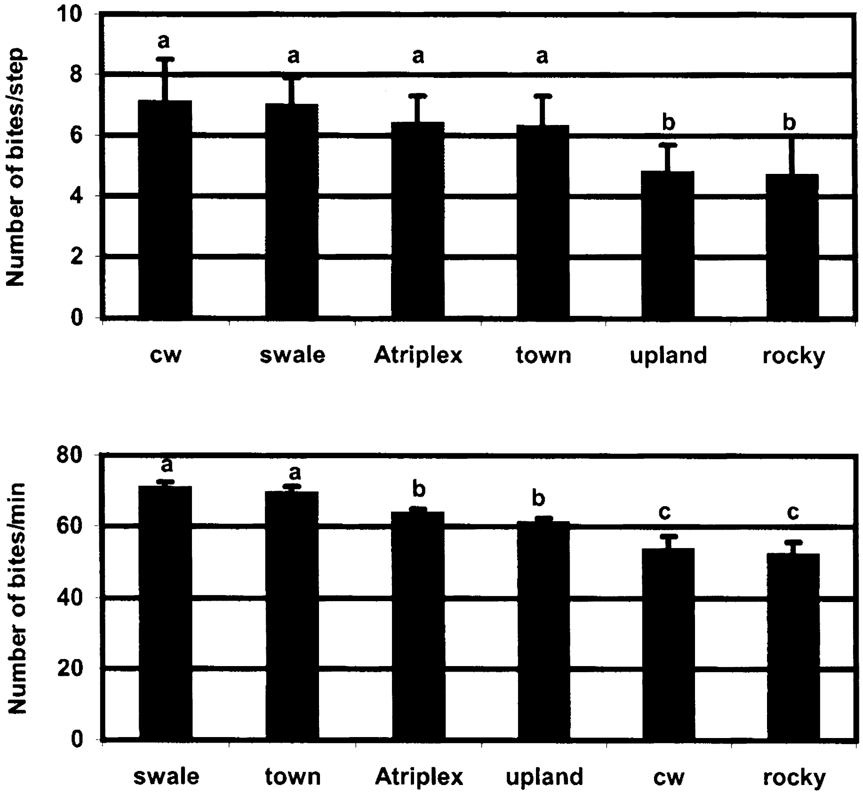

Fig. 2. Least squares means and standard errors of number of bites per step and bites per minute of foraging cattle by habitat ("cw" refers to the crested wheatgrass habitat, "rocky" refers to rocky ridgetops, and "town" refers to prairie dog towns). Sample sizes: swale n = 118, prairie dog town n = 91, *Atriplex* terrace n = 211, cw n = 20, rocky ridgetop n = 24, upland n = 200.

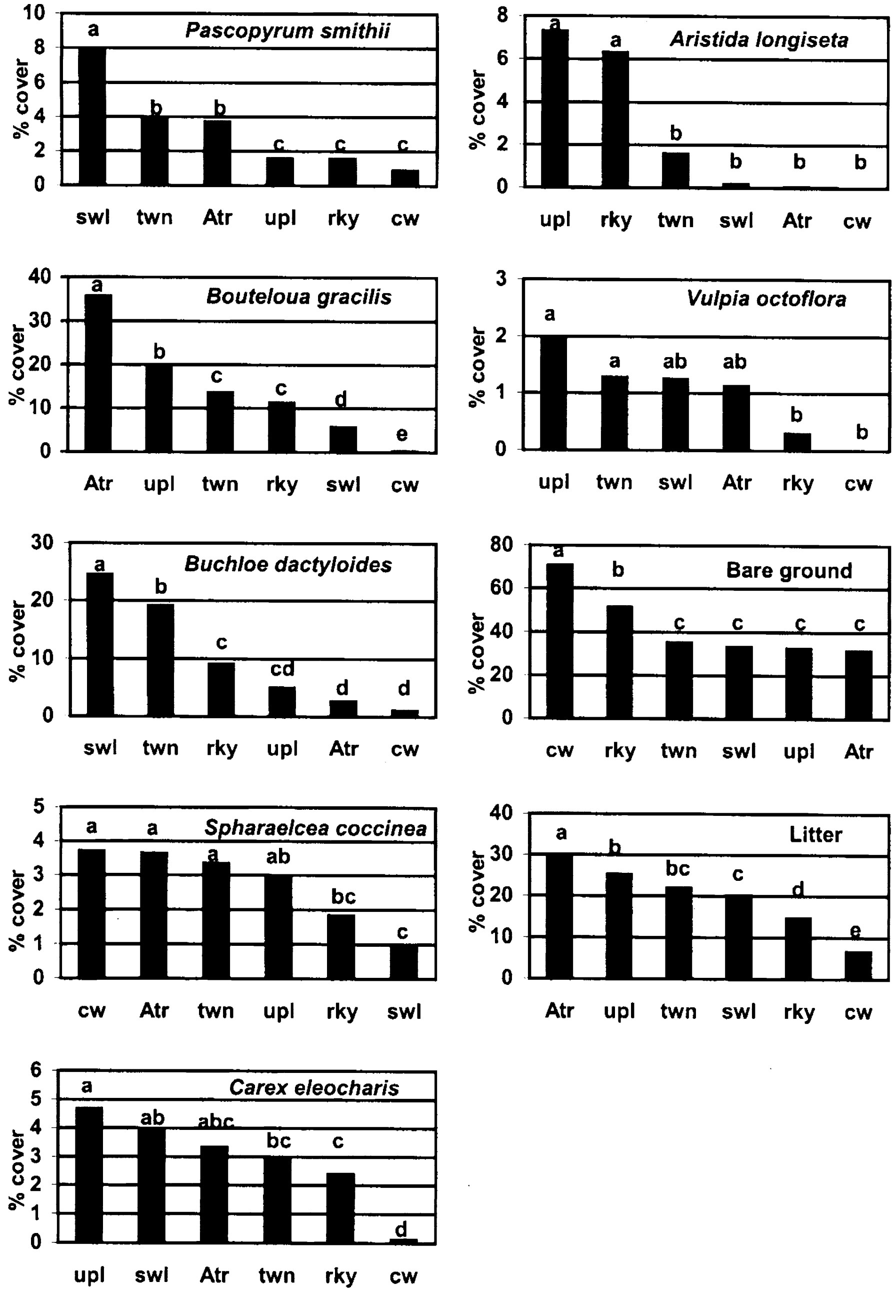

Fig. 3. Average cover (%) for 5 plant species palatable to cattle (left column), 2 non-palatable species (*Aristida longiseta* and *Vulpia octoflora*), and for bare ground and litter on each habitat type. Cover is averaged over June, July, and August of 1999, and across the 3 intensively surveyed pastures on the CPER ("cw" refers to the crested wheatgrass habitat, "rky" refers to rocky ridgetops, "Atr" refers to *Atriplex* terraces, "upl" refers to upland habitat, "swl" refers to swales, and "twn" refers to prairie dog towns). Columns with the same letters were not significantly different at P < 0.05.

great (Bailey 1988, Bailey et al. 1996). It may be that the differences in forage quantity or quality between prairie dog towns and swales on the shortgrass steppe were not sufficiently large for cattle to change their foraging rates.

Our vegetation characterization indicates that plant species palatable to cattle such as western wheatgrass, blue grama, and scarlet globemallow (Vavra et al. 1977), are quite common on these shortgrass steppe prairie dog towns (Fig. 3). Non-palatable plants often had similar or higher cover off of prairie dog towns. The estimate for bare ground cover on prairie dog towns (35.3%) in this study is essentially identical to what Archer et. al (1987) found on the mixed grass prairie of South Dakota (35%). However, Archer et. al (1987) found more than 3 times as much bare ground on prairie dog towns as off, whereas on the shortgrass steppe, we found there to be as much or more bare ground on the other habitats as on prairie dog towns. One important difference found in vegetation on and off prairie dog towns was that the plants growing on prairie dog towns were significantly shorter than those on all of the other habitats. While cattle did not appear to be selecting prairie dog towns to graze on, they also did not significantly avoid them, even though the vegetation was shorter there.

It is not clear why we did not see a preference for prairie dog towns by cattle on the shortgrass steppe. Age of the prairie dog towns may be a factor. The towns used for this study were all relatively young (mean = 5 years); however, areas of prairie dog towns selected for grazing by bison in mixed-grass prairie were of this age (Coppock et al. 1983b). Slope and the location of water tanks were not considered in the analysis of this study; however, the pastures were relatively flat with rolling hills (0–15% slope) and care was taken to select prairie dog towns that did not have water tanks on or adjacent to them. Variability can also occur in the behavior of cows with calves versus steers. However, a combination of pastures with different cattle types was used for this study to obtain an overview of cattle behavior in general.

Year to year weather differences might have an effect on cattle selection of prairie dog towns on the shortgrass steppe. The summer of this study was unusually wet. The total precipitation for 1999 was 550mm, at the upper end of the range of precipitation for the shortgrass steppe. Green (1998) reported that during a wet year on the mixed-grass prairie, bison grazed on prairie dog towns preferentially. He attributed this to the additional moisture causing grasses on surrounding ungrazed habitat to grow taller and seed out, whereas the grazed grasses on prairie dog towns were not seeding out and had high leaf:stem ratios. During a dry year bison did not graze preferentially on the towns. On the shortgrass steppe, Lerwick (1974) found that prairie dogs and cattle switched diets during drought years with prairie dogs consuming more grass and cattle consuming more forbs than in non-drought periods. Variation in weather definitely has an effect on plant-herbivore and herbivore-herbivore relationships, and sur-

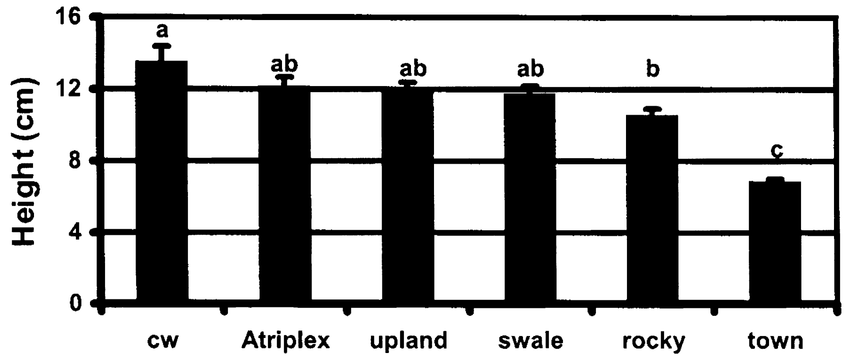

Fig. 4. Mean average height (cm) and standard errors of vegetation for all habitats averaged over July and August, 1999 ("cw" represents the crested wheatgrass habitat, "rocky" refers to rocky ridgetops, and "town" refers to prairie dog towns).

veys conducted on the shortgrass steppe during a drought year might show very different results. However, since 1999 was a wet year, which would be similar to a normal weather year on the mixed-grass prairie, we would expect to see cattle preference for prairie dog towns during the summer of our study if we were to see it at all.

Nitrogen content of plants on and off prairie dog towns was not measured for this study. However, if there was indeed an increase in protein content in the plants on prairie dog towns as shown in the mixed-grass prairie (Coppock et al. 1983a), perhaps this increase on the shortgrass steppe (a place with less moisture) is not great enough to cause a preference but high enough to compensate for the loss in biomass. Therefore the habitat is used as expected and not avoided.

Coppock et al. (1983b) hypothesized that a response by large ungulates to prairie dog towns would likely only be seen in highly productive systems where the difference in habitat on and off towns is greatest. The shortgrass steppe is a very different system from the mixed grass prairie (Milchunas et al. 1998). Atsedu (1995) found differences in nitrogen content increases of grazed plants on the shortgrass steppe to be dependent on grazing histories and intensities. Also, cattle and bison are similar in that both are generalist herbivores, but cattle are more selective feeders (Peden et al. 1974). The examination of cattle use of prairie dog towns on mixed-grass prairie and of bison use of prairie dog towns on shortgrass prairie would provide insights as to whether it is cattle or the shortgrass system that is driving the preferences for prairie dog towns. Furthermore, the issue of carrying capacity is important (Hobbs and Hanley 1990). For example, how large or old does a prairie dog town have to be before it begins to affect the number of cattle that can be sustained on a pasture in the shortgrass steppe? More information is also needed on the effects of prairie dog grazing on the quantity and quality of forage for cattle on the shortgrass steppe.

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Economic implications of off-stream water developments to improve riparian grazing

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Abstract

Livestock grazing in riparian areas is an important management issue on both private and public lands. A study was initiated in northeastern Oregon to evaluate the economic and ecological impacts of different cattle management practices on riparian areas. The effect of off-stream water and salt on livestock distribution and subsequent impact on riparian use, water quality, and livestock production was evaluated. A multi-period bioeconomic linear programming model is used to evaluate the long-term economic feasibility of this management practice with a riparian utilization restriction of 35% for a 300 cow-calf operation. The utilization restriction resulted in economically optimal herd sizes 10% smaller than the baseline herd size. With the management practice, cattle were distributed more evenly, consumed more upland forage before maximum riparian utilization was reached, and gained more weight. The economic impacts of these outcomes were increased with expected annual net returns to the ranch for the project ranging between $4,500 and $11,000 depending on cattle prices and precipitation levels.

Resumen

El apacentamiento de ganado en áreas ribereñas es un importante problema de manejo en terrenos públicos y privados. Se inicio un estudio en el noreste de Oregon para evaluar los impactos económicos y ecológicos de diferentes prácticas de manejo de ganado en áreas ribereñas. Se evaluó el efecto de la disponibilidad de agua y sal lejos de la corriente en la distribución del ganado y los impactos subsecuentes en el uso del área ribereña, la calidad del agua y la producción del ganado. Se uso un modelo de programación lineal de multiperiodos bioeconómicos para evaluar la factibilidad económica a largo plazo de esta práctica de manejo con una restricción de utilización del area ribereña del 35% para una operación de 300 pares de vaca-becerro. La restricción de utilización resultó en tamaños de hato económicamente óptimos 10% menores que el tamaño base del hato. Con la práctica de manejo el ganado se distribuyó mas uniformemente y consumió más forraje de las áreas tierras arriba antes de alcanzar la máxima utilización del área ribereña y ganó más peso. Los impactos económicos de estos resultados fueron incrementos del retorno neto anual esperado del rancho en un rango de $ 4,500 a $ 11,000 dolares dependiendo de los precios y niveles de precipitación.

Properly functioning riparian systems are vital to the health of watersheds and provide an important forage and habitat resource for livestock and wildlife. Recent concerns about water quality and wildlife and fisheries habitat have focused attention on livestock management practices occurring within these areas. The impacts of livestock on riparian systems have been identified (Kauffman and Krueger 1984) and specialized management strategies such as rest rotation, late season grazing and riparian corridor fencing have been developed. However, economic assessments of these management alternatives are often lacking (Skovlin 1984, Armour et al. 1991). When economic analyses are undertaken, projects are often found to not be economically justified (Nielsen 1984, Workman 1986). There is a critical need at this time for economically feasible riparian grazing management strategies that achieve environmental goals.

Bioeconomic models are one method that can be used for evaluating management options. They can combine biological dynamics with economic behavior to help determine an optimal bioeconomic strategy. Standiford and Howitt (1992) developed such a model to evaluate ranch enterprises on California rangelands by incorporating tree canopy, forage and livestock dynamics. Dynamic models have also been developed by Pope and McBryde (1984) and Torell et al. (1991) to determine the intertemporal influence of stocking rates on current and future forage and livestock production.

In this paper, a bioeconomic linear programming model is developed to determine the economic impacts of a grazing management strategy on a 300-head cow-calf ranch. The strategy under evaluation is the placement of an alternative water source and trace mineralized salt in the upper portion of pastures which is designed to influence cattle distribution between riparian and upland areas. A field test of the dispersion project was conducted and the data were used in the development of the bioeconomic model. The purpose of the economic analysis is to compare the optimal (profit maximizing) net returns of a ranch operating with and without off-stream water and salt under varying crop year precipitation levels and market prices (states of nature).

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Table 1. Variable names, definitions, and values used in the ranch model.

Subscripts	
G	Forage location: G1 riparian vegetation, G2 upland vegetation
L	Forage supply: L1 private land, L2 public lease 35%, L3 private lease, L4 hay, L5 over utilization on public. L2 & L5 are summer allotments.
P	Summer pastures: P1 non-project, P2 water project pasture
t	Time (years)
Parameters - Exogenous Variables	
HECTARE$_{G,P}$	Number of hectares in summer allotments
C$_L$	Cost of forage supply per AUD
CALFFWT	Selling weight of heifer calf (cwt) Without project = 5.25, With project = 5.38
CALFMWT	Selling weight of steer calf (cwt) Without project = 5.75, With project = 5.88
CLF	Calving % (includes conception rate, birth rate and death loss) (88%)
COWCST	Variable cost of a cow per month ($14.41)
COWWT	Selling weight of a cow (cwt) Without project = 11.0, With project = 11.27
CULL	Cull cow rate (at least 15%)
DEATH	Cow death rate (1%)
DF$_t$	Discount factor
LEASELMT	Limit to amount of AUDs that can be purchased from private lease (10,350)
OWNLMT	Limit to amount of AUDs off own rangeland (31,470)
PCST	Annual pump cost ($438.40)
PRECP	Median precipitation of crop year (mm)
r	Discount rate (7%)
UTIL$_{G,P}$	Standard utilization levels
YEARWT	Selling weight of yearling heifer (cwt)
YIELD$_G$	Normal forage yield (dry kg per ha) Riparian = 1,301, Upland = 811
Exogenous Parameter	
MKTCALF	Market price for beef calves per cwt Low = $86.12, Median = $100.13, High = $120.32
MKTCOW	Market price for beef cows per cwt Low = $54.82, Median = $59.81, High = $72.13
RAIN	Crop year rain in mm Low = 265, Median = 320, High = 380
Endogenous Variables	
COW$_t$	Mature cows
FIRST$_t$	First calf heifers
HERDt	Herd size
INCOME$_t$	Income for the year
OVER$_{G,P2,t}$	Utilization percentage beyond standard
REPL$_t$	Number of heifer calves held as possible herd replacements
SELLCALFF$_t$	Number of heifer calves sold
SELLCALFM$_t$	Number of steer calves sold
SELLCOW$_t$	Number of cows sold
SELLYEAR$_t$	Number of yearling heifers sold
TERM	Terminal value
VARCST$_t$	Variable costs
PCST	Project cost
X$_{L,t}$	Amount of forage from each supply
Z	Present value of gross margin less dispersion project costs

Model Design

The off-stream water bioeconomic model consists of a set of relationships depicting the objective function, cattle herd equations of motion, and forage growth equations of motion. The model is solved over a 60-year planning horizon.

Objective Function

The objective function (equation 1) of the ranch is to maximize the discounted total gross margin and terminal value less dispersion project costs over a planning horizon of T years. A discount factor (DF_t) of 7% is used in present value calculations. Table 1 gives the definitions for all variables and subscripts used in the paper.

$$\text{Max } Z = \sum_{t=1}^{T} DF_t * (INCOME_t - VARCST_t - PCST) + TERM \quad (1)$$

Livestock revenue ($INCOME_t$), shown in equation 2, is a function of the number of cattle sold, weight of the cattle and the market price received. The market prices were 5 year average prices for Oregon cattle, weighted by class of cattle expected in the herd.

$$INCOME_t = (SELLCOWT * COWWT + SELLYEAR_t * YEARWT) * MKTCOW + (SELLCALFF_t * CALFFWT + SELLCALFM_t * CALFMWT) * MKTCALF \quad (2)$$

The numbers of cattle sold in each age class ($SELLCOW_t$, $SELLYEAR_t$, $SELLCALFF_t$ and $SELLCALFM_t$) are choice variables within the model and optimal numbers of animals for sale are determined. The weights of cattle (*COWWT, CALFFWT* and *CALFMWT*) were defined to be different for the various management schemes studied. Yearling replacement heifers were not considered as sale animals so their weight was not different between treatments. The selling prices (*MKTCOW* and *MKTCALF*) that ranchers receive for their product are a source of risk. To account for this risk, 3 parameter values are assigned from the historical price data set of the region to represent low, median and high market prices.

The annual total variable costs ($VARCST_t$) of the livestock enterprise, shown in equation 3, include both variable costs (*COWCST*) and variable feed costs (C_L).

$$VARCST_t = 12 * (COW_t + FIRST_t) * COWCST + \sum_{t=1}^{5} X_{L,t} * C_L \quad (3)$$

Variable costs per cow are based on a 300 head cow-calf enterprise budget for the mountain region of northeast Oregon (Turner et al. 1998) where the dispersion project study was located. Total feed cost is dependent upon a number of factors. The annual off-stream water and salt project cost (*PCST*) is an exogenously given parameter derived from the initial investment costs amortized over the life of the investment plus the variable costs associated with the riparian improvement system.

Equation 4 denotes the terminal value. It is calculated as the present value of an infinite series of net revenue multiplied by the number of animals in the herd in the last year. The exogenous parameter value (*NETREV*) is calculated from the enterprise budget using the low, median and high market prices depending upon the price condition considered. The parameter HERD is defined below as the number of mature cows, first-calf heifers, and replacement heifers. The purpose of the TERM variable is to force the model to consider future production. In many multiperiod models, the tendency is to liquidate the herd near the end in order to maximize net income. Including the terminal value in the model assumes that the ranch will continue into perpetuity at the final production level and represents the production value of the ranch beyond year T.

$$TERMT = ((HERD_T - SELLCOW_T - SELLYEAR_T)*NETREV) * (\mathrm{r} * (1\text{-}1((1 + \mathrm{r})^\wedge \mathrm{T}))\text{-}1)\text{-}1 \qquad \textbf{(4)}$$

Cattle Equations of Motion

Cow/calf production is based on typical ratios between different animal classes as defined in Turner et al. (1998). There are 4 age classes on the ranch: calf, yearling replacement heifer, first calf heifer and mature cow. All replacement heifers are retained from the calf crop. The calf weaning success rate (CLF) is assumed to be 88%. This is based on a 95% conception rate for cows (all replacement heifers were pregnancy tested in the fall), a 2% death loss during calving and a 5% calf loss after birth (Turner et al. 1998). In November, heifer calves can be sold ($\mathrm{SELLCALFF_t}$) or kept as heifer replacements for the next year ($\mathrm{REPL_{t+1}}$) as represented in equation 5. All steer calves are sold after weaning in the fall (equation 6).

$$SELLCALFF_t = (COW_t + FIRST_t) * CLF * 0.5 - REPL_{t+1} \qquad \textbf{(5)}$$

$$SELLCALFM_t = (COW_t + FIRST_t) * CLF * 0.5 \qquad \textbf{(6)}$$

For the year after their birth, retained heifer calves ($\mathrm{REPL_t}$) are considered part of the herd as yearlings. After being pregnancy tested in the fall, these possible replacements are either sold as yearling heifers ($\mathrm{SELLYEAR_t}$) or kept as part of the herd for the next year ($\mathrm{FIRST_{t+1}}$) as shown in equation 7.

$$\mathrm{REPL_t = FIRST_{t+1} + SELLYEAR_t} \qquad \textbf{(7)}$$

Due to low conception rates and the desire to keep only the best replacements, it is assumed that at least 25% of the possible heifer replacements are culled in November (equation 8).

$$\mathrm{SELLYEAR_t \geq 0.25 * REPL_t} \qquad \textbf{(8)}$$

The size of the herd (equation 9) is a function of the previous year's cow herd, number of replacements kept as first calf heifers from the last 2 years and the number of cows lost due to mortality or culling.

$$\mathrm{HERD_t = COW_t + FIRST_t + REPL_t} \qquad \textbf{(9)}$$

Equation 10 represents the equation of motion for cows.

$$\mathrm{COW_{t+1} = (COW_t + FIRST_t\,)* (1\text{-}DEATH) - SELLCOW_t} \qquad \textbf{(10)}$$

The death loss rate (DEATH) is assumed to be 1%. Equation 11 sets the culling rate of mature cows to be at least 15% that is the typical rate of the study region (Turner et al. 1998).

$$\mathrm{SELLCOW_t \geq COW_t * 0.15} \qquad \textbf{(11)}$$

Calf survival rates are a function of the mother cow's age. To maintain the calf crop success rate of 88%, the herd is restricted by equation 12 to limit first calf heifers to less than one third of the number of cows.

$$\mathrm{FIRST_t \leq (COW_t + FIRST_t) *0.33} \qquad \textbf{(12)}$$

Other resource constraints, represented by equation (13), such as ranch facilities and equipment, limit the herd (cows, first calf heifers and yearling heifers) to a total of 500 animals.

$$\mathrm{HERD_t \leq 500} \qquad \textbf{(13)}$$

Forage Equations of Motion

The typical rancher in the northeast Oregon mountain region supplies a 345 animal unit herd (300 cows at 1 animal unit (AU) and 60 yearlings at 0.75 AU) with hay ($\mathrm{X_{L4}}$) for the duration of winter (Table 1), privately owned spring range and stringer meadows ($\mathrm{X_{L1}}$) for 3 months and Forest Service lands ($\mathrm{X_{L2}}$ and $\mathrm{X_{L5}}$) for 4 months. The model also includes the option of leasing private pasture ($\mathrm{X_{L3}}$).

There are 2 factors that influence the amount of forage available. The first is the amount of precipitation that falls during the crop year (September through June). One study found that 75 to 90% of forage yield fluctuations could be attributed to variations in the amount of precipitation received during the crop year. Sneva and Hyder (1962) found that the response of forage yield to changes in precipitation is consistent on a percentage basis even though productivity among study sites varied. The forecasting model they developed for range herbage production in eastern Oregon is incorporated in the model to adjust forage yields given precipitation parameters.

The number of animal unit days (AUD) available from privately owned pastures ($\mathrm{X_{L1}}$) and privately leased pastures ($\mathrm{X_{L3}}$) are fixed at their long-term averages regardless of precipitation conditions, shown with equations 14 and 15, since the focus of the economic analysis is on summer grazing when the dispersion project can be implemented.

$$\mathrm{X_{L1,t} \leq 31{,}567} \qquad \textbf{(14)}$$

$$\mathrm{X_{L3,t} \leq 10{,}523} \qquad \textbf{(15)}$$

For a minimum duration of 5 months (winter, 152 days), represented in equation 16, the herd is fed a mixture of native and alfalfa hay. Hay may be fed longer than 5 months if summer forage production is low or is needed to maintain a larger herd size.

$$\mathrm{X_{L4,t} \geq (COW_{t+1} + FIRST_{t+1} + 0.75 * REPL_t)*152} \qquad \textbf{(16)}$$

The second factor that determines forage supply is the management decision of the forage utilization levels achieved on private and public pasturelands. In light of research that may link forage utilization level to habitat quality for wildlife and fisheries, the Forest Service is beginning to regulate the maximum utilization level ($\mathrm{UTIL_{g,p}}$) of vegetation from their allotments. This model assumes that the utilization standards are 35% of riparian vegetation (subscript g1) and 50% of upland forage (subscript g2). Federal grazing permits purchased by the model ranch allow for 1,380 AUMs to be consumed. This amount of forage provides feed for 345 animal units for 4 months at regulated utilization conditions when crop year precipitation is at normal levels. Changes in precipitation will cause the quantity of forage produced from the Forest Service lands to vary. In years of low precipitation, the ranch manager must decide to decrease herd size, remove cattle early, and exceed the utilization standard or any combination of the 3.

There are consequences if the manager allows the utilization standard in the riparian zone to be exceeded. The penalty used in this model was based on practices observed in the region. While penalties vary among administrative units, this model assumes the agency will revoke twice the percentage exceeded ($\mathrm{OVER_{g,p,t}}$) from the total permitted amount from the next year's permit. For example, if the monitored riparian pasture is grazed at a 45% utilization level, 10% more than the agency's desired level, then the agency will lower the total permitted number of AUMs by 20% for the next year. Again, the ranch manager would face a decision to reduce herd size, remove cattle early, or exceed the utilization percentage. (Note that the model design does not account for a penalty that is cumulative. It is unlikely that the agency would permit the rancher to continue to exceed the standard without enacting harsher penalties. While the penalty is not an entirely accurate depiction of actual practices, limits of the GAMS software dictated this approach.)

Data collected for this study was for the period of mid July through August, which was only 1.5 months of grazing out of the usual 4 months of public land grazing. For analysis of the dispersion project, the public lease pastures are divided into 1 riparian pasture where the dispersion project can be implemented for 1.5 months (subscript p2) and 2 upland, non-riparian pastures with no dispersion project implemented (subscript p1). The non-project pastures are restricted to the regulated levels. Thus, the utilization standards only apply to the pasture grazed from mid July to the end of August when off-stream water and salt could be provided.

Forage supplied from public lands is divided into 2 categories. X_{L2} is vegetation consumed at or below the regulated utilization levels while X_{L5} represents consumption above the limits. Using Sneva and Hyder's (1962) forage production forecasting model, equation 17 predicts the amount of forage available for consumption at desired Forest Service levels.

$$X_{L2,t} \leq \sum_{g=1}^{2} \sum_{g=1}^{2} ((RAIN_t * 12.59^{-1}) * \\ 111 - 10.6) * 100^{-1} * YIELD_g * \\ (25 * HECTARE_{g,p} * (UTIL_{g,p} \\ - 2*OVER_{g1,p2,t-1}))^{-1} \qquad \textbf{(17)}$$

The exogenous number of hectares of riparian and upland area in the pastures is designated as $HECTARE_{g,p}$. Sneva and Hyder's (1962) regression equation for the forage yield index is $(RAIN_t/12.59) * 111 - 10.6) * 100^{-1}$ where $RAIN_t$ is an exogenous parameter that can be set at a low, median or high value, depending upon the crop year precipitation condition desired. The calculated amount of forage produced during a median year of crop year precipitation ($YIELD_g$) is divided by 11.36 kg/AUD to convert the equation into terms of animal unit days.

Nonproject pasture utilization ($UTIL_{g,p1}$) is set at the agency's desired utilization level of 35% riparian usage and 50% utilization for the uplands. Utilization on the second public lease pasture ($UTIL_{g,p2}$) depends upon whether off-stream water and salt is provided. It also is an endogenous figure within the model set for the P2 pasture. The percent of the riparian vegetation that is consumed beyond 35% the previous year in the treatment period pasture, P2 (equation 18), is $OVER_{g1,p2,t-1}$. It also acts as the agency's penalty and used in the calculation of available forage in equation 17. Equation 18 allows for grazing above the restricted levels and represents the forage available for consumption as X_{L5}.

$$X_{L5,t} \leq \sum_{g=1}^{2} \sum_{p=1}^{2}((RAIN_t * 12.59^{-1}) \\ * 111 - 10.6) * 100^{-1} * YIELD_g \qquad \textbf{(18)} \\ * 25^{-1} * HECTARE_{g,p} * OVERg_{1,p2,t}$$

The physical limit to vegetation utilization is set at 75% (equation 19).

$$UTIL_{g,p} + OVER_{g,p,t} \leq 0.75 \qquad \textbf{(19)}$$

The ratio between riparian and upland utilization may be influenced by the management decision of implementing the dispersion project. It is represented in equation 20 with α as the riparian:upland utilization ratio. This equation forces the model to have higher over-utilization on riparian areas (g1) compared to upland areas (g2) when over-utilization occurs. This over-utilization of riparian areas will be proportionately at least as great as that which occurs on the uplands.

$$OVER_{g1,t} \geq \alpha * OVER_{g2,t} \qquad \textbf{(20)}$$

Equation 21 represents forage demand for the entire year and ties together herd size and forage demanded. Cow/calf pairs are calculated as one animal unit and yearlings are 0.75 of an animal unit. Calves, bulls and horses are assumed not to consume from the forage available.

$$\sum_{L=1}^{5} XL,t \geq (COWt + FIRSTt + 0.75 \\ * REPLt)*365 \qquad \textbf{(21)}$$

Data Collection

The field-test of providing off-stream water and salt to cattle was conducted on the Eastern Oregon Agricultural Research Center's Hall Ranch in northeastern Oregon during mid July through August of 1996 and 1997. Utilizing a complete randomized block design, the study area was divided into 3 blocks. Each block was further divided into 3 treatment pastures. The 3 treatments included a control pasture with no grazing, a pasture with the off-stream water and salt project (dispersion pasture) and a pasture containing no alternative water or salt (non-dispersion pasture). In grazed pastures, cow-calf pairs were stocked at a rate of 1.17 ha per pair for 42 days to achieve 50% total vegetation utilization.

Cow and calf body weights and condition scores were determined prior to turnout and at the end of the study period. An analysis by treatment (dispersion versus non-dispersion pastures) of the 2 years of data in cattle weight gains and changes in cow body condition scores were conducted using the SAS (SAS Institute 1990) general linear models procedure (Table 2). Cattle provided off-stream water and salt did show improved weight gains ($P < 0.01$). Cows in dispersion pastures gained 0.27 kg/day more than cows without off-stream water and salt. There was no significant change in body condition scores for cows between treatments ($P < 0.56$). Calves with off-stream water and salt gained on average 0.14 kg/day more than calves in non-dispersion pastures ($P < 0.01$). This translated into improved animal performance that increased revenue received when cattle were sold.

Forage utilization in the riparian and upland portions of study pastures was estimated (Dickard 1998) using the Bureau of Land Management's utilization formula, shown in equation 22 (USDI 1996). Production weights were sampled in the control and treatment pastures to derive the utilization estimate.

$$\text{(control plot - treatment plot) /} \\ \text{control plot = \% utilization} \qquad \textbf{(22)}$$

Data collected at the Hall Ranch suggest the ratio between riparian and upland utilization is influenced by off-stream water and salt. [Utilization can be difficult to estimate (Burkhardt 1997). The method used here was on a total vegetation production basis. The utilization values listed here may not be "exact" but should be considered an indication of the riparian and upland utilization ratio that is achieved when the off-stream water and salt project is used.] When off-stream water and salt was provided, a larger percentage of upland vegetation was grazed compared to riparian vegetation. If cattle have to be removed when utilization reaches 35% in the riparian area, more upland forage can be consumed before reaching this restriction if cattle are attracted out of the riparian area. The study shows only 25% of the upland for-

Table 2. Comparison by treatment of average daily gain (kg/day) for cattle and change in body condition scores for cows, 1996 and 1997.

Treatment	Cow average daily gain	Calf average daily gain	Change in cow body condition score
	--------------------------------(kg/day)------------------------------		
Dispersion pasture	0.70 ± 0.02^a	1.01 ± 0.005^a	0.08 ± 0.05^a
Non-dispersion pasture	0.42 ± 0.02^b	0.87 ± 0.005^b	0.04 ± 0.04^a

^{a,b} Means (± standard errors) in the same column followed by different superscript significantly differ ($P < 0.01$).

Table 3. Riparian utilization standard and resulting upland utilization for public lands.

	Nonproject Pastures (pl)	Project Pasture (p2) without Off-Stream Water	Project Pasture (p2) with Off-Stream Water
Riparian Vegetation	0.35	0.35	0.35
Upland Vegetation	0.5	0.25	0.5

age in a non-project pasture will have been grazed when the 35% utilization level is reached in the riparian area. Table 3 lists the allowable utilization levels if the manager complies with the desired utilization limitations. Thus the α in equation 20 is influenced by the use of the dispersion project as shown in equation 23 (non-dispersion) and 24 (dispersion). More upland forage (g2) is consumed before reaching the limits of riparian utilization (g1) in the dispersion pastures in equation 20.

$$\text{OVER}_{g1,t} \geq 1.4 * \text{OVER}_{g2,t} \qquad \textbf{(23)}$$

$$\text{OVERg1,t} \geq 0.7 * \text{OVER}_{g2,t} \qquad \textbf{(24)}$$

The assumption has been made that the cattle are grazing in the same distribution ratio between the riparian and upland throughout the grazing season. Based upon GIS analysis of distribution patterns, this appeared to be true for cattle in pastures with off-stream water and salt (Dickard 1998). In contrast, the non-dispersion project pastures showed cattle concentrated in the riparian areas early in the grazing period and then moved more to the uplands in the latter parts of the grazing period.

Solution Method

The bioeconomic model is solved using the General Algebraic Modeling System (GAMS) developed by Brooke et al. using the GAMS/MINOS solver (Modular Incore Nonlinear Optimization System) developed by Murtagh and Saunders (Gill et al. 1992). A 60-year time horizon was chosen to allow the model to reach an equilibrium state and to capture the economic value of variables over the lifetime of the ranch. The equilibrium states of the model run with and without the dispersion project were compared to determine economic feasibility.

For simplification in the interpretation of the model results, the economic analysis of the dispersion impacts is run with a 7% discount rate. The 9 states of nature representing combinations of precipitation and market price conditions have been assigned numbers to simplify display of model results. The model number refers to the levels of crop year precipitation and cattle prices with 1 = low, 2 = median and 3 = high. When a p is present, off-stream water and salt are provided in the uplands of the summer pasture.

Results

The dispersion project has 3 significant impacts on annual gross margin. The first is the direct cost of the dispersion project. The annual dispersion project costs are the sum of the investment cost spread over the lifetime of the equipment and the increases in variable costs such as labor. The second impact is the benefit of better cattle distribution. This allows more forage to be consumed in the uplands of pastures with off-stream water and salt before the riparian utilization limit is reached. This translates into more animal units allowed to graze or fewer AUMs purchased from other sources such as leased pasture and hay. The third impact is the increase in weight gain for cows and calves grazing in pastures with the dispersion project. Model results will be examined under 2 policy scenarios of with and without a riparian area utilization standard and overgrazing penalty. Comparison of those results should indicate the marginal effects on the long-term ranch operation.

Scenario A. Riparian Utilization Penalty

Scenario A assumes that there is a 35% utilization limit on public land riparian areas. If utilization above this level occurs, a reduction in the ranch's permit is invoked for the next year. This penalty is set as a disincentive to exceed the utilization limit. Table 4 is a detailed presentation of the number of cows stocked under each state of nature. Herd size fluctuates based on precipitation, price level and use of the dispersion project. Forage consumption also fluctuates with precipitation, price and use of the dispersion project as shown in Table 5. Private lease as a forage supply option is undertaken only when prices are in the median and high cate-

Table 4. Long run equilibrium number of cows for ranches operating with and without the dispersion project under scenario A (penalty for exceeding 35% utilization of riparian vegetation on public lands) at 7% discount rate.

	Precipitation					
	Dry		Median		Wet	
Price	Non-project	Project	Non-project	Project	Non-project	Project
Low	239	264	266	295	294	331
Median	281	307	307	33	336	373
High	281	306	307	337	336	373

Table 5. Long run equilibrium decision levels for forage usage (in AUD) under scenario A (penalty for exceeding 35% utilization of riparian vegetation on public lands) at 7% discount rate.

	Feed Source			
Model	Own forage	Public lease	Private lease	Hay
11[a]	31,740	27,446	0	42,236
11p	31,740	33,465	0	46,532
21	31,740	33,871	0	46,821
21p	31,740	41,299	0	52,122
31	31,740	40,979	0	51,894
31p	31,740	49,967	0	58,307
12	31,740	27,446	10,350	49,622
12p	31,740	33,465	10,350	53,918
22	31,740	33,871	10,350	54,207
22p	31,740	41,299	10,350	59,508
32	31,740	40,980	10,350	59,280
32p	31,740	49,967	10,350	65,693
13	31,740	27,446	10,350	49,622
13p	31,740	33,465	10,350	53,918
23	31,740	33,871	10,350	54,207
23p	31,740	41,299	10,350	59,508
33	31,740	40,980	10,350	59,280
33p	31,740	49,967	10,350	65,693

[a] Model number refers to crop year precipitation and prices, respectively, where 1 = low, 2 = median, 3 = high and "p" indicates the dispersion project.

gories. Herd size is reduced by approximately 42 cows during low cattle prices rather than leasing the more expensive forage. Under the condition of limiting riparian utilization to 35% on public lands and low cattle prices, the 300-cow ranch cannot support the herd if off-stream water and salt are not provided during median precipitation years. In all model versions, the maximum allowable level of forage is consumed from privately owned range, which is restricted regardless of precipitation conditions to 1 month of feed for 345 animal units. If all pastures had been allowed to fluctuate under the various crop year precipitation levels, herd size would have more dramatic decreases in dry years, remain constant in median years and higher increases in wet years. Under all price conditions, hay is fed only during the required 5 months of winter. The highest allowable level of forage use, under desired riparian utilization levels, is consumed from the public lease. The maximum value for public forage changes depends upon the precipitation conditions and the use of the dispersion project (Table 4). For the median rain and price model, an extra 7,430 AUDs (or 240 AUMs) of forage consumption are supported with improved distribution between riparian and upland areas. This yields enough forage to support an additional 34.5 animal units for 7 months.

In all states of nature, the dispersion project increases the ranch's average annual gross margin. Table 6 illustrates the change in average annual ranch gross margin realized when cattle are provided off-stream water and salt during a month and half of summer grazing. Increases of $3,800–$13,000 are found by implementing the dispersion project, depending upon precipitation and price conditions. Even in low price and drought conditions, the additional $3,800 in average annual gross margin indicates a rapid payback period for the project. Initial investment costs for the dispersion project are approximately $2,400, which is spread over its useful life of 10 years.

Table 6. Change in average annual gross margin less dispersion costs when dispersion project is implemented under scenario A (penalty for exceeding 35% utilization of riparian vegetation on public lands) at 7% discount rate.

	Precipitation		
Price	Dry	Median	Wet
Low	+ $3,820	+ $4,526	+ $5,303
Median	+ $6,595	+ $7,289	+ $11,737
High	+ $9,327	+ $11,075	+ $13,008

An analysis of the increased $7,300 in average annual gross margin for the median price and precipitation state of nature shows approximately half ($3,800) is from the increased weight gain of cattle grazing in pastures with the dispersion project. The remaining amount of increase can be attributed to the income from the sale of the extra 20 calves, 2 yearling heifers and 5 culled cows that are produced by the larger herd.

To compensate for the reality of imperfect information, expected values were determined by assigning probabilities to the different states of nature. The crop year precipitation data has a normal distribution with a standard deviation of 66 mm. The probability of precipitation being equal to or less than the low value is 20%. The probability of rain being greater than or equal to the high value is 17%. This yields a 63% chance that the value will be near the median value (within plus or minus 1 standard deviation from the median value). Cattle prices exhibit autocorrelation because of their tendency to follow a trend in the price cycle. In other words, cattle prices do not generally jump from a low price in 1 year to a high price in the following year. Therefore, the probability of switching between low, median and high values is extremely low. To compensate for this fact, 3 expected values of the dispersion project, one for each price level, are calculated according to the probability of the precipitation states.

Table 7. Expected value for off-stream water and salt in terms of change in average annual gross margin under scenario A (penalty for exceeding 35% utilization of riparian vegetation on public lands) at 7% discount rate.

	Precipitation			
Price	20% probability of a dry year	63% probability of a normal year	17% probability of a wet year	Expected value
Low	20% * $3,820	63% * $4,526	17% * $5,303	$4,517
Median	20% * $6,595	63% * $7,289	17% * $11,737	$7,358
High	20% * $9,327	63% * $11,075	17% * $13,008	$11,054

Table 7 is the payoff matrix for the expected value of the off-stream water and salt project. During the period of low cattle prices which Oregon ranchers were facing during the study, the project has an expected value of $4,500 in increased annual gross margin less the annual cost of implementing the dispersion project. As cattle prices increase, the expected value increases to $7,400 and $11,100 for median and high prices.

Scenario B. Project on Own Pasture with no Penalty

The dispersion project's expected value can also be calculated for situations in which the rancher is allowed a higher utilization level. For example, many range managers graze their own riparian lands at a 50% utilization level. The model is modified to reflect this type of situation to determine if the project would increase annual gross margin. The penalty in the forage equation of motion (eq. 17) is removed from the model and the allowable utilization percentages are increased as shown in Table 2. Table 8 illustrates the calculated expected change in annual gross margin when the project is implemented under these conditions. The expected value of providing off-stream water and salt is $2,400, $3,300 and $4,000 under low, median and high price levels, respectively. These increases in expected gross margin are created from the additional weight gain of the culled cows and sold calves.

Table 8. Expected value for off-stream water and salt in terms of change in average annual gross margin less the dispersion project costs under scenario B (riparian utilization of vegetation set at 50% on public lands) at 7% discount rate. (Expected value determined by multiplying the change in gross margin for that state of nature by the probability of that precipitation state occurring).

	Precipitation			
Price	20% probability of a dry year	63% probability of a normal year	17% probability of a wet year	Expected value
Low	20% * $2,122	63% * $2,428	17% * $2,764	$2,424
Median	20% * $3,476	63% * $3,314	17% * $3,699	$3,312
High	20% * $3,191	63% * $4,109	17% * $4,536	$3,976

Conclusions

Regardless of precipitation and price conditions, the off-stream water source and salt dispersion project examined in this study has a positive net return for ranches dealing with riparian grazing concerns. Better distribution of cattle allows for more upland forage to be consumed before reaching desired riparian utilization levels. The cows and calves also show higher weight gains when given access to off-stream water and salt. As riparian utilization becomes more restrictive, providing off-stream water and salt may be a way that traditional grazing levels can remain while environmental objectives (reduced livestock impacts in the riparian area) are also obtained. Part of the dispersion returns comes from the assumption that riparian utilization is a key factor in determining when cattle are removed from public lease pastures. However, criticism about utilization as a management tool must be considered. First, the vegetation sampling for utilization analysis is often done after cattle are removed. This means that a rancher will not know until after the fact that riparian utilization has exceeded the standard. To avoid this, a rancher would have to dedicate additional labor to periodic sampling during the grazing season. In addition, the correct method for utilization analysis is subject to debate (Oregon State University 1998). There will continue to be conflict between the ranching industry and public agencies if utilization becomes the "measuring stick" for management.

There are indirect economic benefits of the dispersion project not captured by the model. The only captured economic values are the increased weight gains of cull cows and calves and the increase in numbers of sale animals over the non-project conditions. The weight gain on the brood cows (non-sale animals) can also be associated with the improved health of cows and better calving success rates (Hart et al. 1988). As riparian areas recover, they also can provide the rancher with higher quality and quantity of forage (Elmore and Beschta 1987). More biological research needs to be conducted in riparian lands on the interaction of grazing levels and future forage production yields.

There are also social benefits that may have accrued from implementing off-stream water and salt in livestock pastures. In addition to an economic assessment, 3 other focus areas were included in the dispersion project study. They include riparian area assessment, biodiversity counts and animal behavior and performance. The initial ecological assessments collected for the project are beginning to be determined and may show improvements in riparian area health. With a positive economic feasibility assessment completed on the dispersion project, it opens the door for discussion with range managers on improving riparian grazing with a method that should be non-threatening to their livelihood. More interdisciplinary studies like the one conducted at the Hall Ranch in the summer of 1996 and 1997 are needed so that all ecological, economic and social aspects are included in finding a sustainable solution to grazing in riparian areas. Bioeconomic models such as the one presented here are a movement toward a better method of comparison when complex biological systems are involved.

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Economics of sale weight, herd size, supplementation, and seasonal factors

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Abstract

A growth function for range calves is estimated using a polynomial function of calf age that accounts for weather variation, sex, prior calf weights relative to a norm, and a compensatory gain factor. Data on rainfall plus calf weights at birth and when calves were roughly 3, 8, 12, and 20 months of age are used to estimate the growth function. This function is then used to determine the economic trade-off between herd size and calf sale weights, for both spring and fall sale dates. In addition, the profitability of feeding supplement is evaluated by increasing the rate of gain beyond that projected by the the polynomial age growth function for southeast and central Arizona grazing environments when forage and nutrients are limited. Using prices from 1980 to 1998, results indicate that the most profitable herd mix, sale date, and feeding protocol for the southeast Arizona region is 204 kg calves with no supplemental feeding and sales occurring in May. Supplemental feeding and sales occurring at 250 kg head^{-1} in May is the most profitable herd mix for the central Arizona region. More favorable average daily gain rates for May sales from the central versus southeast is why supplemental feeding is marginally better for the central region than feeding no supplement.

Key Words: optimal calf sale weight, livestock supplementation effects, livestock marketing, polynomial age growth function, rainfall

Resumen

Se estimó una función de crecimiento para becerros en pastizales usando una función polinomial de la edad del becerro que toma en cuenta la variación de clima, el sexo, los pesos de becerro relativos a la norma y un factor de ganancia compensatoria. Datos de precipitación, del peso de los becerros al nacimiento y del peso cuando tenían aproximadamente 3, 8, 12 y 20 meses se usaron para estimar la función de crecimiento. Luego esta función se uso para determinar los sacrificios económicos entre el tamaño del hato y los pesos de venta de los becerros, tanto para fechas de venta de primavera como de verano. Adicionalmente, se evaluó la rentabilidad de suplementar para incrementar la tasa de ganancia más alla de lo proyectado por la función polinomial de edad de crecimiento para ambientes de apacentamiento del sudeste y la región central de Arizona cuando el forraje y los nutrientes son limitantes. Usando precios de 1980 a 1998, los resultados indican que la mezcla de hato, fecha de venta y protocolo de alimentación más rentables para la región sudeste de Arizona es becerros de 204 kg sin suplementación y las ventas realizadas en Mayo. La alimentación suplementaria y las ventas en Mayo con pesos de 250 kg cabeza^{-1} es la mezcla de hato mas rentable para la región central de Arizona. Las tasas promedio de ganancia diaria de peso mas favorables en Mayo de la región central versus la región sudeste es la razón por la que la alimentación suplementaria es marginalmente mejor para la región central que el no suplementar.

The trade-off between sale weight and timing of sales is complicated by seasonal forage and price conditions along with variation in the price spread between light and heavy calves. Generally, lighter calves sell for a higher price per unit of weight than heavier calves and calf prices in the spring are greater than in the fall, but exceptions to these generalities occur. In addition, variability in seasonal rainfall and the ability to feed supplement complicates analyzing trade-offs between rates of gain, sale weight, herd size, and the timing of calf sales.

Some ranches have adopted a rather rigid selling practice for their calves to take advantage of seasonal forage availability and aggregate numbers for a given sale to attract more buyers. For example, ranchers in the central region of Arizona typically sell calves in the spring while southeast Arizona ranchers generally sell in the fall. Both regions sell mainly according to the time of year, irrespective of the weight of their calves, and very few feed substantial supplements. Because Arizona ranchers often question the economic trade-offs between calf sale weights, herd size, rates of gain and feeding supplement, and a spring versus fall sale date, the primary objective of this analysis was to address these issues. More specifically, the profitability of an Animal Unit (AU) grazing resource is quantified with and without supplemental feeding under the different sale weights of either 159, 204, 250, 295, or 340 kg head^{-1} for May and November sale dates from 2 different Arizona regions. In addition, the economic impact of a fertility increase in conjunction with supplemental feeding and the profitability of heavier calf weights during "extra grass" years are evaluated.

Quantifying the future rate of gain for a calf kept on the ranch is a critical element for evaluating the profitability of different marketing dates. Selling calves at a heavier weight generally comes with an opportunity cost of reducing the number of cows that can be maintained on the ranch, thus also reducing the number of calves that can be sold. Several studies have looked at animal performance under different range conditions with a production focus and little economic analysis (e.g., Clayton et al. 1983, Fox and Black 1977, Tess and Kolstad 2000). Notable exceptions are Van Tassell et al. (1987) and Lambert (1989). Van Tassell et al. (1987) quantified variations in calf weights from different

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managerial, biological, and weather variables. Six separate models were used to estimate calf weights at 6 different ages. The model developed herein differs since it estimates calf weight as a continuous function of age from birth to 20 months of age. Variation in birth dates and subsequent single-day weighing dates for all calves after birth allows for calf weights to be estimated as a continuous function of age.

Lambert (1989) used a discrete stochastic programming model to evaluate the retention of fall-weaned calves and their optimal rate of gain under different states of nature and price expectations. The purchase of additional winter feed rations was required to retain calves and maintain the size of the cow herd. Given that feeding hay as an energy source to southwestern range cows is quite costly and generally kept to a minimum, this study evaluates the cost of heavier calf weights as a tradeoff with reduced cow numbers rather than as additional feeds purchased. This framework identifies the best herd mix for the fixed range resource. Supplemental feeding is considered, but retaining calves to reach heavier weights still does not occur without some reduction in cow numbers. This analysis also evaluates seasonal market and production factors associated with calf and cull cow sales occurring in either the spring (mid-May) or fall (mid-November.)

Materials and Methods

Calf weight data was collected from the registered Hereford herd of the San Carlos Apache Tribal Ranch, Arsenic Tubs, Ariz. (N33°20'30", W109°48'46") for the 8 years of 1980, 1981, 1983 to 1986, 1988, and 1989. These years were the most complete and current we could find for calf weights from birth to 20 months of age. A birth date and calf weight at birth was recorded for each calf. In addition, weights were taken when the entire calf crop was at an average age of roughly 3, 8, 12, and 20 months of age. Weight and animal combinations are such that we have 1,368 calves and 5,862 unique calf weights. There was not a complete set of weight data for all calves. Most of the missing weights were associated with 3-month weights. Different calving dates provide age variation around each weighing date so that calf weight was estimated as a continuous function with respect to age.

More formally, calf *i*'s weight (kg head^{-1}) at the *j*th weighing ($WT_{i,j}$, $j = 1, 2, 3, 4$, and 5, and corresponds to weights taken at birth and roughly 3, 8, 12, and 20 months of age) was estimated as

$$WT_{i,j} = GFRS_{i,j} + \left(D_j \delta_{wj}(WT_{i,j-1} - GFRS_{i,j-1})\right)_{j\geq 2} + \left(D_j \delta_{CGj} CG_{i,j}\right)_{j=5} + \varepsilon_{i,j} \quad \textbf{(1)}$$

where

$$GFRS_{i,j} = \left(\sum_{a=0}^{8} \beta_i Age^{a}_{i,j} + \left(D_j \delta_{rj} Rain^{j-1 to j}_{i,j}\right)_{j\geq 3}\right)(1 - DH_i\delta_h), \text{ and} \quad \textbf{(2)}$$

$$CG_{i,5} = [(WT_{i,4} - WT_{i,3}) - \sum_{a=0}^{8} \beta_i (Age^{a}_{i,4} - Age^{a}_{i,3})][1 - DH_i\delta_h]. \quad \textbf{(3)}$$

The term $GFRS_{i,j}$ corresponds to calf weight (kg head^{-1}) estimated as an 8th order polynomial growth function of calf age in months ($Age_{i,j}$) plus a rainfall component[1] ($Rain^{j-1 to j}_{i,j}$), and this weight is adjusted lower by a constant percentage (δ_h) for heifers. The term $Rain^{j-1 to j}_{i,j}$ is the rainfall (cm) accumulated for the months between the prior and current weighing periods (*j*-1 to *j* for $j \geq 3$) minus the 30-year-average rainfall for these same months, as reported by the Western Regional Climate Center (1961–1998) for the San Carlos Reservoir. The polynomial growth function has flexibility to allow for the dip in calf weight that occurs from weaning and seasonal forage availability. Rainfall effects were not considered for birth and 3-month weights since cows will generally pull down their body condition to provide milk for a young suckling calf if rainfall and forage has been poor (Sprinkle 2000). Similarly, compensatory gains were not considered for weigh dates other than the 20-month weighing since a calf obtains most of its nutrients from the cow between birth and the 3-month weighing.

Compensatory gain at the 20-month weighing or $CG_{i,5}$ is accounted for by using the difference between the actual weight change from the 12th- and 8th-month weighings versus the weight change expected from the polynomial growth function of calf age adjusted for sex differences. How a calf's actual weight compares to its norm based on age, sex, and rainfall at its previous weigh date (i.e., $WT_{i,j-1}-GFRS_{i,j-1}$) identifies calves that are consistently above or below their projected norm, whereas $CG_{i,5}$ accounts for the unusual or non-consistent weight patterns. For example, a calf that was above the polynomial growth curve after accounting for sex differences at its 8-month weighing but below this curve at its 12-month weighing can realize an extra or compensatory weight gain at its 20-month weighing through $CG_{i,5}$.

The dummy variable D_j equals 1 at the *j*th weighing; otherwise, its value equals 0. Similarly, DH_i equals 1 or 0 if the *i*th calf is a heifer or steer. $\varepsilon_{i,j}$ is a normally distributed error term with mean 0 and variance σ^2. Parameters estimated include an 8th order polynomial function of age that describes a growth path for steers from birth to 20 months of age (β_0,...,β_8), coefficients that quantify rainfall effects on 8-, 12-, and 20-month weighings (δ_{r3}, δ_{r4}, δ_{r5}), values that describe how actual calf weights relative to their norm at prior weighings impact calf weights (δ_{w3}, δ_{w4}, δ_{w5}), compensatory gain at the 20-month weighing (δ_{CG5}), and the percentage weight discount for heifers relative to steers (δ_h). Equation (1) was estimated using the least squares maximum likelihood procedure in TSP™ v4.5 (1999).

To gain insights into the trade-off between different sale weights and dates, real profits in constant 1999 dollars for 2 different ranching regions were simulated from 1980 through 1998 using either mid-May or mid-November sale dates for steer calves that weighed either 159, 204, 250, 295, or 340 kg head^{-1}. These weights correspond to the median of Cattle-Fax's sale weight categories so that 159 kg head^{-1} refers to sale prices within the weight range of 136 to 181 kg head^{-1} (i.e., 300 to 400 lb head^{-1}) and similarly for the heavier sale weights. The 2 regions examined have distinct seasonal forage differences. The southeast region of Arizona is dependent upon the summer monsoon rains for warm season grass production, while central Arizona is more dependent upon winter rains for its production of cool season grasses and legumes such as jojoba (*Simmondsia chinensis*).

Table 1 shows the average daily gains estimated for different sale weights and dates by region plus the equivalent cow numbers that can be maintained for each scenario. Rates of gain for the 2 regions were set up to mirror each other with the

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[1] The i subscript is maintained for the rainfall variable to denote variation in rainfall from 1 year to the next, even though rainfall is the same for all calves within a given year.

Table 1. ADG (kg day^{-1}) and equivalent cow numbers^{a}.

	Southeast Arizona		Central Arizona	
Calf Weight	May Sales	Nov. Sales	May Sales	Nov. Sales
kg head^{-1}		(kg day^{-1})		
No Supplemental Feeding		(equivalent cow numbers)		
Birth to 159	0.723	0.803	0.803	0.723
	(1.000)	(1.000)	(1.000)	(1.000)
159 to 204	0.661	0.587	0.587	0.587
	(1.000)	(1.000)	(1.000)	(1.000)
204 to 250	0.180	0.200	0.200	0.180
	(0.743)	(0.763)	(0.763)	(0.74)3
250 to 295	0.694	0.771	0.771	0.694
	(0.688)	(0.710)	(0.710)	(0.688)
295 to 340	0.445	0.494	0.494	0.445
	(0.606)	(0.631)	(0.631)	(0.606)
Supplemental Feeding				
204 to 250	0.714	0.608	0.608	0.714
	(0.920)	(0.927)	(0.927)	(0.920)
250 to 295	0.714	0.608	0.608	0.714
	(0.839)	(0.853)	(0.853)	(0.839)
295 to 340	0.714	0.608	0.608	0.714
	(0.762)	(0.780)	(0.780)	(0.762)

^{a}Equivalent cow numbers in parentheses were obtained by reducing available Animal Unit Years for cows by 0.5, 0.6, and 0.7 for the number of days it took calves that would be sold to go from 204 to 250, 250 to 295, and 295 to 340 kg head^{-1}, respectively. No distinction was made for weights less than 204 since these calves always reached their weight before 8 months of age, within the normal bounds of a one-year breeding and calving cycle.

most favorable gains occurring prior to November and May sales for the southeast and central regions. The most favorable forage conditions under supplementation assume a growth rate of 0.803 kg day^{-1} for weights from birth to 159 kg and 0.794 kg day^{-1} for weights from 204 to 340 kg head^{-1}. These rates of gain were reduced by 10% when forage is less abundant in each region prior to the animal's sale date. These growth rate assumptions and the 10% reduction applied when forage is less abundant were derived from conversations with University of Arizona colleagues and Arizona ranchers. To calculate the cows that could be supported on an Animal Unit Year (AUY) of forage, reductions of 0.5, 0.6, and 0.7 AUYs were charged for the number of days it took calves to go from 204 to 250, 250 to 295, and 295 to 340 kgs, respectively. For example if it took 180 days for a calf to go from 204 kg to 250 kg, the AUY reduction would be 0.5*(180/365), where 0.5 is the assumed Animal Unit equivalency for this average calf weight. The AUY reduction for producing calves heavier than 204 kg head^{-1} has the effect of reducing total cow numbers and thereby reducing the number of calves available for sale. No opportunity cost of fewer cows is added when going from 159 to 204 kg sale weights since 204 kg calves are weaned at about 7 months of age, which allows ample time for cows to breed back in a year-round calving system.

Birth dates and supplement requirements to meet the daily rates of gain in Table 1 are described in Table 2. Birth dates were calculated working backwards from the sale date and the corresponding rate of gain for each protocol. The amount of supplement required is dependent upon sale weight, sale date, and region. Prior to weaning, calves less than 204 kg head^{-1} consume little forage so that supplemental feeding was only considered for calves above this weight level. The amount of supplement fed ranged from 45 to 181 kg AU^{-1}, varying in average annual cost from \$10.31 to \$41.23 AU^{-1}. The cost (\$/kg) of a 50:50 corn meal and cottonseed meal mixture was charged using Arizona corn meal and cottonseed feed costs for the quarter fed as reported by U.S. Department of Agriculture, Agricultural Prices (1980–1998). Because some ranchers may be able to obtain more of a wholesale than retail price for supplement, we did not charge additional labor or fuel expenses for distributing supplement to the cow herd. However, the distribution costs for supplement may be very important, depending on the terrain of the ranch.

Another expense item that varied with different sale date and weight options was the opportunity cost of sale. That is, calves sold at 204 kg could have been sold at 159 kg and so forth. The opportunity cost of funds was charged at a real annual interest rate of 4%. All other cost items except for grazing expenses were obtained from Economic Research Service's cow-calf production costs for the West (USDA 1982–1998). Cash grazing costs were calculated using the grazing fees and accompanying percentages of grazing land in Arizona owned by the State (33%), Bureau of Land Management (17%), Forest Service (40%), or Private entity (9%) as reported in Mayes and Archer (1982). Common variable and fixed cash expenses for all sale weight and date combinations are available in Tronstad et al. (2001). Gao (1996) also provides more detail about the cost items incorporated.

Cull cows were assumed to weigh 454 kg head^{-1}, irrespective of the herd's mix or production protocol. In addition, a calf crop percentage of 80% per exposed cow, calf death loss after birth of 2.5%, and a culling percentage of 16% with a 4% annual death loss for cows was applied to all scenarios. The calf crop percentage of 80% per exposed cow falls within the range of values given in Teegerstrom and Tronstad (2000). Calf and cow death loss-

Table 2. Supplement requirements and calculated birth dates by sale date, sale weight, and location.

Calving Date			Supplement Required 50:50 Corn & Cottonseed Meal Ration	
SE AZ May Sales	Central AZ Nov. Sales	Sale Weight	Calf	Calf-Cow
		(kg head^{-1})	(kg head^{-1})	(kg pair^{-1})
27 Nov.	30 May	159	—	—
21 Sept.	24 Mar.	204	—	—
19 July	19 Jan.	250	92	0
17 May	17 Nov.	295	113	23
14 Mar.	14 Sept.	340	136	45
Nov. Sales	May Sales			
16 June	14 Dec.	159	—	—
16 April	14 Oct.	204	—	—
18 Feb.	18 Aug.	250	0	45
23 Dec.	22 June	295	0	92
27 Oct.	26 April	340	0	136

Note: Expert opinion was used to determine the supplement requirements needed to attain the ADG rates described in Table 1.

Table 3. Range calf growth model and corresponding parameter estimates.

Variables	Description	Corresponding Parameters	Parameter Estimates	t-values
Constant	β_0 equals estimated birth weight	β_0	37.143	52.277
$Age_{i,j}$	(kg head^{-1}). $Age_{i,j}$ indicates age of	β_1	96.924	13.246
$Age^2_{i,j}$	calf *i* in months at the *j*th weighing	β_2	-65.850	-9.509
$Age^3_{i,j}$	for each of the corresponding	β_3	22.565	9.384
$Age^4_{i,j}$	8th order polynomial terms.	β_4	-3.806	-9.106
$Age^5_{i,j}$	Polynomial order associated with the age	β_5	0.345	8.569
$Age^6_{i,j}$	growth function was determined by applying	β_6	-0.172E-01	-7.890
$Age^7_{i,j}$	the Schwartz (1978) criteria of estimating	β_7	0.446E-03	7.169
$Age^8_{i,j}$	$WT_{i,j}$ as a function of $\sum_{a=0}^{8} \beta_i Age^a_{i,j}$.	β_8	-0.470E-05	-6.467
DH_i	Dummy variable that is 1 if heifer and 0 if steer.	δ_h	-0.497E-01	-10.344
$(WT_{i,1} - GFRS_{i,1})$	Impact of the difference in animal *i*'s weight at	δ_{w2}	0.534	2.120
$(WT_{i,2} - GFRS_{i,2})$	their prior weighing versus that expected by	δ_{w3}	0.274E-01	1.839
$(WT_{i,3} - GFRS_{i,3})$	$GFRS_{i,j-1}$ at the *j*th weighing (*j*=2,3,4, and 5	δ_{w4}	0.406	28.269
$(WT_{i,4} - GFRS_{i,4})$	or the 3, 8, 12, and 20-month weighings,	δ_{w5}	0.763	35.872
	respectively.)			
$CG_{i,20}$	Compensatory gain effect at the 20-month weighing for animal *i*.	δ_{CG}	-0.497E-01	-5.868
$Rain^{2to3}_{i,3}$	Centimeters of rainfall from the *j*-1 to *j* month	δ_{r3}	2.001	17.120
$Rain^{3to4}_{i,4}$	weighing in a given year less the 30-year-average	δ_{r4}	0.727	11.378
$Rain^{4to5}_{i,5}$	rainfall for these same months (j = 3, 4, and 5).	δ_{r5}	0.614E-01	0.375
D_j	Dummy variable that is 1 if it is the *j*th weighing or 0 otherwise.			

Notes: Refer to equations 1 through 3 for a formal description of the variables and model estimated. The model's adjusted R-squared was 0.947 and standard errors used to obtain t-ratios were calculated using the Robust White procedure, using TSP™ v4.5.

es are mid-range to those reported by Tronstad and Gum (1994). The calf crop is assumed to be a 50:50 mix of steers and heifers. For a 100-AU ranch selling 159 or 204 kg calves, a total of 100 cows plus 20 heifers are exposed to the bull every year. The combined weight of heifer calves selected as replacements at weaning plus bred heifers will exceed the average weight of the 80-cow AUYs in the herd. But cows may die throughout the year and not just at weaning, offsetting the larger grazing needs of the combined heifer calf and bred heifer AUYs. Irrespective, the same heifer development costs are equally imputed for all scenarios. Out of the 100 cows, 16 are culled and 4 are expected to die. The 80% assumed fertility results in 96 calves born and the 2.5% calf death loss results in 93.6 calves at weaning. To replenish the cows that are culled or die, 42.7% (20/46.8) of all heifers are retained each year as replacements with 80% fertility. Thus, a 100-AU ranch selling 159 kg or 204 kg calves would expect to sell 16.0 cows, 46.8 steer calves (i.e., 120*0.8*0.975*0.5), and 26.8 heifer calves annually.

Results

Calf weights were estimated as a function of age, sex, climate, calf weights at the previous weighing relative to an expected weight, and a 20-month compensatory gain as described in equation (1). Table 3 provides the parameter estimates and corresponding statistics for this model. Note that the model to estimate calf weights is constructed so that if climate and prior calf weights have been at their norms, weight is simply an 8th order polynomial function of calf age in months with a constant weight percentage differential between steers and heifers. Figure 1 graphically describes this polynomial growth function for a steer calf from birth to 20 months of age as plotted against the actual calf weight data. Estimated calf weights from equation (1) are presented in Figure 2. Unlike logistical growth functions, the polynomial framework has flexibility to allow for the dip in calf weight that occurs from weaning and seasonal forage availability. An 8th order polynomial was selected from polynomial orders of 3 to 10 that were estimated, applying the Schwarz (1978) criteria to calf weight estimated as only a function of calf age. On average, calf weights at the 12-month weighing were 3.84 kg head^{-1} less than at the 8-month weighing. At any given age, heifer calves were estimated to weigh 2.25 kg head^{-1} less than a steer calf.

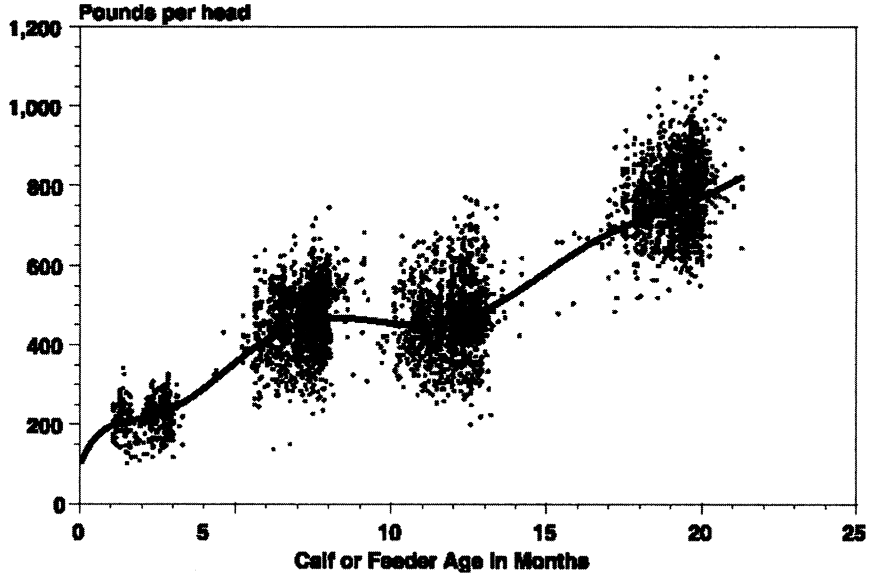

Fig. 1. Calf scale weights and estimated polynomial age growth function for steer calves.

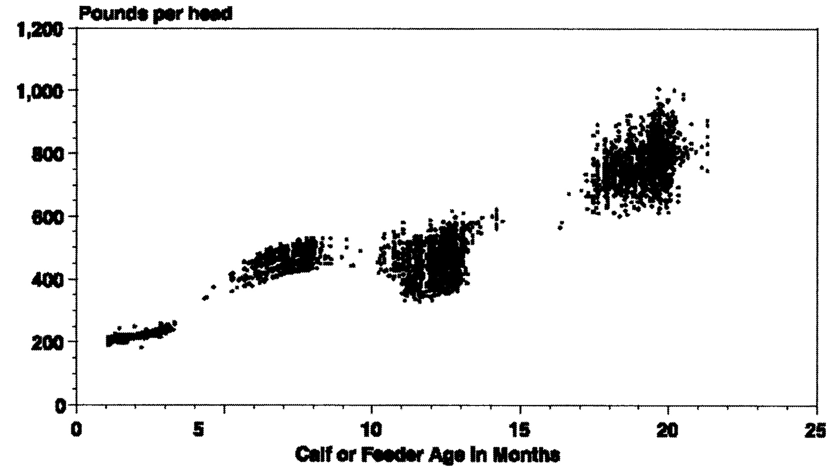

Fig. 2. Modeled calf weights based on equation 1.

If rainfall is above (below) the 30-year average for the months prior to a weighing, calves would be expected to weigh more (less) than otherwise at their current weighing. Rainfall between the prior and current weighing is used as a proxy to estimate forage conditions being above or below their long-term average. As indicated by the estimated rainfall parameters (Table 3), if the accumulated rainfall between the 3- and 8-month weighings was above the 30-year average by 1 cm, calves were estimated to weigh 2 kg head^{-1} more at the 8-month weighing than if rainfall was equal to the 30-year average. The magnitude and statistical significance of the rainfall variable decreases as the animal increases in age. This result is attributed to the 20-month compensatory gain effect and the greater importance of lagged weight components as the animal increases in age. That is, these factors were able to better capture both genetic and environmental components as the calves increased in age compared to the rainfall variable.

Using the weight gains estimated above, Cattle-Fax (1981–1998) prices for calf and cow sales, and the opportunity cost of forage described in Table 1 (i.e., reduced cow numbers for heavier calf weights), the average and standard deviation of 1999 real returns for different sale dates and weights is given in Table 4. A sale weight of 204 kg head^{-1} for May with no supplemental feeding is the most profitable alternative for the southeast Arizona region. An average real return of \$120.45 AUY^{-1} for the southeast was realized for the 19 years from 1980 to 1998. The most profitable scenario for the central Arizona region was a 250 kg sale weight with a production protocol of May sales and supplemental feeding. Supplemental feeding is more attractive for the central than southeast region because May sales have the most favorable rate of gain for the central Arizona region. The return in going for the 250 kg head^{-1} May sale weight feeding supplement is only \$4.30 AUY^{-1} or 3.6% higher than the lighter 204 kg head^{-1} weight class, but an impact in fertility would likely increase the return from feeding supplement as described below.

While the returns associated with the heaviest 2 sale weights of 295 and 340 kg head^{-1} are consistently low, the risks or standard deviations associated with these weights are generally lower as well. The highest 2 weight classes of 295 and 340 kg head^{-1} have a standard deviation that is on average 19% less than the more profitable lighter sale weights. However, the highest standard deviation of returns is also from feeding supplement and selling 340 kg head^{-1} feeders in the southeast region during November. Feeding large quantities of supplement adds a cost that significantly decreases profitability when the price of heavy feeders is low. However, supplemental feeding can really boost revenues by bringing more calves and weight to market when prices for heavier feeders are strong in the fall. Combined cost and seasonal market forces make this production and marketing protocol the most risky.

While cull cow sales make up only 20% to 23% of total revenues, they account for the largest share of the profit differential between May and November sales. Of the \$17.14 profit difference between May and November sales for 204 kg calves from southeast Arizona not fed supplement, cull cow sales account for 52% of the favorable revenue difference between these months. Steer and heifer calf sales account for 33% and 15% of the favorable May sale revenue difference. For 250 kg sale weights from the central region feeding supplement, cull cow sales account for 46% of the favorable difference in May over November revenues, while steer and heifer sales account for only 37% and 17% of this difference. However, if cull cow weights for a ranch are less for May than November instead of being equal as

Table 4. Average 1999 real return and standard deviation[a] of returns, (\$ AUY^{-1}), 1980–98.

	Southeast Arizona		Central Arizona	
Sale Weight	May Sales	Nov. Sales	May Sales	Nov. Sales
(kg head^{-1})	-----	--------- (\$AUY^{-1})	---------	-----
No Supplemental Feeding				
159	63.94 (67.04)	50.82 (62.38)	64.28 (67.11)	50.48 (62.32)
204	120.45 (73.80)	103.31 (69.58)	121.09 (73.92)	102.68 (69.47)
250	23.86 (54.01)	25.53 (54.21)	38.90 (56.66)	11.05 (51.58)
295	4.07 (49.52)	18.43 (53.20)	24.95 (53.12)	-2.02 (49.43)
340	-62.06 (39.09)	-31.89 (44.42)	-30.32 (44.25)	-63.38 (38.86)
Supplemental Feeding				
250	110.68 (73.22)	108.48 (71.58)	125.39 (74.10)	94.03 (70.78)
295	89.75 (69.95)	100.92 (72.87)	109.39 (71.73)	81.55 (71.15)
340	57.11 (66.56)	85.11 (93.18)	83.21 (69.53)	54.93 (68.91)

[a] The sample standard deviation of returns is in parentheses below the average of annual real returns.

Table 5. Average 1999 real return and standard deviation[a] of returns (\$ AUY^{-1}) for extra grass year scenarios, 1980–98.

	Southeast Arizona		Central Arizona	
Sale Weight	May Sales	Nov. Sales	May Sales	Nov. Sales
(kg head^{-1})	----------	(\$$\text{AUY}^{-1}$)	----------	
Supplemental Gains at No Supplement Cost				
250	131.57	118.82	135.85	114.72
	(73.41)	(71.62)	(74.21)	(70.85)
295	121.15	121.63	130.33	112.65
	(70.29)	(72.87)	(71.96)	(71.14)
340	99.04	130.58	114.68	96.49
	(67.06)	(76.59)	(69.92)	(68.79)
Non-Supplemental Gains with No AUY Reduction				
250	164.39	147.21	165.39	146.26
	(79.48)	(77.06)	(79.67)	(76.88)
295	199.26	190.50	200.63	189.18
	(84.65)	(86.43)	(84.91)	(86.18)
340	237.49	235.73	239.28	233.99
	(92.88)	(96.61)	(93.21)	(96.29)

[a]The sample standard deviation of returns is in parentheses below average annual real returns.

assumed, this would diminish the favorable revenue difference of May over November cull cow sales.

Without feeding supplement, the estimated polynomial age growth function is essentially flat after reaching 7 months of age or 204 kg head^{-1} for the next 5.5 months. However, supplemental feeding is able to remove the long flat period for range calves from 7 to 12.5 months of age. Feeding supplement at the level described in Table 2 to attain the accompanying Average Daily Gains (ADGs) described in Table 1 increases average AUY^{-1} profitability for 250 kg calves sold in May by \$86.82 and \$86.49 for the southeast and central regions, respectively. Even though supplemental feeding is not always the most profitable option, it consistently increases the return for sale weights above 204 kg head^{-1}, anywhere from \$83 to \$119 AUY^{-1}.

Table 5 illustrates what the return to different sale weights and dates would be if a rancher had "extra grass" so that supplemental gains were obtainable without feeding supplement or no reduction in AUYs was charged for selling calves at heavier weights. These values are to provide an illustrative benchmark that can be used to interpolate an abundant forage situation rather than suggest that supplemental gains or no AUY reduction will be attained in an "extra grass" year. Even when supplemental gains are available at no extra feed cost, 250 kg head^{-1} sales are the most profitable except for November sales in the southeast region. In general, the opportunity cost associated with foregone calf numbers and lower prices does not outweigh the benefit of heavier calf weights, even when supplemental gains are imposed with no added feed cost. But if no AUY reduction is charged for producing heavier calves, the heaviest calf weight of 340 kg head^{-1} yields the highest return with May sales still somewhat preferred over November sales for both regions.

While supplemental feeding removes the long flat growth period for range calves, it may also have an impact on fertility of the herd. The value (\$ AUY^{-1}) of a 1% increase in fertility associated with feeding supplement is given in Table 6, utilizing the supplemental ADGs described in Table 1. The value of a 1% increase in fertility is about \$5.50 AUY^{-1} for all supplemental fed sales. Using the returns given in Table 4, it would take an increase in fertility from feeding supplement of more than 1.78% ((120.45-110.68)/5.49) before it would be more profitable to sell calves at 250 rather than 204 kg head^{-1} for May sales in southeast Arizona. Because supplemental feeding and May sales of 250 kg head^{-1} is the most profitable option for the central Arizona region, fertility would have to decline by –0.78% ((121.09-125.39)/5.53) before it would not pay to feed supplement and increase the May sale weight from 204 to 250 kg head^{-1}. The value of a 1% increase in fertility accompanied with supplemental feeding is about the same for all sale weight categories because the supplemental fed rates of gain described in Table 1 are roughly the same for all calves above 204 kg head^{-1}.

Discussion and Conclusions

This study shows that the benefit of higher sale weights was not enough to overcome lower calf prices and fewer calf and cull cow sales for calf weights above 204 kg head^{-1} without feeding supplement. Supplemental feeding removes the nearly 0 rate of gain for calves from 7 to 12.5 months of age, so that for the central Arizona region 250 kg head^{-1} calf sales in May fed supplement is the most profitable option. May sales were found to be more profitable than November sales, even with lower ADG rates. More favorable market conditions for May than November sales are the main reason why May sales were often more profitable than November sales.

In calculating cost and return estimates for cow-calf ranches in Arizona, Teegerstrom and Tronstad (2000) conducted focus groups in 5 different regions to gain insights into typical production practices. They reported a typical sale weight for steers of between 204 to 250 kg head^{-1}, depending on the ranching region. This result is consistent with the most profitable sale weight category of 204 kg head^{-1} for the southeast and 250 kg head^{-1} for the central Arizona regions. With regards to sale date, a fair number of ranchers market their calves in the fall rather than the spring, and May was determined as the most profitable sale time for both regions. Given that the difference in profitability between May and November

Table 6. Value of a 1% increase in fertility[a] associated with supplemental feeding.

	Southeast Region		Region Central Region	
Sale Weight Category	Mid-May	Mid-Nov.	Mid-May	Mid-Nov.
(kg head^{-1})	----------	---------- (\$$\text{AUY}^{-1}$)	----------	----------
250	\$ 5.49	\$ 5.40	\$ 5.53	\$ 5.36
295	\$ 5.52	\$ 5.60	\$ 5.62	\$ 5.51
340	\$ 5.40	\$ 5.46	\$ 5.59	\$ 5.46

[a]For fertility changes up to 85.5% after the increase and starting with an initial fertility rate above 34.2%. Given a 100 AUY ranch with fertility rates above 85.5%, bred cows will need to be sold or less than 20 heifer calves will need to be retained for breeding to keep the herd at a constant AUY. Fertility rates below 34.2% are unable to sustain the cow herd even with 100% of the heifer calves retained for breeding. Value of fertility utilizes the ADGs associated with feeding supplement as described in Table 1.

sales was found to be relatively small in comparison to alternative sale weights, small differences in biological productivity from what was assumed in this analysis could shift results to favor November sales, especially for the southeast Arizona region. In addition, rates of gain were adjusted from a calculated weight gain using expert opinion for fall and winter calving dates and changes in the values assumed could sway results. This indicates that formal studies on these relationships should be considered. High labor and distribution costs to remote and difficulty in accessing range sites could also make supplemental feeding less attractive than what we have determined in our analysis. However, each rancher can adjust the return values presented to fit their own cost and production values in evaluating alternative sale dates and weights.

It is also important to note that a more flexible sale date, weight combination, and supplemental feeding strategy could have generated more net return than the "fixed strategies" above. For example, a strategy that can take advantage of market opportunities for feeding calves to a heavier weight when corn prices are high and forage is available would outperform the best "fixed strategies" presented of always producing 204 or 250 kg calves for sale in May. That is, when corn prices are so high that heavier calves sell for a higher price kg^{-1} than light calves, a rancher benefits from both the higher price received and more kgs sold by keeping calves until they are at a heavier weight class.

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Spatial and temporal patterns of cattle feces deposition on rangeland

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Abstract

The objective of this study was to identify and model environmental and management factors associated with cattle feces deposition patterns across annual rangeland watersheds in the Sierra Nevada foothills. Daily cattle fecal load accumulation rates were calculated from seasonal fecal loads measured biannually on 40 m^2 permanent transects distributed across a 150.5 ha pasture in Madera County, Calif. during the 4 year period from 1995 through 1998. Associations between daily fecal load per season, livestock management, and environmental factors measured for each transect were determined using a linear mixed effects model. Cattle feces distribution patterns were significantly associated with location of livestock attractants, slope percentage, slope aspect, hydrologic position, and season. Transects located in livestock concentration areas experienced a significantly higher daily fecal load compared to transects outside of these concentration areas ($P < 0.001$). Percent slope was negatively associated with daily fecal load, but this association had a significant interaction with slope aspect ($P = 0.02$). Daily fecal load was significantly lower during the wet season compared to the dry season ($P = 0.002$). Daily fecal loading rates across hydrologic positions were dependent upon season. Our results illustrate the opportunities to reduce the risk of water quality contamination by strategic placement of cattle attractants, and provide a means to predict cattle feces deposition based upon inherent watershed characteristics and management factors.

Resumen

El objetivo de este estudio fue identificar y modelar los factores ambientales y de manejo asociados con los patrones de deposición heces fecales de bovinos a través de cunecas hidrológicas de pastizal anual en los pie de monte de la Sierra Nevada. Se calcularon las tasas diarias de la carga acumulativa de heces fecales de bovinos a partir de las cargas fecales estacionales medidas bianualmente en transectos permanentes de 40 m^2 distribuidos a través de un potrero de 150.5 ha en el condado de Madera, Calif., las mediciones se realizaron en un durante un periodo de 4 años, de 1995 a 1998. Las asociaciones entre la carga fecal diaria por estación, el manejo del ganado y los factores ambientales medidos para cada transecto se determinaron usando un modelo lineal de efectos mixtos. Los patrones de distribución de la heces del ganado estuvieron significativamente asociados con la localización de atrayentes del ganado, el porcentaje de pendiente, el aspecto de la pendiente, la posición hidrológica y la época del año. Los transectos localizados en áreas de concentración de ganado experimentaron una carga diaria de heces fecales significativamente mayor que la de los transectos fuera de estas áreas de concentración ($P < 0.001$). El porcentaje de pendiente estuvo asociado negativamente con la carga diaria de heces, pero esta asociación tuvo una interacción significativa con el aspecto de la pendiente ($P = 0.02$). La carga diaria de heces fecales fue significativamente menor durante la época húmeda en comparación con la época seca ($P = 0.002$). La carga diaria de heces fecales fue significativamente menor durante la estación húmeda en comparación con la estación seca ($p = 0.002$). Las tasas de carga diaria fecal a través de las posiciones hidrológicas fueron dependientas de la época del año. Nuestros resultados ilustran las oportunidades para reducir el riesgo de contaminación de la calidad del agua mediante la ubicación estratégica de atrayentes del ganado y provee medios para predecir la deposición de heces fecales de ganado bovino basado en las características inherentes del a cuenca hidrológica y factores de manejo.

Key Words: water quality, pathogens, grazing distribution, watershed management

Rangeland watersheds on the west slope of the Sierra Nevada Mountain Range serve as important source areas for California's drinking water supply, particularly the San Francisco Bay Area and the rapidly urbanizing Central Valley. These annual rangelands are grazed by cattle both year around and seasonally. Atwill (1996) reviews concerns raised by drinking water municipalities, public health officials, and regulatory agencies about the potential risk that pathogens (*Cryptosporidium parvum* and *Giardia lamblia*) contained in cattle feces on rangelands poses to drinking water supplies. Systematic assessment of the linkages between rangeland cattle production and transmission of water-borne pathogens to humans requires evaluation of the prevalence of pathogens in cattle herds (Atwill et al. 1999a), identification of associations between livestock management and pathogen prevalence (Atwill et al. 1999b), and investigation of the hydrologic transport of pathogens from cattle fecal deposits to water-bodies (Tate et al. 2000a, Atwill et al. 2002).

The spatial and temporal pattern of feces deposition by cattle grazing annual rangeland watersheds is also an important factor determining the risk rangeland beef cattle production poses to

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water quality. The *timing* of feces deposition relative to rainfall-runoff events, and the *proximity* of deposition to watershed areas contributing runoff, such as riparian areas, determine much of the potential for pathogens in fecal deposits to be transported to downstream water-bodies and potentially into drinking water supplies. Successful management of cattle feces distribution to reduce risk to water quality requires an understanding of the management and environmental factors determining the spatial distribution of livestock feces across annual rangeland watersheds during both wet (transport potential high) and dry (transport potential low) seasons. While there is significant information available about cattle grazing distribution and behavior on rangelands (Bailey et al. 1996), there is limited information available to quantitatively predict the temporal and spatial distribution of livestock feces on annual rangelands.

In general, cattle distribution patterns are variable and determined by the interactions of topography, water location, supplemental feed placement, forage abundance and quality, season, livestock species and class, and livestock cognitive abilities (Bailey et al. 1996). On annual rangeland in California, Wagnon (1968) concluded that cattle distribution, as measured by forage use, was determined by vegetation type, forage production, slope percentage, and season. The overall negative effect which increasing percent land slope has on cattle distribution and resultant forage utilization has long been established (Mueggler 1965, Cook 1966, Ganskopp and Vavra 1987). Holechek et al. (1998) and Bailey et al. (1996) reach a general consensus that cattle use diminishes rapidly as site slope exceeds 10%. Larsen (1996) concluded that cattle fecal distribution tends to be non-uniform and variable across a landscape, estimating that 0.4% to 2.0% of a pasture may be covered by fecal deposits. On rangeland in southeastern Utah, Buckhouse and Gifford (1976) reported 0.2% of the land surface covered with cattle fecal deposits at a stocking rate of 2 ha AUM^{-1}.

The ability of managers to modify livestock distribution with practices such as water development, salt and feed placement has been well documented. Lange (1969) coined the term "piosphere" to describe the distinct trail, vegetation, and fecal load patterns radiating out from sheep watering troughs in South Australia. Miner et al. (1992) and Clawson (1993) found that the location of water troughs could be used to control cattle distribution and reduce time spent near riparian areas on eastern Oregon rangelands. Larsen (1989) reports cattle fecal loading as high as 7400 deposits ha^{-1} (4.5% land surface coverage) below bedding trees in Oregon, and a loading of 6,067 deposits ha^{-1} near winter feeding areas. Bailey and Welling (1999) found that the density of cattle fecal pats was 560% greater in areas with supplemental feed (3.3 pats 100 m^{-2}) compared to areas without supplemental feed (0.5 pats 100 m^{-2}) on foothill rangeland in Montana. Bailey et al. (2001) illustrated the potential for managers to modify cattle distribution and forage utilization by strategic placement of supplemental feed in areas cattle would normally under-utilize. Harris et al. (1998, 2002) were able to manipulate traditional cattle travel patterns by placement of water and supplemental feed.

The first objective of this study was to identify the environmental and management factors determining spatial and temporal patterns of cattle fecal deposition across annual rangeland watersheds in California's Sierra Nevada foothills under ambient year-long cattle grazing. Our second objective was to develop a data-driven predictive model to estimate cattle fecal loading under specific environmental and management scenarios in this landscape.

Methods

Study Site

The study was conducted on a 150.5 ha pasture at the San Joaquin Experimental Range (SJER) located in the Sierra Nevada foothills in Madera County, Calif. (37°6'8"N 119°43'33"W). Climate at SJER is Mediterranean with an average annual precipitation of 485 mm occurring almost entirely as rainfall November through May. Vegetation across the pasture is oak savannah with annual grassland understory. Blue oak (*Quercus douglasii* Hook & Arn.) and interior live oak (*Quercus wislizenii* A.DC.) dominate the overstory, while annual grasses and forbs such as wild oats (*Avena fatua* L.), rip-gut brome (*Bromus diandrus* Roth), soft chess (*Bromus mollis*, L.), and redstem filaree (*Erodium cicutarium* (L.) L'Her) dominate the annual grassland understory.

The study pasture has a general aspect of north to northwest, with slopes ranging from 0 to 35%. Elevation of the pasture ranges from 335 m to 457 m. The pasture is drained by an intermittent creek that normally flows from January through March. Field surveys were conducted during storm events occurring January through April of 1995 to identify pasture areas which directly contribute surface runoff to the intermittent stream. The extent of this area varied through the wet season and during individual storms. This area of the pasture was termed the variable source area (VSA) following Hewlett and Hibbert (1967) and Bernier (1985). Based upon the field survey and topography, the VSA for the study pasture was defined as the area within 3 m of the thalwag of the intermittent stream draining the pasture and its ephemeral tributaries as well as the seasonal wetland swales throughout the pasture. Following this definition, the VSA represented 15.8 ha or approximately 10% of the total pasture area.

The 150.5 ha pasture was grazed continuously with a 16 to 24 head fall calving, cross-breed cow-calf herd throughout the study period (October 1995 through September 1999). The number of cows varied across years based upon seasonal and annual forage production dynamics. Annual stocking rates accounting for all herd animals for the 1995, 1996, 1997 and 1998 water year were 0.14, 0.16, 0.11, and 0.13 AU ha^{-1} yr^{-1}, respectively.

Study Design

The study was a longitudinal survey of cattle fecal loading stratified across a set of management practices and environmental factors. In October 1995, 54 permanent 40 m^2 (30.5 m long by 1.3 m wide) belt transects were established across the study pasture. In October 1997, an additional 20 transects were established to increase the sample size to 74 transects. Transects were established across the pasture in a stratified random design. Transects were established perpendicular to slope contour. Stratifications were hydrologic position (ridge, hillslope, or VSA) and livestock concentration area (yes or no). Ridge (1995–96 n = 4; 1997–98 n = 6), hillslope (1995–96 n = 29; 1997–98 n = 42), and VSA transects (1995-96 n = 16; 1997–98 n = 18) were randomly placed within each hydrologic position. Lastly, livestock concentration area transects (1995–96 n = 5; 1997–98 n = 8) were established within 30 m of all stock water troughs (2) and supplemental feed and salt sites (3) within the pasture. Slope (%), aspect (north, south), hydrologic position (hillslope, ridge, VSA), surface rock cover (%), oak overstory canopy cover (%), cattle trail through transect (yes, no), and vertical and horizontal distance (m) to nearest livestock concentration site were measured for each transect.

Daily Fecal Load Accumulation Rate

Daily cattle fecal load accumulation rate on a dry weight basis (kg ha^{-1} day^{-1}) was measured in each transect for the wet (1-Oct through 30-Apr) and dry (1-May through 30-Sep) season of the 1995–96, 1996–97, 1997–98, and 1998–99 water years (1-Oct through 30-Sep). Four years of data were collected for 54 transects (established October 1995), and 2 years for 74 transects (additional 20 established October 1997).

On about 1-Oct and about 1-May of each water year, dry weight fecal load (kg ha^{-1}) in each transect was measured and all fecal material was cleared from the transect, allowing determination of wet and dry season fecal material accumulation. Dry weight fecal load (kg ha^{-1}) in each transect was measured using the comparative fecal load methodology (Tate et al. 2000b). This methodology is an ocular estimation technique where the dry weight of each individual fecal pat in the transect is estimated and the fecal load of the transect is calculated as the sum of individual fecal pat dry weights in the transect. Daily fecal load accumulation rate on a dry weight basis (DFLAR) (kg ha^{-1} day^{-1}) was then calculated for each plot for each of the 2 seasons for each of the 4 years by dividing the fecal load per sample period by the number of days in that sample period.

Statistical Analysis and Model Development

The basic data structure was a biannual repeated measure of cattle feces accumulation across 54 transects for 4 years and an additional 20 transects for 2 years, resulting in 511 complete data records. The association between the daily fecal load accumulation rate per season (wet, dry) and the various transect management and environmental factors was determined using a linear mixed effects model (Pinheiro and Bates 2000). Examination of residual errors demonstrated marked heteroscedasticity within the daily fecal load accumulation rate data which was overcome by a square root transformation of this data in conjunction with the use of an exponential variance function (Pinheiro and Bates 2000).

In the linear mixed effects analysis, management and environmental factors were modeled as fixed effects; transect was modeled as a random or group effect (74 unique transects read either 4 to 8 times); and the outcome variable was the square root of the daily fecal load accumulation rate ($\text{DFLAR}^{0.5}$) for each transect. Each management and environmental factor and all 2-way interactions were offered to the model in a forward stepping algorithm with a P-value of ≤ 0.10 required for entry into the final model. Final model coefficients were estimated using restricted maximum likelihood, and P-values for each coefficient was estimated using the Wald statistic (Pinheiro and Bates 2000).

Results

Linear Mixed-Effects Model

After controlling for substantial group or random effects, in part a result of repeated measures on each transect, a variety of management and environmental factors were determined to be significantly ($P < 0.1$) associated with daily fecal load accumulation rate (Table 1). The overall fit of the model predicting the square root of daily fecal load accumulation rate ($\text{DFLAR}^{0.5}$) is illustrated by the agreement between the observed values and those predicted by the linear mixed effects model (Fig. 1).

The coefficients in Table 1 quantify the expected effect of each factor on $\text{DFLAR}^{0.5}$. For the categorical factors in the model (year, concentration site, aspect, season, and hydrological position) the coefficient represents the expected effect of each level (e.g. 1996, 1997, 1998 for year) of the factor relative to the reference level (e.g. 1995 for year) for the factor. For slope, the only continuous factor in the model, the coefficient represents the incremental change in $\text{DFLAR}^{0.5}$ per incremental change in percent slope. Surface rock cover (%), oak overstory canopy (%), vertical and horizontal (m) distance to nearest livestock concentration site, and presence of a cattle trail in the transect were not significantly associated with daily fecal load accumulation rate ($P > 0.10$).

Management Factors

Transects located in livestock concentration areas experienced a significantly higher $\text{DFLAR}^{0.5}$ (0.14 kg ha^{-1} day^{-1}) compared to transects outside of these concentration areas ($P < 0.001$) (Table 1). There was a significant year effect such that

Table 1. Linear mixed-effects model predicting square root of daily fecal load accumulation rate ($\text{DFLAR}^{0.5}$) (kg ha^{-1} day^{-1}) by cattle grazing annual rangeland at San Joaquin Experimental Range, 1995–98. Coefficients quantify the expected effect of each factor on $\text{DFLAR}^{0.5}$. For the categorical factors (year, concentration site, aspect, season, and hydrological position) the coefficient represents the expected effect of each factor level relative to the reference level. The coefficient for slope represents the incremental change in $\text{DFLAR}^{0.5}$ per incremental change in percent slope.

Model Term	Coefficient	95% CI[2]	P-value
Intercept	0.48	0.41, 0.55	0.0001
Year			
19951	0.0	-	-
1996	0.02	-0.003, 0.040	0.08
1997	-0.03	-0.04, -0.02	0.0001
1998	-0.01	-0.020, -0.003	0.008
Concentration Site			
Yes[1]	0.0	-	-
No	-0.14	-0.20, -0.07	0.0001
Slope	-0.007	-0.010, -0.004	0.0002
Aspect			
North[1]	0.0	-	-
South	-0.01	-0.05, -0.01	0.65
Season			
Dry[1]	0.0	-	-
Wet	-0.04	-0.06, -0.02	0.002
Hydrologic Position			
Ridge[1]	0.0	-	-
Hillslope	-0.06	-0.10, -0.01	0.02
VSA[2]	-0.03	-0.050, 0.001	0.06
Slope x Aspect			
Slope-North[1]	0.0	-	-
Slope-South	0.003	0.0003, 0.006	0.03
Season x Hydrologic Position			
Wet-Ridge[1]	0.0	-	-
Wet-Hillslope	0.03	-0.008, 0.06	0.13
Wet-VSA	-0.01	-0.03, 0.001	0.06

[1] Reference category for each categorical variable.

[2] 95 % confidence interval for coefficient (lower, upper).

[3] Variable source area.

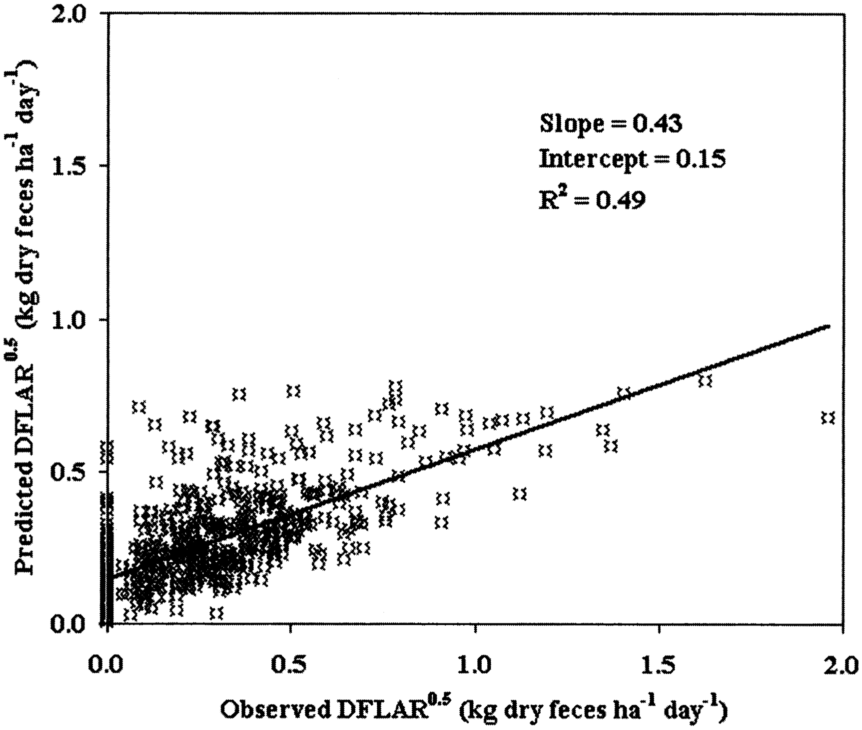

Fig. 1. Square root of observed daily cattle fecal load accumulation rate (DFLAR$^{0.5}$) versus DFLAR$^{0.5}$ predicted by a linear mixed effects model containing year (1995, 1996, 1997, 1998), livestock concentration site (Yes, No), slope (%), aspect (north, south), season (wet, dry), hydrologic position (ridge, hillslope, variable source area), a slope by aspect interaction, and a season by hydrologic position interaction.

daily fecal load accumulation rate was lower during 1997 and 1998 compared to 1995, while 1996 was higher than 1995 (Table 1, Fig. 2). The significance of year in the model may indicate the sensitivity of this fecal loading estimation method to changes in stocking rate.

Environmental Factors

Percent slope of the transect was negatively associated with daily fecal load accumulation rate, but this association had a significant interaction with aspect (P = 0.02) such that for every 10% increase in slope, DFLAR$^{0.5}$ decreased by 0.07 kg ha^{-1} day^{-1} for north facing slopes yet decreased by only 0.04 kg ha^{-1} day^{-1} for south facing slopes (Fig. 3). South-facing slopes tended to accumulate more cattle fecal material relative to equivalently sloped north-facing slopes. The difference between the cattle fecal loading rates for north-facing as compared to south-facing slopes becomes negligible as percent slope approaches 0 (Fig. 3), indicating that the effect of aspect on DFLAR$^{0.5}$ is most pronounced at steeper slopes. This point is corroborated by the lack of significance for the main term of aspect (P = 0.65) (Table 1).

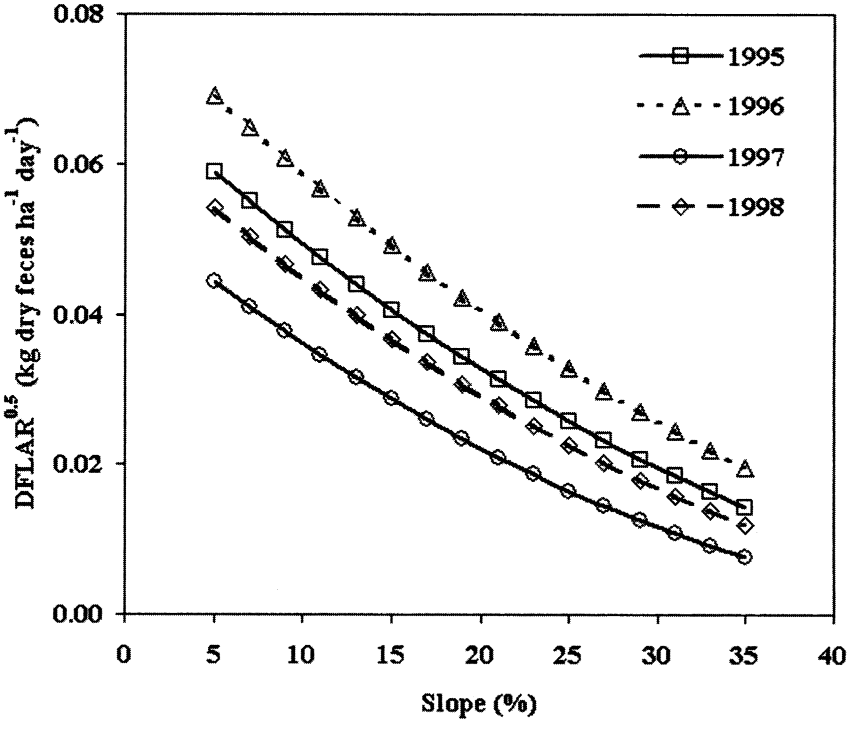

Fig. 2. Predicted square root of daily fecal load accumulation rate (DFLAR$^{0.5}$) for each study year as a function of slope (%).

Daily fecal load accumulation rate was significantly lower during the wet season compared to the dry season (P = 0.002, Table 1, Fig. 3 and 4). Hydrologic position within the watershed was associated with the rate of fecal accumulation, such that ridges accumulated more fecal material than hillslopes and the variable source area (Fig. 4). The association between hydrological position and cattle fecal material deposition was in part influenced by the prevailing season, in that there was a significant interaction term between season and hydrologic position (P < 0.001). Relative to ridges and the variable source area (VSA), hillslopes experienced the least reduction in fecal accumulation during the wet season compared to the dry season (Fig. 4).

Discussion

These results indicate that a complex and interacting set of management and environmental factors must be considered when measuring, predicting, or managing feces loading by cattle across annual rangeland watersheds. The data-driven statistical model reported in Table 1 explicitly predicts the spatial-temporal distribu-

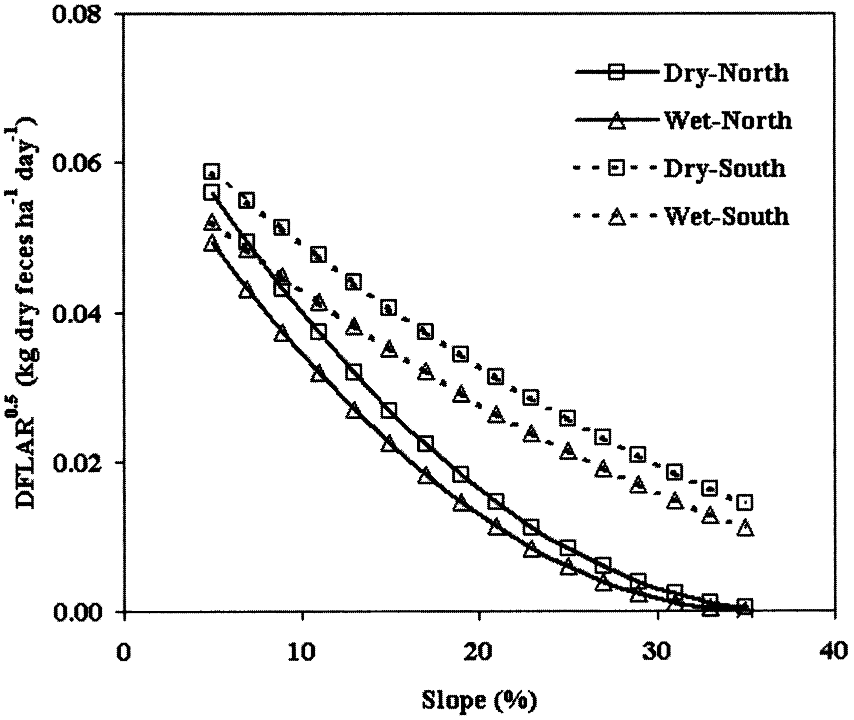

Fig. 3. Predicted square root of daily cattle fecal load accumulation rate (DFLAR$^{0.5}$) as a function of season (wet, dry), aspect (north, south), and slope (%). Units for DFLAR$^{0.5}$ are kg dry feces ha^{-1} day^{-1}.

tion of daily fecal material accumulation rate across an annual rangeland watershed. Fecal loading patterns likely do not correlate perfectly with variables used to describe grazing distribution (forage utilization patterns) or livestock behavior (time spent foraging, loafing, traveling). While there is certainly overlap in the factors determining livestock grazing behavior and fecal loading on a given landscape, there are also factors unique to each of these components of livestock grazing. Ideally, a single robust model predicting both livestock activity (grazing distribution and behavior) and resultant environmental impacts (fecal loading, forage utilization, riparian area damage) will be developed.

Our work shows that water troughs and supplemental feed significantly increase daily fecal accumulation rate at, and near, sites where these attractants are located. This result illustrates the potential for management to increase or decrease risk of manure-borne contaminants to water quality based upon the location of livestock attractants within a watershed or riparian pasture. Placement of a cattle attractant near a stream will increase daily fecal loading rate and risk to water quality, while strategic placement away from the stream can decrease fecal loading and associate risks near the stream. Previous studies have reported substantially higher cattle fecal loading near supplemental sites and bedding areas (Larsen 1996, Bailey and Welling 1999). Our results correlate well with research illustrating the potential to modify cattle distribution and forage utilization by strategic placement of supplemental feed (Bailey et al. 2001, Harris et al. 1998, 2002). Managers should place cattle attractants in watershed and pasture areas which have limited surface runoff connection to streams or other water-bodies.

Ridges and hillslopes are the most hydrologically remote areas, while the variable source areas (VSA) are the most hydrologically connected areas on rangeland watersheds in the south Sierra Nevada foothills. Cattle fecal loading rate across these landscape positions is dependent upon season (Fig. 4). Fecal loading rate was significantly greater in the VSA during the dry season compared to the wet season. However, loading rates in the VSA declined dramatically, to levels equal to hillslope positions, during the wet season. The affinity of livestock for VSAs during the dry season can be attributed to the presence of green feed and water during the first half of the season (May–July) according to work on the San Joaquin

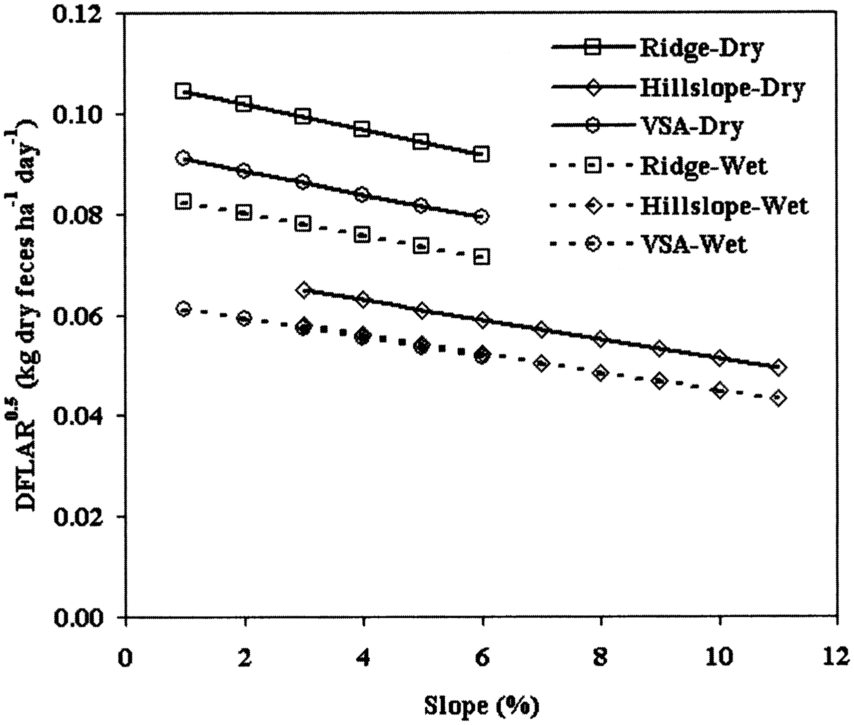

Fig. 4. Predicted square root of daily cattle fecal load accumulation rate (DFLAR$^{0.5}$) as a function of season (wet, dry), hydrologic position (ridge, hillslope, variable source area (VSA)), and slope (%).

Experimental Range (SJER) by Wagnon (1968). During the wet season, green feed and surface water (pools and puddles) are uniformly available across these watersheds providing cattle little incentive to selectively utilize swales and other riparian areas. Harris et al. (1998) found similar seasonal trends in the spatial distributional patterns of livestock on the SJER.

Regardless of season, ridge positions were associated with higher fecal loading rates than either hillslope or VSA positions. Based upon 3 years of observations of beef cattle activity across 4 pastures, Wagnon (1963) reported that beef cattle at the SJER spent 58 to 85% of their annual feeding time on open slopes and 22 to 25% on swales. Wagnon (1963) does not differentiate cattle feeding time spent on hillslope v. ridge positions. Ridges at SJER are characterized by open canopy conditions and slopes less than <5% while hillslopes are characterized by slopes ranging from 5 to 35% with variable brush, canopy and rock cover (Wagnon 1968). The higher fecal loading rate on ridges might be explained by the affinity of cattle for ridge positions relative to hillslopes because of the low slope, open conditions, and favorable microclimate of this landscape position. The apparent preferential deposition of fecal material by cattle on ridges is an association upon which managers can capitalize upon by strategic placement of cattle attractants in these hydrologically remote areas.

As land slope in the study pasture increased to 35%, fecal loading by cattle was significantly reduced. Fecal loading rate decreased 50 to 99% at locations with a 20 to 30% slope compared to sites with a 1 to 5% slope. In a theoretical landscape grazing distribution model, Bailey et al. (1996) discuss the use of slope as an abiotic factor constraining site forage value as slope increases. While slope is clearly a factor determining cattle distribution across rangeland landscapes, both Mueggler (1965) and Cook (1966) clearly illustrate that the effect of slope on cattle use of an area is not a simple relationship. Cook (1966) found significant interactions between slope (%) and other variables (distance to water, % maximum slope between site and water, etc.) when attempting to predict site use by cattle on mountain range in northern Utah.

We found that slope and aspect (north, south) interacted to determine fecal loading rates. We observed preferential deposition of fecal material by cattle along steeper slopes facing south compared to steeper slopes facing north. However, the magnitude of the effect of aspect on fecal loading rate diminished substantially as slope approaches zero (Fig. 3). In this landscape, aspect can account for differences in microclimate, as well as in the occurrence, amount and composition of forage production. Combinations of favorable forage and microclimate create conditions preferred by the cattle at higher slopes with a southerly aspect compared to a northerly aspect.

We found significantly lower daily fecal loading rates (on a dry weight basis) during the wet season compared to the dry season. Forage quality, digestibility, and moisture content is higher on annual rangeland during the winter growing season compared to the summer dormant season. George et al. (1984) defined the annual forage production curve for SJER. While the growing season can last from October through April, the bulk of forage production occurs from roughly March through April. The period October through February is often characterized as "the inadequate green season", when forage growth is limited due to cold temperatures. Forage during the period May through September is composed of the dry residual forage produced during the period October through April, with some green forage remaining in the swales until mid June.

The reduced daily fecal loading rate (on a dry weight basis) observed in this study during October through April relative to the May through September dry season may be a result of several factors: 1. Inadequate feed availability during the period October through February; 2. Greater forage use efficiency resulting in less available preferred forage creating less fecal output; and 3. More rapid erosion and decay of deposited feces. Without direct measurements of forage amount, quality, intake, fecal output, and feces decay across the wet season it is difficult to determine which factors contributed to the lower daily fecal loading rates observed in this study. For future work, we recommend that timing of fecal load measurements be matched to identifiable changes in forage production and quality. On annual rangeland we recommend sampling to capture the October through February inadequate green season, March through April to capture the rapid spring growth season, May through June to capture the period when green forage remains in swales while upland forage is dry, and July through September when forage is dry throughout the landscape.

Conclusions

Spatial and temporal patterns of cattle fecal deposition across oak savannah watersheds in California's southern Sierra Nevada foothills is dependent upon a complex and interacting group of management and environmental factors. We were able to successfully identify and model the effect of many of these variables. However, information on seasonal forage production, forage quality, and microclimate across the landscape is required to fully interpret spatial and temporal fecal loading associations identified in our study. Factors we found to affect cattle feces distribution included location of livestock attractants, slope, aspect, topographic position, and season. Our results illustrate some of the opportunities available to grazing managers on these rangelands to reduce the risk to water quality from cattle feces by strategic placement of supplemental feed grounds and stock water troughs. Our results also provide a means to predict cattle feces deposition, allowing identification and prioritization of risk to water-bodies across this landscape based upon both inherent watershed characteristics and management factors on this range type.

For future studies, it would be beneficial to integrate the examination of livestock distribution, behavior, resultant environmental impacts, microclimate, forage, and topographic factors simultaneously across a single landscape. Numerous efforts have been, and continue to be, conducted where only livestock distribution and behavior, or only livestock environmental impacts are measured. A comprehensive approach across several range types is required before livestock distribution - behavior - management - inherent site characteristics - environmental impacts can be understood and predicted at multiple spatial and temporal scales.

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Saltcedar recovery after herbicide-burn and mechanical clearing practices

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Abstract

Mechanical clearing and herbicide-burn treatments were compared to evaluate saltcedar (*Tamarix chinensis* Lour.) control and recovery along the Rio Grande on the Bosque del Apache National Wildlife Refuge, Socorro, N.M. The herbicide-burn treatment included an aerial application of imazapyr (±)-2-[4,5-dihydro-4-methyl-4-(1-methylethyl)-5-oxo-1*H*-imidazol-2-yl]-3-pyridinecarboxylic acid] + glyphosate [N-(phosphonomethyl)glycine] (0.6 + 0.6 kg ai ha^{-1} rate) followed 3 years later by a prescription broadcast fire that eliminated > 99% of the standing dead stems. Six years after initial herbicide application, saltcedar mortality was 93%. Mechanical saltcedar clearing entailed removing aerial (trunks and stems) growth by blading, stacking and burning debris, followed by removal of underground plant portions (root crowns) by plowing, raking, and burning stacked material. Saltcedar mortality 3 years after mechanical clearing averaged 70%, which was deemed unsatisfactory. Thus, root plowing, raking, and pile burning was repeated. Three years later, after the second mechanical clearing, saltcedar mortality was 97%. Costs for the herbicide-burn treatment averaged \$283 ha^{-1}, whereas mechanical control costs were \$884 ha^{-1} for the first surface and root clearing and an additional \$585 ha^{-1} for the second root clearing. Riparian managers should consider environmental conditions and restoration strategies prior to selecting a saltcedar control approach. Although control costs were significantly lower for the herbicide-burn treatment compared to mechanical clearing in this study, the choice of methods should always consider alternative control strategies for saltcedar. Frequently, combinations of methods result in more efficient, cost-effective results.

Key Words: Riparian restoration, imazapyr, glyphosate, prescribed fire, root plowing, root raking, brush control

Resumen

Se compararon tratamientos de aclareo mecánico y herbicida-quema para evaluar el control y recuperación del "Saltcedar" (*Tamarix chinensis* Lour.) a lo largo del río grande en el Refugio Nacional de Fauna Silvestre Bosque del Apache en Socorro, N.M. El tratamiento de herbicida-quema incluyo una aplicación aérea de imazapir (±)-2-[ácido 4,5-dihidro-4-metil-4-(1-metiletil)-5-oxo-1*H*-imidazol-2-yl]-3-piridinecarboxilico] + glifosato [N-(fosfonometil)glicine] (0.6 + 0.6 kg ia ha^{-1}) seguido tres años después de quema prescrita que eliminó > 99% de los tallos muertos en pie. Seis años después de la aplicación inicial del herbicida la mortalidad del "Saltcedar" fue de 93%. El aclareo mecánico del "Saltcedar" comprendió la remoción aérea del crecimiento (troncos y tallos) mediante el corte de las plantas, apilamiento y quema de los residuos seguido de la remoción de las porciones subterráneas (raíces y coronas) de las plantas mediante barbecho rastrillado y quema del material apilado. La mortalidad del "Saltcedar" 3 años después del aclareo mecánico promedio 70% el cual fue considerado insatisfactorio, Así, el barbecho, rastrillado y quema del material apilado se repitió, tres años después del segundo aclarelo mecánico la mortalidad del "Saltcedar" fue de 97%. Los costos del tratamiento de herbicida-quema promedio \$283 ha^{-1} mientras que los costos del control mecánico fueron de \$884 ha^{-1} para la primer remoción del material vegetal superficial y de la limpieza de las raíces y un costo adicional de \$585 ha^{-1} para la segunda limpieza de raíces. Los manejadores de las áreas ribereñas deben considerar las condiciones ambientales y las estrategias de restauración antes de seleccionar una de ellas para el control del "Saltcedar". Aunque los costos de control fueron significativamente bajos para el tratamiento de herbicida-quema, comparados con el aclareo mecánico de este estudio, la elección de los métodos siempre debe considerar estrategias alternativas para control del "Saltcedar". Frecuentemente la combinación de métodos produce en una mayor eficiencia de resultados costo-efectividad.

Saltcedar (*Tamarix* spp.) are exotic deciduous trees that escaped from cultivation into the wild in the late 1800s (Allred 2002, Robinson 1965). Today, the trees prevail in monocultural thickets and in mixed riparian communities along most rivers in the southwestern United States (Brotherson and Field 1987, Brock 1994, Frasier and Johnsen 1991). In New Mexico, saltcedar is common particularly along the Rio Grande in riparian areas formerly occupied by cottonwood (*Populus* spp.), willow (*Salix* spp.), and other native vegetation (Friedman et al. 1998). Collectively, *Tamarix* is composed of several genetically linked forms or ecotypes over its broad distribution range (DiTomaso and Bell 1996). With the exception of *T. aphylla* L. Karst. and T. *parviflora* DC., most species are difficult to distinguish from each other. *T. chinensis* Lour., *T. gallica* L., and *T. ramosissima* Ledeb. are occasionally grouped together in the literature as the same species and each has been reported as common along the

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Rio Grande (Baum 1978, DiTomaso 1998). According to Allred (2002), *T. chinensis* has nomenclatural priority and is the same species as *T. ramosissima*, whereas *T. gallica* does occur but is uncommon along the Rio Grande. Aside from taxonomical consideration, these species possess similar growth and ecological characteristics that make them more or less receptive to the same control practices (Everitt 1980, 1998).

During the later half of the 20th century, numerous saltcedar control initiatives by various governmental agencies and private entities have been undertaken along the Rio Grande in New Mexico (McDaniel et al. 2000, Scurlock 1998). Reasons for controlling saltcedar include a wide range of goals, such as restoring native species in riparian communities, conserving water for irrigation and municipal use, improving stream water conveyance efficiency, protecting or enhancing habitat for endangered species, and clearing areas for agricultural and residential use. In the 1950s, saltcedar control with phenoxy herbicides including 2,4-D (2,4-dichlorophenoxy acetic acid), silvex (2,4,5-tricloropropionic acid), and 2,4,5-T (2,4,5-trichlorophenoxy acetic acid) at rates of 1.2 kg ai ha^{-1} or higher, was employed along the Rio Grande (Anonymous 1951, Busch et al. 1992). Guidelines for control with phenoxy herbicides were developed by several sources and foliage suppression rather than plant kill was the expectation from spraying (De Loach 1989). Recent research has focused on using imazapyr (±)-2-[4,5-dihydro-4-methyl-4-(1-methylethyl)-5-oxo-1*H*-imidazol-2-yl]-3-pyridinecarboxylic acid] for saltcedar control along the Rio Grande (Taylor and McDaniel 1998a) and Pecos rivers (Duncan and McDaniel 1998) in New Mexico. Duncan and McDaniel (1998) reported about 90% saltcedar mortality after aerially applying imazapyr at a 1.2 kg ai ha^{-1} rate or as a mixture of imazapyr and glyphosate [N-(phosphonomethyl)-glycine] at a 0.6 + 0.6 kg ai ha^{-1} rate to foliage in late summer. Following herbicide treatment, prescribed fire or chaining has been used to remove dead standing saltcedar stems prior to further riparian restoration (Taylor and McDaniel 1998b).

Root plowing has been a common mechanical method for removing saltcedar on the flood plain bordering the Rio Grande (McDaniel et al. 2000). This implement severs the root crown from the remaining root mass when the blade is dropped to a soil depth of 31 to 46 cm (Hollingsworth 1973). According to Horton (1960), root plowing gave more than 90% control when this treatment was conducted during hot and dry weather, which accelerates dessication of cut stems and roots. Hollingsworth (1973); however, was skeptical of root plow treatments and reported that "the use of root plowing as a control for saltcedars all but ceased (along the Rio Grande) because soil covers stems and roots resulting in regrowth and lack of control." Taylor and McDaniel (1998a) reported that root crowns should be raked from beneath the soil surface following root plowing to increase mechanical control success. DeLoach (1989) suggested that because root plow results were inconsistent for saltcedar control, additional research was needed to achieve better results.

The Bosque del Apache National Wildlife Refuge (NWR) has included saltcedar control as part of its continuing wildlife habitat improvement program since the refuge was established in 1939 (Bosque del Apache NWR, unpublished annual narrative reports). In the late 1980s renewed efforts to control saltcedar focused on rehabilitating riparian and wetland habitats in areas once naturally flooded by the Rio Grande (Taylor and McDaniel 1998b). Herbicide spraying and prescribed fire have been included as part of an ongoing effort to remove saltcedar. But the majority of rehabilitation has been accomplished, thus far, by mechanical methods using heavy equipment. This study's objective was to compare these 2 strategies for removing saltcedar: aerial herbicide spraying and prescribed fire (herbicide-burn); and root plowing and raking control (mechanical clearing). Specifically, saltcedar regrowth after treatment and costs associated with each treatment strategy were examined.

Materials and Methods

Research Area

The experiment was conducted outside the active Rio Grande floodplain on the Bosque del Apache NWR near Socorro, New Mexico (57' 47' N, 55' 24'W', 1300 m). In the early 1940s, a series of wet years resulted in the most significant flooding recorded in the Middle Rio Grande Basin during the 20th century (Whitney 1995). Partly in response to the resulting damage, the Flood Control Act of 1948 was passed, which authorized construction of an 86-km, low-flow conveyance channel adjacent to the site from San Acacia to Elephant Butte Reservoir. This structure, completed in the early 1950s with levees and roads, was built on the western edge of the river's current channel and served to isolate the study area from the present active river flood plain (Fig. 1). Over time, the low-flow conveyance channel and other flood control structures have restricted river movement and associated natural processes that

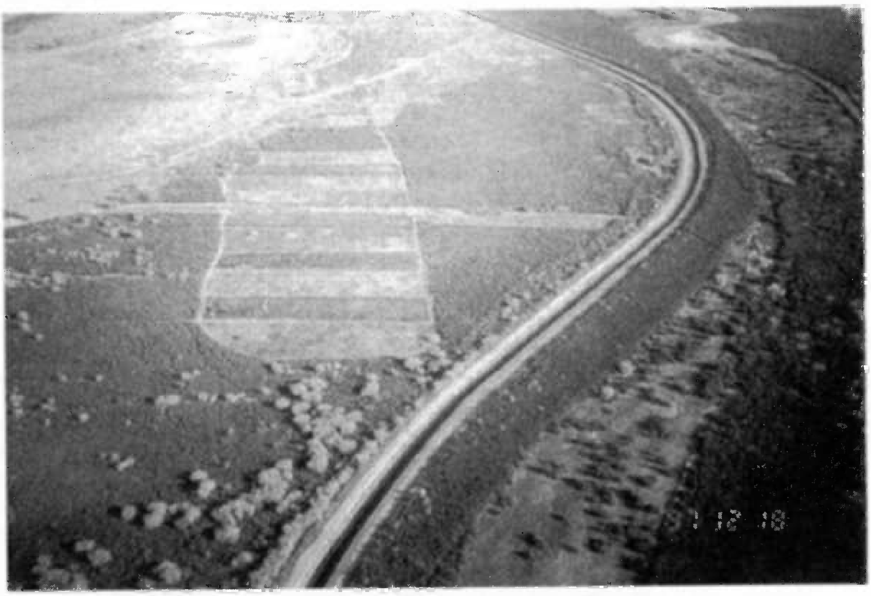

Fig. 1. Oblique aerial view of experimental plots located within a saltcedar thicket at the Bosque del Apache National Wildlife Refuge, Socorro, N.M. A low-flow conveyance channel (near center) with levees and roads serves to isolate this former portion of the flood plain from the Rio Grande (right side). Note scattered Fremont cottonwood trees in the lower left.

influence establishment and maintenance of native riparian vegetation communities (Howe and Knopf 1991, Taylor et al. 1999). In addition, several major wildfires have swept through the study area since the 1950s, resulting in the elimination of most fire-intolerant native trees and shrubs. Thus, when this study was initiated, the area was dominated by saltcedar as a near monocultural thicket.

The flood plain soil in the study area was formed through centuries of river cutting and deposition activities and, therefore, is a highly variable mix. In our 2- by 8-km study area (Fig. 1), soil surface textures within short distances varied from loose sands to tight silts and clays. Soil salinity, mapped by electromagnetic induction (Sheets et al. 1994), indicated the electrical conductivity of soils in the area to be mostly above 8.0 ds m^{-1}. This level indicates high soil salinity, and suggests that survival and productivity of cottonwood and other native trees is likely to be poor (data not shown) (Taylor and McDaniel 1998b). Depth to water table ranged from 0.6 to 2.3 m and averaged 1.5 m. Except for a few remnant Fremont cottonwood (*Popular fremontii* S. Wats.) and black willow trees (*Salix nigra* Marsh) on old channel banks bordering the study area, saltcedar was the principal woody plant within experimental plots. Saltgrass (*Distichlis spicat*a (L.) Greene) and alkali sacaton (*Sporobolus airoides* Torr. Torr.) grew sparsely in the understory and, we speculate, would likely be the major vegetation had saltcedar not established.

Experimental Design and Saltcedar Control Treatments

Herbicide-burn and mechanical clearing treatments were applied to 10 plots, resulting in 5 replications for each treatment in a completely randomized design. Plots measuring 82 by 305 m (2.5 ha) were arranged side-by-side with 10 m buffers (graded roads) placed between each plot.

The herbicide treatment consisted of an imazapyr plus glyphosate mixture (0.6 + 0.6 kg ai ha^{-1}) in water with a 0.25% v v^{-1} nonionic surfactant, and a 0.07% v v^{-1} drift control agent. A Cessna T188™ aircraft applied the herbicide on 30 August 1994, between 0700 and 0830 hours with 16 and 19° C air temperature, 65 and 92% relative humidity, and wind below 1 m $second^{-1}$. The airplane speed was calibrated for 49 m $second^{-1}$, and the wing was fitted with a streamline boom with nozzles (D8-SS) positioned 45° aft to deliver a 65 liters ha^{-1} total spray volume. The 5 sprayed plots remained undisturbed until early October 1997, when prescribed broadcast burns were conducted to remove dead standing saltcedar stems. Each herbicide plot was burned separately with fires ignited using a truck-mounted terra-torch[1]. Conditions during prescribed burning included 28 to 32° C air temperature, 31 to 42% relative humidity, and wind speeds of 1 to 3 m $second^{-1}$. In 20 to 30 minutes, fire removed nearly all the standing dead and desiccated saltcedar stems within a plot. An exception was in 1 sprayed plot where about 15% of the woody material did not burn, because saltcedar skeletons were scattered too widely to carry the fire.

Table 1. Activities, time, and cost associated with saltcedar herbicide-burn and mechanical clearing treatments on the Bosque del Apache National Wildlife Refuge, N.M.

Treatment/Activity	Hours	Cost
		(\$ ha^{-1})
Herbicide-burn		
Herbicide (imazapyr & glyphosate)	—	202
Aerial application	4	18
Prescribed burning	12	63
Total	16	283
Mechanical clearing[1]		
1st Clearing		
Aerial growth cutting, raking, stacking, and pile burning	140	477
Root plowing, root raking, stacking, and pile burning	100	407
2nd Clearing		
Root plowing, root raking, stacking, and pile burning	102	585
Total	342	1,469

[1]These cost were based on local comparable prices for equipment lease, fuel, routine maintenance, and labor.

Mechanical clearing involved a 2-stage approach, in which saltcedar aerial trunk and stem growth was removed first and then root material was extracted from the soil. In June 1995, saltcedar aerial growth was cleared in the 5 experimental plots using two, D-7 class bulldozers. Fitted with front-mounted blades, the bulldozers pushed over the standing stems and cut them near the soil surface. A 1.9-m^{-3} capacity, articulating loader adapted with a brush rake worked behind the bulldozers to gather and stack the cut debris into piles. These piles were allowed to dry for about a month before being doused with diesel fuel and ignited. Clearing aerial growth required 140 hours and took about a month to complete (Table 1). In September 1995, root plowing was accomplished using 1 of the D-7 bulldozers equipped with a 6 m wide blade that severed the roots about 40 cm below the surface. The second D-7 bulldozer was fitted with a hydraulic, 6.4-m wide root rake containing teeth 1.2 m in length and spaced 38 cm apart to rake root material into windrows. The articulating loader later consolidated windrowed material into piles that subsequently were burned. Three years after the initial clearing operation, saltcedar regrowth was common in the 5 mechanically cleared experimental plots, thus a second clearing operation was necessary. In June 1998, all mechanical plots were retreated using the root plowing, root raking, gathering and pile burning sequence. This operation required about 102 hours to complete (Table 1).

Vegetation Sampling

Prior to treatment in August 1994, 4 parallel permanent belt transects were spaced evenly 50 m apart in each experimental plot. Transects, 4 m wide and 50 m long, were used to determine saltcedar density (plant units ha^{-1}), and a 50 m tape was placed at the belt transect's center to determine canopy cover intercept (percent cover) (Burnham et al. 1980). Saltcedar was multistemmed, thus a plant unit was defined as a single plant with stems originating from a common root crown near or just below the soil surface. Live stems converging near the base of each plant unit were counted separately and were recorded as live basal stems per plant unit. Pretreatment density and percent cover estimates of live saltcedar were later compared with similar measurements taken after treatment in autumn 1995, 1996, 1997, 1998, 1999, and 2000. Percent saltcedar control was determined yearly by

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[1]Firecon, Inc., P.O. Box 657, Ontario, Ore. 97914

comparing live saltcedar density in experimental plots with the pretreatment densities. Partially defoliated or damaged plants were considered alive. At both ends of a transect (0 and 50 m point), a modification of the point-center quarter technique (Bonham 1989) was used to measure distance to the nearest live saltcedar plant in each of 4 quarters to determine plant spacing (m). To avoid overlapping other transects, only plants within 25 m of the center point were recorded. Height (m), width (m), and the number of live basal stems per plant unit were measured on each of the nearest saltcedar plants. Canopy volume (m^3) was computed by multiplying height and diameter measurements. Data collected were distributed normally and error variances were homogeneous for all variables analyzed, including plant density, cover, plant spacing, height, volume, and live basal stems per plant unit. A repeated measures analysis of variance, with treatment as the main plot factor and survey year as the repeated measures factor, was used to analyze data using SAS (1985) procedures. If F-tests detected significant treatment differences ($P > 0.05$) then Fisher's LSD ($\alpha = 0.05$) was used as a mean separation technique.

Results

Pretreatment Conditions

According to records kept by the Bosque del Apache NWR, at least 3 wildfires passed through the study area since the 1940s. The most recent wildfire in spring 1986 killed most aerial saltcedar vegetation and many charred stems were still standing when pretreatment measurements were taken in August 1994. Because fire does not kill saltcedar roots, there was prolific sprouting from buds on the buried root crown. This resulted in saltcedar regrowth of relatively uniform stature and height, similar to that of the residual charred stems. Pretreatment measurements indicated no significant difference among the experimental plots in plant density, cover, spacing, height, volume, or live basal stems per plant unit (Table 2). Saltcedar density averaged 7,112 plant units ha^{-1}, and live stems originating near the plants base ranged from as few as 4 to as many as 130 stems per plant unit. Canopy cover determined by line intercept ranged from 34 to 90% and averaged 56% while plant spacing ranged from 0.1 to 9.3 m and averaged 1.3 m. Plant height ranged from 0.6 to 6.0 m and averaged 2.3 m, whereas plant volume ranged from 0.01 to 13 m^3 and averaged 0.9 m^3.

Table 2. Pretreatment saltcedar measurements averaged from 10 experimental plots 2.5 ha in size on the Bosque del Apache National Wildlife Refuge near Socorro, N.M. in October 1994.

Measurement	Mean	Standard Error
Density (plants ha^{-1})	7,118	1,316
Canopy cover (%)	56	7
Plant spacing (m)	1.3	0.13
Plant height (m)	2.28	0.14
Plant volume (m^3)	0.90	0.22
Live basal stems per plant unit (no.)	31.5	4.4

Treatment Comparisons

Treatment-by-year interactions occurred for all variables, including plant density, cover, spacing, height, volume, and live basal stems per plant unit. The interactions were expected because the initial mechanical clearing effort provided inconsistent saltcedar control by plot and resulted in variable data the first 3 years after treatment. The second mechanical clearing provided high and consistent saltcedar control across experimental plots. Thus, after this operation, there were no differences in measured variables for the next 3 years. In contrast, the herbicide treatment gave consistent saltcedar control results across all experimental plots every year.

Live plant densities were lower in herbicide-burn plots compared with mechanically cleared plots in 1995, 1996, and 1997, but herbicide-burn plots had higher plant densities in 1998 and 2000 (Table 3). Treatments did not differ in 1999. Few plants possessed foliage in herbicide-treated plots the first 3 years after treatment. In 1998, the first year after prescribed fires, saltcedar regrowth from burned stumps and buried root crowns was easily noticed, and plant density increased compared to previous years. Saltcedar density contin-

Table 3. Mean saltcedar plant density (plants ha^{-1}), canopy cover (%), spacing (m), height (m), volume (m^3), and live basal stems per plant unit (no. plant unit^{-1}) in herbicide-burn and mechanical clearing treatments in 1995 through 2000 on the Bosque del Apache National Wildlife Refuge, N.M.

Treatment/Year	Density	Canopy Cover	Spacing	Height	Volume	Basal Stems
	(plants ha^{-1})	(%)	(m)	(m)	(m^{-3})	(no. plant unit^{-1})
Herbicide-burn						
1995	6a[1]A[2]	0.0aA	0.0aA	0.0aA	0.0aA	0.0aA
1996	83aA	0.8aA	0.0aA	0.0aA	0.0aA	0.0aA
1997	137aA	1.3aA	0.0aA	0.0aA	0.0aA	0.0aA
1998	287bB	2.9bB	4.2aB	1.4bB	0.6aB	8.3aB
1999	452aC	6.3aC	5.3aC	2.0aC	1.9aC	7.0aB
2000	522bC	11.5bD	5.2aC	2.7aD	3.2aD	12.3aC
Mechanical clearing						
1995	937bA	5.0aAB	6.8bB	0.4bA	0.1bA	1.6aA
199	2287bB	13.0bBC	3.2bA	1.5bB	0.5bB	6.3bBC
1997	2142bB	17.0bC	2.7bA	1.9bC	1.5bB	7.8bB
1998	52aA	0.4aA	5.2aAB	0.5aA	0.1bA	4.9bC
1999	200aA	4.0aAB	10.6bC	2.3aD	2.0aB	8.1aB
2000	180aA	4.7aAB	10.7bC	2.7aE	3.1aC	12.5aD

[1] Treatment means by year followed by the same lower case letter are not different ($P > 0.05$).

[2] Year means within a treatment followed by the same upper case letter are not different ($P > 0.05$).

ued to increase in herbicide-burn plots in 1999 and 2000 compared to previous years, but these were not different from each other. On mechanically cleared plots, plant density was lower in 1995, 1998, 1999, and 2000, than in 1996 and 1997. Higher densities in 1996 and 1997 reflected poor control achieved after the initial clearing effort.

Percent cover was less than 1% on mechanically cleared and herbicide-burn plots in 1995, but saltcedar cover was higher in mechanically cleared plots in 1996 and 1997 (Table 3). Saltcedar cover was higher in herbicide-burn plots than in mechanical plots after the second clearing in 1998 and 2000, but no differences were found in 1999. The prescribed fires apparently stimulated saltcedar sprouting resulting in an increased percent cover each year after burning relative to pre-burn years. Saltcedar cover increased rapidly on mechanically cleared plots from 1995 to 1997. After re-clearing in 1998, percent cover did not increase in 1999 or 2000.

Saltcedar were more widely spaced in herbicide-burn than mechanically cleared plots in 1995, 1996, and 1997 (Table 3). Following burning and reclearing activities, spacing was similar between treatments in 1998. But in 1999 and 2000, plant spacing was greater on mechanically cleared plots. Within herbicide-burn plots, plant spacing was greater prior to burning compared with that recorded afterwards. Plant spacing in mechanical plots was similar to 1995 and 1998, immediately after clearing activities. However, spacing was much greater in 1999 and 2000 than 1996 and 1997, reflecting more successful control following the second clearing effort.

Plant height and volume were less in herbicide-burn plots compared with mechanically cleared plots in 1995, 1996, and 1997. But in 1998, herbicide-burn plots recorded greater height and volume (Table 3). In 1999 and 2000, plant height and volume were nearly the same among treatments. Saltcedar height and volume on mechanically cleared plots were lowest and not different in 1995 and 1998, following clearing activity; growth was rapid in subsequent years following these events.

The number of live basal stems per plant unit was similar on herbicide-burn and mechanically cleared plots in 1995, but not in 1996 or 1997 when more stems were found on saltcedar growing within mechanically cleared plots (Table 3). Stems increased on saltcedar following burning in 1998, but there were no treatment differences in the number of live basal stems per plant unit in 1999 or 2000. Live basal stem numbers were lowest in 1995, following the first mechanical clearing activity. They increased after the second clearing in 1998, and were highest in 2000.

Discussion

Saltcedar Control in the Herbicide-Burn Treatment

Chemically treated saltcedar needles discolored 2 to 3 weeks after the mixture of imazapyr plus glyphosate was applied in late August 1994. But foliage did not shed until mid-November; about the same time that saltcedar normally defoliates and enters winter dormancy in this area. On the Bosque del Apache NWR, saltcedar usually initiates new stem and needle growth in early April but none of the sprayed plants had any green foliage when the site was visited in May 1995. During the first post treatment survey in October 1995, a total of 2,840 plants were observed from transects in the sprayed plots, but only 2 had any green growth. These plants possessed the highly restricted, gnarled primordial growth from axillary buds on lower stems that typifies imazapyr damage (Duncan and McDaniel 1998). More live saltcedar plants were counted in October 1996 (39 total live, 99% control) and October 1997 (66 total live, 98% control). But again, these plants had mainly gnarled primordial growth. It was noticed that surviving plants usually occurred in a streaked pattern, suggesting a reduced amount of herbicide may have been intercepted by the canopy because the spray swath did not provide complete overlap coverage.

After data collection in October 1997, prescribed burns were conducted separately within each sprayed plot, and the heat created eliminated nearly all (>99%) of the dead standing saltcedar stems. Prescribed burning was conducted safely, despite the close proximity of adjacent expanses of untreated monocultural saltcedar. Burn prescription conditions required moderate air temperature, high relative humidity, and light wind, resulting in relatively high moisture content of adjacent live saltcedar fuels. Under such conditions, fuel ignition was difficult if not impossible in these adjacent stands. One year after burning, during the 1998 evaluation, we noticed that the stems of dead saltcedar always burned completely to the ground, whereas most sprouting plants still had 1 or 2 standing charred stems. This indicated that these stems were probably alive before the fire and were too succulent to burn completely. Sprouting was evident from either the lower portions of these stems or from the root crown. By comparing plant density prior to treatment in the herbicide-burn plots to that recorded in October 2000, saltcedar control was estimated to be 93%. Herbicide cost \$202 ha^{-1} and aerial application and other minor labor costs were \$18 ha^{-1}. Prescribed burning costs were about \$63 ha^{-1} and combined, the total treatment cost was about \$283 ha^{-1} (Table 1).

Saltcedar Control in the Mechanical Clearing Treatment

Nearly 140 hours, over a 4-week period from late June to mid-July 1995, were required to surface cut, rake, stack, and burn saltcedar aerial growth in the 5 plots randomly assigned for mechanical clearing. Because of overheating problems, heavy equipment usually was only operated for 3 to 4 hours in the early morning. Root plowing, raking, stacking, and pile burning required 100 hours to complete and was delayed by the onset of summer rains in July and August. This work started in early September after the rains ended and continued through November 1995. Surface aerial clearing costs totaled about \$477 ha^{-1}, and costs related to root material removal totaled about \$407 h^{-1}. These expenses were based on comparable local equipment lease, fuel, routine maintenance, and labor costs. Three years after the initial mechanical clearing effort, saltcedar control among experimental plots ranged from 54 to 88% and averaged 70%, which was deemed unacceptable. The second saltcedar clearing effort was performed in June and July 1998 under hotter and drier conditions, and few live saltcedar remained after this operation. Saltcedar removal costs during the second effort were about \$585 ha^{-1}. Machine hours were increased during this operation by the presence of a weedy annual plant community primarily composed of kochia (*Kochia scoparia* L. Roth *ex* Schrad.) and Russian thistle (*Salsola kali* L.), which hindered root removal. Combined costs for the 2 mechanical clearing treatments totaled \$1,469 ha^{-1} (Table 1).

Poor saltcedar control following the first mechanical clearing effort was reflected through greater plant density and cover than sprayed plots during the first 3 years after treatment (Table 3). Plant height, volume, and live basal stems per plant unit also were greater in mechanically cleared plots. Timing of the initial clearing operation largely contributed to poor mechanical control. Aerial growth was not cleared until mid-July which delayed root plowing and raking until after the summer rainy season. By the time root work began in early September, cooler weather and moister substrates prevailed. Clearing aerial growth should have been accomplished during cooler winter weather to avoid overheating equipment and to allow for longer operating periods. Ideally, root plowing and raking should have been completed prior to the summer rainy season, as was conducted during the second clearing operation in this study.

Management Implications

Removing saltcedar is a necessary first step towards restoring riparian habitats along many Southwestern river systems (Taylor 1999). Areas that become saltcedar thickets are likely to remain as such indefinitely unless interventive steps are taken to remove plants. In our study area, as an example, saltcedar established in the 1940s following significant flooding events. Periodic wild fires through the area enabled saltcedar to thrive at the expense of fire-intolerant native trees and shrubs (Busch 1995). When this study began in 1994, there were virtually no other plant species present except saltcedar and, by all indications, the plant community would remain this way into the foreseeable future.

When selecting a control strategy for saltcedar, it is important to consider factors related to the plant and its environment, such as the plant's age, growth characteristics and associated vegetation. Areas with dense, even-aged saltcedar and little associated vegetation are better suited for the herbicide-burn treatment than areas that have mixed riparian vegetation. Imazapyr and glyphosate are nonselective herbicides and potentially can kill other desirable plants. Thus, this treatment in combination with prescribed fire should not be used where protection of native species is required (Duncan and McDaniel 1998). Similarly, mechanical clearing can be nonselective and shares many of the same environmental drawbacks as an herbicide-burn treatment when desirable plant protection is needed.

Applied by itself, imazapyr is more effective than glyphosate for saltcedar control (Duncan and McDaniel 1997). Imazapyr's activity is enhanced when above and below-ground plant parts are proportional because the chemical is readily moved in both xylem and phloem after root or foliar absorption. Imazapyr is rapidly absorbed into the foliage (within 24 hour) with plant death resulting primarily from acetolactate synthase inhibition. Secondary effects include disruption of photosynthate translocation, hormone and enzyme activity, and interference in DNA synthesis and cell growth (Weed Science Society of America 2002). According to Sprenger et al. (2002), spraying saltcedar regrowth within 1 or 2 years following surface removal of trunks and shoots (i.e. by burning or mechanical removal) should be discouraged, presumably because of the imbalance created in source/sink relationships.

When conducting mechanical clearing treatments, root crown removal is critical for assuring control (Horton 1960). Operators must be cognizant of root plowing depths to ensure that root crowns are indeed severed from the remaining root mass and then pulled from the soil using raking implements. The root mass is smaller and the crown is closer to the surface on younger plants than on older, more mature vegetation, thus, determination of the optimal depth for root plowing must be adjusted accordingly.

Frequently, wet conditions or high water tables in floodplain habitats preclude using heavy equipment or render their use for removing root material ineffective due to excessive soil moisture. The herbicide-burn treatment for saltcedar control would, therefore, be attractive to managers in areas where equipment access is not possible. Imazapyr currently is registered for noncropland areas and for riparian and wildlife restoration in New Mexico, whereas glyphosate is registered for noncropland and aquatic habitats. Imazapyr may be used in low-lying areas after water has receded. Imazapyr and glyphosate degrade rapidly through microbial breakdown and photolysis, and movement is limited in the soil even when treated sites are inundated by water (Sisneros 1991, Taylor 1999). Imazapyr has soil residual activity (Sisneros 1991), but no ill effects on germinating seedlings or planted materials were reported after saltcedar was aerially sprayed during other studies on the Bosque del Apache NWR (Taylor and McDaniel 1998a, Sprenger et al. 2002).

Once saltcedar is removed, follow-up restoration work can be markedly different depending on water availability for flooding or irrigation. On the Bosque del Apache NWR, a network of canals and irrigation ditches throughout the refuge allows water from the Rio Grande to be used to mimic flooding and promote native seed germination to naturally vegetate sites (Stromberg 1997, Rood et al. 1998, Taylor et al. 1999). Native trees and shrubs should be planted on sites without flooding potential (Swenson and Mullins 1985, Anderson and Ohmart 1982, Anderson and Laymon 1989, Taylor and McDaniel 1998b). Herbaceous weeds often are serious competitors to planted vegetation (Anderson and Laymon 1989). Therefore ground disturbance, such as that incurred through clearing saltcedar vegetation mechanically, could be avoided using the herbicide-burn control approach.

Where flooding is used to promote natural riparian vegetation regeneration, soil disturbance and/or sediment depostion is required (Segelquist et al. 1993, Stromberg 1997, Rood et al. 1998, Sprenger et al. 2002). Saltcedar clearing by mechanical practices provides this disturbance and opens areas to sunlight needed for seedling growth and survival (Taylor et al. 1999). The herbicide-burn treatment also opens saltcedar canopies and, when flooded with sediment-laden flows, enhances the establishment and survival of replacement native riparian plants with minimal soil disturbance.

Cost and time greatly influence strategic choices related to saltcedar control and riparian restoration. In this study, for an additional 7% control achieved using the 2 mechanical clearing treatments, costs were 520% higher than the herbicide-burn treatment. The herbicide application was made in a single morning and burning accomplished in 1 day. By comparison, the initial mechanical clearing operation was conducted over a 6-month period (June to November), and the second operation was completed over a 2-month period (June to July). To reduce costs where thorough control is needed or soil disturbance is required as part of a restoration strategy, treatment combinations should be considered. As an example, saltcedar aerial growth can be removed using the herbicide-burn treatment for less than half the cost of mechanical surface aerial clearing. This method also reduces wear and tear on heavy equipment. If resulting resprout densities are unacceptable and/or if soil disturbance is needed for subsequent restoration, follow-up root plowing and raking can be used, which still provides a savings compared to using only the mechanical clearing treatment.

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Comparison of 2 techniques for monitoring vegetation on military lands

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Abstract

The U.S. Army is responsible for preparing a well-trained combat force while maintaining the ecological diversity and integrity of the lands it manages. The ability to efficiently collect data that accurately capture plant community diversity and percent composition is imperative to proper monitoring and land management of military lands. To ensure that the dual goals of military training and land stewardship are met on an army-wide basis, the U.S. Army Land Condition-Trend Analysis (LCTA) Program was developed. The LCTA Program specifies the Army's standard methodology for the collection, analysis, and reporting of natural resource data used for land inventory and monitoring. However, the LCTA sampling technique was developed in Colorado and Texas and little information is available on whether these methods are suitable for vegetation inventory and monitoring in other grassland ecosystems. This study compares LCTA measures of species richness and composition with quadrat sampling in the transitional area between the tall- and mixed-grass prairies of Camp Gilbert C. Grafton (South Unit) in North Dakota. Species richness was 67% higher when sampling with quadrats than using the LCTA technique, suggesting that LCTA samples did not detect a third of the plants present. Compared with the quadrat technique, LCTA samples overestimated the community contribution of *Bouteloua gracilis* (H.B.K.) Lag. ex Steud. (blue grama) and underestimated proportions of forbs and sedges. Moreover, LCTA samples are labor intensive and time consuming to collect. Other sampling methods may be needed to detect shifts in species composition towards a less desirable plant community or decreases in biodiversity that may be due to land-use. Thus, it is important for Camp Gilbert C. Grafton (South Unit) to re-evaluate the current standard methodology for monitoring the impacts of military training. Since military installations are located in many different ecosystems, it may be necessary for other installations to likewise examine the usefulness of LCTA techniques in their ecosystems.

Key Words: diversity, species richness, grassland vegetation, plant community, prairie, Land Condition Trend Analysis

Resumen

El ejército de E.U.A es responsable de preparar una fuerza de combate bien entrenada y a la vez de mantener la diversidad ecológica y la integridad de los terrenos que el maneja. La habilidad para colectar eficientemente datos que reflejen certeramente la diversidad de la comunidad vegetal y el porcentaje de composición es imperativo para un monitoreo y manejo apropiado de los terrenos del ejercito. Para ayudar a asegurar en forma general que la doble meta del entrenamiento militar y propiedad de la tierra se cumplen en el ejercito, se desarrollo el Programa de Análisis de la Tendencia de la Condición de la Tierra del Ejercito de los Estados Unidos (LCTA). El programa LCTA especifica la metodología estándar del ejercito para la colección, análisis y reporte de datos de los recursos naturales usados para llevara a cabo el inventario y monitoreo de los terrenos. Sin embargo, la técnica de muestreo del LCTA se desarrollo en Colorado y Texas y hay poca información disponible respecto a si estos métodos son apropiados para el inventario y monitoreo de otros ecosistemas de pastizal. Este estudio compara mediciones de riqueza de especies y composición con muestreo de cuadrantes en el área transicional entre las praderas de zacates altos y las de zacates mixtos del Campo Gilbert C. Grafton (Unidad Sur) en North Dakota.. La riqueza de especies fue 67% mayor cuando se uso el muestreo de cuadrantes que cuando se uso la técnica de LCTA, sugiriendo que las muestras del LCTA no detectaron un tercio de las plantas presentes. Comparada con la técnica de cuadrantes, las muestras del LCTA sobreestimaron la contribución que el *Bouteloua gracilis* (H.B.K.) Lag. ex Steud. ("Blue grama") hace a la comunidad y subestimó proporciones de hierbas y juncos. Más aún, para colectar las muestras del LCTA se requiere de un trabajo intensivo y mucho tiempo. Pueden necesitarse otros métodos de muestreo para detectar desviaciones en la composición de especies hacia una comunidad vegetal menos deseable o disminuciones en la biodiversidad que pueden ser por el uso de la tierra. Así, es importante para el Campo Gilbert C. Grafton (Unidad del Sur) revaluar la metodología estándar actual para monitoreo de los impactos del entrenamiento militar. Ya que las instalaciones militares esta localizadas en muy diferentes ecosistemas, puede ser necesario para otras instalaciones examinar la utilidad de las técnicas del LCTA en sus ecosistemas.

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The U.S. Army is responsible for managing nearly 5.1 million hectares of land on 186 major installations worldwide (U.S. Department of Army 1989). As a result of the limited acreage available and a dramatic increase in the acreage needed for military training and modern weapons testing, these areas have come under intensive use (U.S. Department of Army 1978). The risk of deterioration in land condition comes with increased land use, including accelerated soil erosion and reduced vegetative cover (Barker et al. 1998). Military lands must be carefully managed to preserve the functional and structural integrity of the natural communities, ensure long-term sustainability for future training needs, and to provide a realistic training environment.

In addition to its responsibility for preparing a well-trained combat force, the U.S. Army must maintain the ecological diversity and viability of the lands in its care. Many of these lands are intensively used for a variety of military training activities, but they are also managed for non-military values such as fish and wildlife, recreation, and agriculture. Additionally, the National Environmental Policy Act of 1969 and Army Regulation 200-2 require the Army to minimize any significant short-term and long-term environmental impacts on natural resources (Goran et al. 1983). Furthermore, rare and endangered species, and the habitat necessary to maintain those species on army land, are protected by the Threatened and Endangered Species Act (U.S. Dept. of Interior 1973). Recent legislative trends in environmental impact analysis require quantification of impact estimates. Thus, there is a need to establish cause-effect relationships between Army activities and environmental impacts. Knowledge about these impacts and their short and long-term effects help Army personnel to plan training programs that minimize adverse effects on local ecosystems.

To help ensure that the dual goals of military training and environmental compliance are met on an army-wide basis, the U.S. Army Land Condition-Trend Analysis (LCTA) Program was developed (Diersing et al. 1992). The LCTA program is the Army's standard methodology for the collection, analysis, and reporting of natural resource data used in land inventory and monitoring (Wolff 1990). The objectives of the LCTA program are to promote the principles of sustained yield, land stewardship, and multiple uses of military land resources (Tazik et al. 1992). Specific objectives are to: "1) evaluate the capability of land to meet the multiple-use demands of the U.S. Army on a sustained basis, 2) delineate the biophysical and regulatory constraints to use of the land, 3) monitor changes in land resource condition and evaluate change in terms of current land use, 4) develop and refine land management plans to ensure long-term resource availability, 5) characterize installation natural resources, and 6) implement standards in collection, analysis, and reporting of the data acquired that enable Army-wide data compilation" (Tazik et al. 1992).

The effects of disturbance, such as that caused by military maneuvers, are often quantified by collecting data on vegetation and monitoring for decreases in vegetation abundance (Brady et al. 1995, CEMML 2001). Measuring environmental impact involves inventory of natural resources and monitoring for those resources over time to determine whether ecological changes have occurred. Due to potential threats of exotic plant invasions, the desire to protect native plant diversity, and the need to maintain a realistic military training environment, sampling techniques need to accurately quantify the status and trends of plant diversity on all military installations. Since military installations are scattered throughout the United States, comprising all of the ecoregions and habitat types of North America, it is extremely difficult to develop a "standard" vegetation monitoring technique that can be applied across all military lands, yet this is what has been attempted with the LCTA program. The LCTA program's sampling methods were initially developed in the shortgrass steppe of Colorado and southern mixed prairie of Texas and have subsequently been implemented on military installations across the U.S. (Tazik et al. 1992).

An independent review panel found the LCTA methods to be technologically sound (USALIAC 1989), even though little information is available on whether the LCTA protocol is suitable for vegetation inventory and monitoring in other grassland ecosystems. In this study, we compared the "standard" protocol currently being used by military installations (LCTA) with a technique that is widely used by plant ecologists and is the standard methodology for vegetation monitoring in mixed grass prairie (Bonham 1989).

Like any other sampling protocol, the LCTA method has its strengths and weaknesses. The LCTA sampling method determines ground cover, surface disturbance, and vertical distribution of the vegetation. Information derived from LCTA samples is also used in evaluating soil erosion status, military concealment cover, wildlife habitat, and botanical composition, and for ground-truthing remotely sensed imagery (Tazik et al. 1992). The major limitation of the LCTA method in the mixed grass prairie is the amount of time needed to gather information from a transect. The second limitation is the low amount of area sampled (60 cm^2) per transect, the standard area sampled for all installations on a per transect basis. This may be overcome if a large number of points are sampled, but again, time constraints may not allow monitoring teams to cover large areas. An additional limitation of the LCTA method is that it is not recommended for use in areas where canopy cover is less than 5% or greater than 35% (CEMML 2001). The vegetation at Camp Gilbert C. Grafton (South Unit) is quite complex with nearly 100% canopy cover (Photo 1).

Photo 1. ***Poa pratensis—Stripa*** **spp. community at Camp Grafton South.**

Alternatives to the LCTA sampling procedures include the use of traditional quadrats, such as 0.10 m^2 Daubenmire frames. If the LCTA rod is viewed as a very narrow, vertically oriented quadrat, then these frames or quadrats can be seen as larger, horizontally oriented counterparts with their own strengths and weaknesses. The larger quadrat allows a greater area to be sampled in a short period of time and greater flexibility in size of quadrats used. However, quadrat sampling does not measure military concealment cover nor vertical distribution of the vegetation.

Observed differences between data obtained using the LCTA protocol and quadrats in the field led to this study, which compared the 2 methods to determine which technique best captures baseline vegetation conditions at Camp Grafton South, an area developed in 1983 to support the training needs of the North Dakota Army National Guard. This training site is also used by the North Dakota Air National Guard; Army National Guard units from other states; the U.S. Army Reserve; various Reserve Officer Training Corps units; and active component units of the U.S. Army, Navy, and Air Force. The North Dakota Army National Guard recently introduced tracked vehicles to some of its land units ("mechanized units"). These vehicles have the potential to negatively affect the natural environment, posing new management challenges to the training site (Barker et al. 1998). Milchunas et al. (2000) concluded that long-term disturbance from mechanized military maneuvers can cause plant mortality and indirectly affect plant communities through soil compaction and by altering competitive relationships within the plant community. With the addition of tracked vehicles, vegetation and soil properties need to be monitored on these installations to ensure that no irreparable harm will occur to the sites' natural resources.

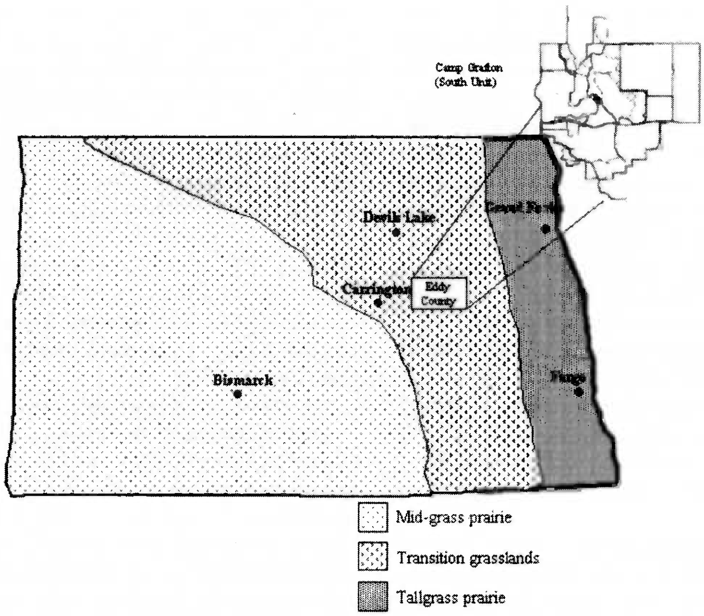

Fig. 1. Location of Eddy County and Camp Gilbert C. Grafton (South Unit) within North Dakota and the major vegetation zones across the state (modified from Küchler 1964 and Barker and Whitman 1988 and 1989).

The LCTA program was used as part of a larger effort that also included quadrat sampling methods to describe the native vegetation of the transitional grasslands of Camp Grafton South. Initial observations indicated that quadrats consistently detected more species than did sampling using the LCTA techniques, that LCTA sampling failed to detect a large proportion of the forbs and sedges present, and that LCTA samples resulted in higher percent composition estimates of dominant grasses than did quadrat samples (K. Sedivec, personal communication). The objective of this study was to compare the LCTA monitoring technique with quadrat sampling to describe the species richness and percent composition of vegetation on a military installation in east-central North Dakota in an area known as the transitional grasslands.

Methods

Study Area

Camp Gilbert C. Grafton (South Unit) is located approximately 56 km southwest of Devils Lake, North Dakota, and has an area of approximately 3,470 ha (Barker et al. 1998) (Fig. 1). This study was conducted in the southeast corner of Eddy County, between 47°40' to 47°45' N Lat and 98°35' to 98°43' W Long (Fig. 1), in the Drift Prairie physiographic zone of the Transitional Grasslands prairie region (Barker and Whitman 1989). Vegetation in these transitional grasslands is a combination of mixed-grass and tallgrass prairie plants (Whitman and Wali 1975, Barker and Whitman 1989). Küchler (1964) classified the potential natural vegetation of this northern transition grass prairie as a moderately dense, short to medium tall Wheatgrass-Bluestem-Needlegrass (*Agropyron-Andropogon-Stipa*) association. The transitional grassland type lies between the Bluestem prairie to the east and the drier Wheatgrass-Needlegrass association to the west. The study area is administered by the North Dakota Army National Guard and has been grazed by cattle for many years.

The vegetative plant communities within the study area were designated high-, mid- and low-prairie based on topography and drainage (Fig. 2). The high-prairie

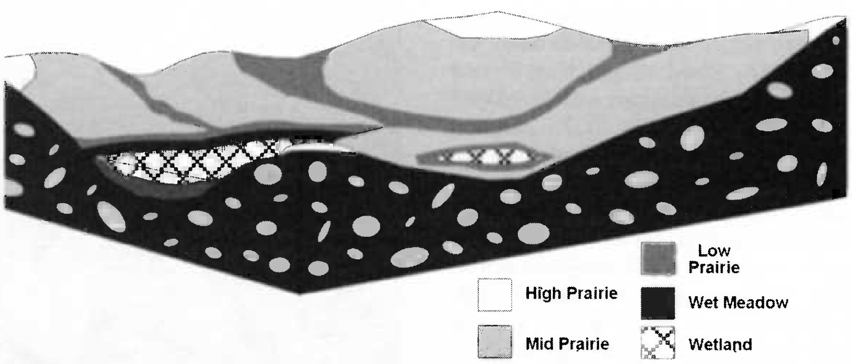

Fig. 2. Hypothetical block diagram of Camp Grafton South, modified from Dix and Smeins (1967).

(upland) was classified as an area that includes steep shoulder slopes and tops of knolls that lose most of their moisture to runoff. The mid-prairie (midland) was classified as areas that include back slopes with moderate infiltration. The low-prairie (lowland) was classified as an area that occupies the footslope and toeslope positions on the landscape. A visible zonation of plant communities occurred across these 3 topographic areas.

Average annual precipitation (29-year average) at the McHenry weather station was 47.3 cm per year (NOAA 1995-1997). Annual precipitation was 63.2 cm, 47.5 cm, and 29.4 cm for 1995, 1996, and 1997, respectively. The 29-year average precipitation was 8.7 cm in June, 6.7 cm in July, and 6.9 cm in August. Precipitation was below the 29-year average for June and above the average for July for all 3 years. Precipitation was below the 29-year average for August, totalling 5.5 cm, 3.1 cm, and 3.5 cm for 1995, 1996, and 1997, respectively.


Photo 2. Sampling vegetation using LCTA methodology. (Note vertical rod).

Sampling Methods

The Land Condition-Trend Analysis (LCTA) vegetation surveys consist of 3 main components: line point transect aerial cover surveys, line point transect ground cover surveys, and belt transect surveys (Tazik et al. 1992). The line transect aerial cover survey characterizes canopy cover, species composition and distribution (Photo 2). The line transect ground cover survey characterizes basal cover, species composition, distribution, and surface disturbance. Data from the line transect surveys were recorded using a modified point intercept method (Levy and Madden 1933, Goodall 1952, 1953, Mueller-Dombois and Ellenberg 1974). Forty-five, 100 m transects were randomly located on native prairie at Camp Grafton South during the springs of 1995–1997 (15 per year) using the GIS software program IDRISI (Fig. 3). According to Tazik et al. (1992), the number of plots established at any given installation should be based on the size and variability of the area. As a rule of thumb, there should be approximately 1 plot per 200 ha. The CGS comprises 3,470 ha, suggesting that 18 transects would be sufficient to monitor the natural resources at this installation. This study evaluated 45 transects, 2.5 times the recommended number (Tazik et al. 1992). Transects were proportionately allocated, using total hectares of vegetation type within the upland (n = 18), midland (n = 17) and lowland (n = 10) communities, and were located in the field with a hand-held global positioning system (GPS) receiver.

Using the Army's LCTA Program methodology, 100 points were sampled along each line transect, beginning at the 0.5 m point and continuing at 1 m intervals along the measuring tape (Tazik et al. 1992). A 1 m tall, 6 mm diameter measuring rod was placed perpendicular to the ground at each point. The pre-

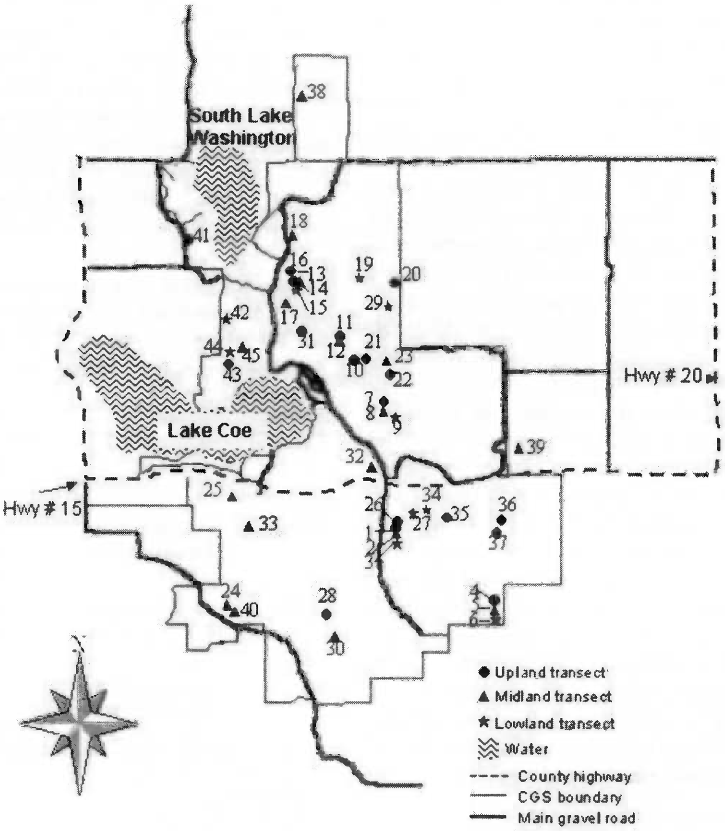

Fig. 3. Location of 45 grassland transects at Camp Grafton South.

sence/absence of forb and graminoid species were determined by recording vegetation contacts ("hits") on the measuring rod. If a species touched the rod at more than 1 place, only 1 "hit" was recorded for that point, indicating presence of that species.

Quadrats were also sampled to detect the presence/absence of graminoid and forb species. Quadrats were sampled every 5 m along the 100 m transects using a 0.25 m^2 frame for forb frequency and, within the 0.25 m^2 frame, a 0.1 m^2 frame to determine frequency of graminoid species, after Biondini et al. (1989), Stohlgren et al. (1998) and Daubenmire (1959). The larger 0.25 m^2 frame was used to determine presence/absence for forbs due to the inherent spatial patchiness of forb species (Biondini et al. 1989). The LCTA and quadrat samples were taken at the same locations and transects at the same time. Plant species nomenclature followed the Great Plains Flora (Great Plains Flora Association 1986).

Data Analysis

We calculated species richness for each transect to determine whether the 2 sampling techniques equally measured plant community diversity. Species richness was calculated as the total number of species observed along each transect. Additionally, the percent composition of selected species was calculated as an index of community dominance. *Carex* spp., *Stipa* spp., *Artemisia frigida* Willd. (fringed sagebrush), *Helianthus rigidus* (Cass.) Desf. (stiff sunflower) and *Bouteloua gracilis* (H.B.K.) Lag. ex Steud. (blue grama) were selected as species of interest because they were representative of the communities in the study area, present in most transects, and detected using both sampling techniques.

Presence/absence (frequency) data collected using LCTA techniques can be used to characterize plant community composition and serve as baseline data to detect changes in vegetation over time (Price et al. 1995). However, because frequency data are highly dependent on the size of the area sampled (Bonham 1989), we converted the presence/absence measures to percent composition. We calculated percent composition as the proportion that each species of interest contributed to the local community (Skinner 1995) by dividing the number of "hits" (or number of quadrats in which the species was present) along each transect by the sum of all "hits" for all species encountered:

$$\text{Percent composition} = \frac{\text{no. of hits of species A}}{\text{total no. of hits for all species}} \times 100 \qquad \textbf{(1)}$$

Table 1. Summary statistics. "LCTAspp" is species richness as measured by the LCTA Method and "quadratspp" is species richness as measured using quadrats for the upland, midland and lowland communities at Camp Grafton South.

Topographic Position	Variable	N	Mean	Std . Deviation	Minimum	Maximum
Upland	LCTAspp	18	12.83	4.74	7	22
	quadratspp	18	20.11	8.68	9	38
Midland	LCTAspp	17	12.71	5.65	6	26
	quadratspp	17	22.06	10.76	9	48
Lowland	LCTAspp	10	11	6.39	5	23
	quadratspp	10	16.8	8.05	8	30
All	LCTAspp	45	12.38	5.41	5	26
	quadratspp	45	20.11	9.4	8	48

Wilcoxon's signed-rank test for 2 related samples was used to test for significant differences in the distributions of the data collected with the 2 sampling protocols. Wilcoxon's test was run first on all transects and then individually on lowland, midland, and upland transects. Wilcoxon's signed-rank test was conducted on the percent composition in the same manner as for species richness.

Results

Species richness. The quadrat sampling resulted in consistently higher values for species richness than the Land Condition-Trend Analysis (LCTA) Program's sampling method (Table 1). This was true for all 3 topographic areas (upland, midland, and lowland prairie). Sampling with larger quadrats detected about 67% more species on average than did the LCTA method (Table 1). The difference between species richness as measured by the 2 methods was statistically significant (Table 2). Sampling with quadrats detected as many or more species than the LCTA method, with the exception of 1 upland transect (Table 2). On the upland, midland, and lowland communities, the quadrat method detected 36, 42, and 34% more species, respectively, than did the LCTA Program methodology.

Percent composition. Percent composition of *Carex* spp. was greater when sampled with the quadrats than with LCTA methods in 39 of 45 transects and the differences in values obtained by the 2 methods were statistically significant for all three topographic areas (Table 3). Sampling with LCTA methods resulted in higher percent composition for *Stipa* spp. in upland and midland transects (Table 4). For fringed sagebrush and stiff sunflower, percent composition values were larger when measured with quadrats than when measured with LCTA methods in upland and midland transects, but the differences were not statistically significant in lowland transects (Tables 5 and 6). Percent

Table 2. Results of Wilcoxon signed-ranks test. "LCTAspp" is species richness as measured by the LCTA method and "quadratspp" is species richness as measured using quadrats for the upland, midland, lowland and all grassland communities at Camp Grafton South.

Topographic Position	Ranks	N	Mean Rank	Sum of Ranks	Z	Asymp. Sig. (2-tailed)
Upland	Negative ranks[1]	1	1.50	1.50	-3.446[4]	.001**
	Positive ranks[2]	15	8.97	134.50		
	Ties[3]	2				
Midland	Negative ranks[1]	0	--	--	-3.519[4]	.000**
	Positive ranks[2]	16	8.50	136.00		
	Ties[3]	1				
Lowland	Negative ranks[1]	0	--	--	-2.819[4]	.005**
	Positive ranks[2]	10	5.50	55.00		
	Ties[3]	0				
All	Negative ranks[1]	1	2.00	2.00	-5.625[4]	.000**
	Positive ranks[2]	41	21.98	901.00		
	Ties[3]	3				

*Significant at 0.05 level

**Significant at 0.01 level

[1] quadratspp < LCTAspp

[2] quadratspp > LCTAspp

[3] quadratspp = LCTAspp

[4] based on negative ranks

Table 3. Results of Wilcoxon signed-ranks test. "LCTACarex" is percent composition of *Carex* spp. as measured by the LCTA method and "quadrat *Carex*" is percent composition of *Carex* spp. as measured using quadrats for the upland, midland, lowland and all grassland communities at Camp Grafton South.

Topographic Position	Ranks	N	Mean Rank	Sum of Ranks	Z	Asymp. Sig. (2-tailed)
Upland	Negative ranks^1	0	0.00	0.00	-3.724^4	.000**
	Positive ranks^2	18	9.50	171.00		
	Ties^3	0				
Midland	Negative ranks^1	0	0.00	0.00	-3.180^4	.001**
	Positive ranks^2	13	7.00	91.00		
	Ties^3	4				
Lowland	Negative ranks^1	0	0.00	0.00	-2.521^4	.012*
	Positive ranks^2	8	4.50	36.00		
	Ties^3	2				
All	Negative ranks^1	0	0.00	0.00	-5.442^4	.000**
	Positive ranks^2	39	20.00	780.00		
	Ties^3	6				

*Significant at 0.05 level
**Significant at 0.01 level

Table 4. Results of Wilcoxon signed-ranks test. "LCTAStipa" is percent composition of *Stipa* spp. as measured by the LCTA method and "quadratStipa" is percent composition of *Stipa* spp. as measured using quadrats for the upland, midland, lowland and all grassland communities at Camp Grafton South.

Topographic Position	Ranks	N	Mean Rank	Sum of Ranks	Z	Asymp. Sig. (2-tailed)
Upland	Negative ranks^1	16	9.94	159.00	-3.201^4	.001**
	Positive ranks^2	2	6.00	12.00		
	Ties^3	0				
Midland	Negative ranks^1	14	9.50	133.00	-2.675^4	.007**
	Positive ranks^2	3	6.67	20.00		
	Ties^3	0				
Lowland	Negative ranks^1	3	4.00	12.00	-1.244^5	.214
	Positive ranks^2	6	5.50	33.00		
	Ties^3	1				
All	Negative ranks^1	33	24.64	813.00	-3.711^4	.000**
	Positive ranks^2	11	16.09	177.00		
	Ties^3	1				

*Significant at 0.05 level
**Significant at 0.01 level
[1] quadratspp < LCTAspp
[2] quadratspp > LCTAspp
[3] quadratspp = LCTAspp
[4] based on negative ranks
[5] based on negative ranks

Table 5. Results of Wilcoxon signed-ranks test. "LCTAARFR" is percent composition of *Artemisia frigida* (fringed sagebrush) as measured by the LCTA method and "quadratARFR" is percent composition of fringed sagebrush as measured using quadrats for the upland, midland, lowland and all grassland communities at Camp Grafton South.

Topographic Position	Ranks	N	Mean Rank	Sum of Ranks	Z	Asymp. Sig. (2-tailed)
Upland	Negative ranks^1	0	0.00	0.00	-2.366^4	.000**
	Positive ranks^2	7	4.00	28.00		
	Ties^3	11				
Midland	Negative ranks^1	0	0.00	0.00	-2.201^4	.028*
	Positive ranks^2	6	3.50	21.00		
	Ties^3	11				
Lowland	Negative ranks^1	0	0.00	0.00	-1.604^4	.109
	Positive ranks^2	3	2.00	6.00		
	Ties^3	7				
All	Negative ranks^1	0	0.00	0.00	-3.516^4	.000**
	Positive ranks^2	16	8.50	136.00		
	Ties^3	29				

Significant at 0.05 level
**Significant at 0.01 level
[1] quadratspp < LCTAspp
[2] quadratspp > LCTAspp
[3] quadratspp = LCTAspp
[4] based on negative ranks

composition of blue grama were greater when measured with the quadrats in midland transects (Table 7). No significant differences between sampling methods were found for *Stipa* spp., fringed sagebrush, stiff sunflower or blue grama on lowland transects.

The raw data revealed the strengths and weaknesses of both sampling methods. The LCTA method detected shrubs more often than did quadrats, but LCTA methods failed to detect a sizable proportion of the forbs present. For example, in upland transect 37 there were 4 species of forbs detected using LCTA methods and an additional 14 forb species were found using quadrats (Table 8). Individually, these forbs had percent compositions of less than 10% but their combined contribution to the community was 55%. Similarly, only about half as many forbs were detected by LCTA as by quadrats in transects 24 and 29 (midland and lowland transects, respectively). Percent composition of dominant grasses also differed substantially between sampling methods. The LCTA method resulted in percent compositions for *Poa pratensis* that were several times higher than the values calculated from data gathered using quadrats (Table 8).

Discussion

Rangeland conservation is increasingly concerned with maintaining native plant diversity, detecting exotic species, and monitoring rare species (Mack 1981, U.S. GAO 1991, National Research Council 1994, Joern and Keeler 1995, Randall 1966, Stohlgren et al 1998). Because rangeland inventory and monitoring needs have increased in the face of decreased funding to monitor rangelands (National Research Council 1994), sampling techniques must be more cost-efficient and information rich than ever before. Military training lands are no exception. As management challenges on military installations become more complex, the sampling techniques used to monitor vegetation must provide relevant information linking land use with environmental change (Brady et al. 1995, Stohlgren et al. 1998). Based on our results, the Land Condition-Trend Analysis (LCTA) Program methodology did not adequately detect rare or subdominant species, a serious limitation to monitoring efforts at Camp Grafton South.

Species richness. Like the work of Stohlgren and coworkers (1998) in the northern mixed prairie, we found that the

Table 6. Results of Wilcoxon signed-ranks test. "LCTAHERI" is percent composition of *Helianthus rigida* (rigid sunflower) as measured by the LCTA method and "quadratHERI" is percent composition of rigid sunflower as measured using quadrats for the upland, midland, lowland and all grassland communities at Camp Grafton South.

Topographic Position	Ranks	N	Mean Rank	Sum of Ranks	Z	Asymp. Sig. (2-tailed)
Upland	Negative ranks[1]	0	0.00	0.00	-2.366[4]	.018*
	Positive ranks[2]	7	4.00	28.00		
	Ties[3]	11				
Midland	Negative ranks[1]	1	1.00	1.00	-2.197[4]	.028*
	Positive ranks[2]	6	4.50	27.00		
	Ties[3]	10				
Lowland	Negative ranks[1]	0	0.00	0.00	-1.000[4]	.317
	Positive ranks[2]	1	1.00	1.00		
	Ties[3]	9				
All	Negative ranks[1]	1	2.00	2.00	-3.294[4]	.001**
	Positive ranks[2]	14	8.43	118.00		
	Ties[3]	30				

*Significant at 0.05 level
**Significant at 0.01 level
[1] quadratspp < LCTAspp
[2] quadratspp > LCTAspp
[3] quadratspp = LCTAspp
[4] based on negative ranks

2 sampling techniques differed in the number of species detected. Sampling with LCTA did not capture as much of the plant diversity of the study area as quadrat sampling. This may not be a serious problem when species richness is low and there are few species to sample, but the vegetation at Camp Grafton South is quite complex, with nearly 100% canopy cover and approximately 600 species present (Dekeyser 1995) (Photo 3). Our results may have been expected, as the LCTA protocol is not recommended for use in areas where canopy cover is less than 5% or greater than 35% (CEMML 2001). Unlike the communities in Texas and Colorado where the LCTA methods were developed, the dense cover at this installation clearly falls outside of this recommended range, indicating that other methods should be investigated for use at this installation.

There are 2 main reasons that the LCTA point-intercept method did not capture the full plant diversity present at Camp Grafton South. First, the vegetation in the study area produces a thick layer of litter that is not disturbed when sampling using a rod (but which is removed when sampling with quadrats). Thus, plants of small stature may have been obscured by the litter and remained undetected when sampling with the LCTA protocol. Second, the LCTA Program sampling technique uses a 6 mm diameter rod to intercept vegetation at 100 points along each transect. This results in a very small area covered (60 cm2) compared with quadrats that each cover 0.1 to 0.25 m^2 of area. However, the LCTA sampling technique also records "hits" by species that are adjacent to the rod and not actually growing in the area covered by the rod itself, but which have leaves that overlap the point where the rod is placed. Thus, the LCTA technique does sample an area greater than the size of the rod itself, but the size of this area is impossible to calculate, since it depends on the growth form and habit of the individual plant species found in the community. Because we are unable to calculate species richness on a per m^2 basis, our comparisons of LCTA and quadrat results should be interpreted with caution. Nonetheless, it is clear that quadrat sampling resulted in a more complete picture of the diversity of the plant community at Camp Grafton South.

Percent composition. The LCTA technique underestimated the percent composition of forbs and sedges, compared with quadrat sampling, due in part to reduced detection of the presence of these subdominant species. Price and coworkers (1995) concluded from LCTA techniques at Fort Hood, Texas, that sampling intensity may be sufficient for major species but insufficient for minor species. Our findings at Camp Grafton South were very similar to those found at Fort Hood, indicating that similar problems may arise even in the more arid areas where the LCTA Program was developed. Price and coworkers (1995) also concluded that minor species often are not normally distributed, making it difficult to detect the minor species using the LCTA method unless a very large number of points were sampled along each transect (CEMML 2001). However, this is not a feasible remedy because of the time it would involve. The LCTA technique took 2 to 2.5 hours per site versus 1 hour when sampling with quadrats.

Detecting and monitoring locally rare species or subdominant species in rangeland is important because less common species are a major component of plant diversity. These subdominant species are the same species that will likely be lost if there is a shift in species composition due to disturbance or invasion of less desirable species (Stohlgren et al. 1998). Camp Gilbert C. Grafton (South Unit) currently has 4 species that are considered threatened in North Dakota, *Carex pseudo-cype-*

Table 7. Results of Wilcoxon signed-ranks test. "LCTABOGR" is relative frequency of *Bouteloua gracilis* (blue grama) as measured by the LCTA method and "quadratBOGR" is percent composition of blue grama as measured using quadrats for the upland, midland, lowland, and all grassland communities at Camp Grafton South.

Topographic Position	Ranks	N	Mean Rank	Sum of Ranks	Z	Asymp. Sig. (2-tailed)
Upland	Negative ranks[1]	10	11.50	115.00	-1.823[4]	.068
	Positive ranks[2]	7	5.43	38.00		
	Ties[3]	1				
Midland	Negative ranks[1]	1	12.00	12.00	-2.118[5]	.034*
	Positive ranks[2]	11	6.00	66.00		
	Ties[3]	5				
Lowland	Negative ranks[1]	3	2.33	7.00	-1.183[5]	.237
	Positive ranks[2]	4	5.25	21.00		
	Ties[3]	3				
All	Negative ranks[1]	14	22.93	321.00	-0.189[5]	.850
	Positive ranks[2]					
	Ties[3]					

*Significant at 0.05 level
**Significant at 0.01 level
[1] quadratspp < LCTAspp
[2] quadratspp > LCTAspp
[3] quadratspp = LCTAspp
[4] based on negative ranks
[5] based on negative ranks

rus L. (cyperus-like sedge), *Carex buxbaumii* Wahl., *Cyprideum calceolus* L.(large yellow lady's-slipper orchid), and *Cypripedium candidum* Muhl. Ex Willd. (small white lady's-slipper orchid) (North Dakota Outdoors 1986). It is imperative that these threatened, rare or subdominant species be monitored through a well-designed vegetation sampling protocol because of their importance to the diversity of the plant community and their contribution to the overall health and structural integrity of Camp Grafton South. Although we do not know the "true" percent composition of species of this landscape, our data suggest that sampling with quadrats is better than LCTA sampling for measuring species compositions at this installation. It may be necessary to conduct studies evaluating various quadrat sizes and numbers of plots to determine the most time-efficient and information rich method. One such method is a species-area curve, which uses nested quadrats to find the relationship between number of species present and area sampled. This method is used to find the minimal area and number of quadrats needed to adequately sample vegetation. Since military installations are located in many different ecosystems, it may be necessary for other installations to develop their own species-area curve and likewise evaluate the usefulness of the LCTA methodology in their ecosystems. Further research is needed to evaluate other sampling techniques and determine the method that most accurately and efficiently captures the data necessary to successfully monitor the training lands of the North Dakota Army National Guard.

Conclusion

The U.S. Army Land Condition-Trend Analysis (LCTA) Program's inventory and monitoring methods may be suitable for the semi-arid ecosystems where they were developed, but fail to accurately portray the community diversity and species composition of North Dakota's complex transitional prairie. The LCTA sampling protocol is currently being used on Army installations worldwide; however, our results suggest that the "one-size-fits-all" approach of using the same sampling methods for all Army installations needs to be re-evaluated. Although there are several advantages to using the LCTA technique, such as measuring military concealment and vertical distribution of the vegetation, military land managers may not be detect a

Table 8. Representative data for upland, midland, and lowland transects at Camp Grafton South. Transect 37 represents a community located in the high prairie (upland), transect 24 is located in the mid prairie (midland), and transect 29 is located in the low prairie (lowland) portion of the study area.

Transect	Species	Plant Group[1]	LCTA percent composition	Quadrat percent composition
37	*Bromus inermis*	G	1.55	0.962
	Calamovilfa longifolia	G	1.55	1.92
	Poa pratensis	G	76.7	19.2
	Stipa viridula	G	3.10	8.65
	Ambrosia psilostachya	F	0.775	3.85
	Galium boreale	F	0.775	2.88
	Helianthus rigidus	F	0.775	2.88
	Monarda fistulosa	F	2.33	4.81
	Agropyron caninum	G	0.775	--
	Schizachyrium scoparium	G	0.775	--
	Stipa comata	G	0.775	--
	Amorpha canescens	S	2.33	--
	Symphiocarpos occidentalis	S	7.75	--
	Carex eleocharis	G	--	5.77
	Carex heliophila	G	--	9.62
	Dicanthelium wilcoxianum	G	--	0.962
	Achillea millefolium	F	--	0.962
	Anemone cylindrica	F	--	8.65
	Artemisia ludoviciana	F	--	2.88
	Asclepis viridis	F	--	3.85
	Aster ericoides	F	--	1.92
	Astragalus flexuosus	F	--	0.962
	Cirsium flodmanni	F	--	0.962
	Equisetum laevigatum	F	--	1.92
	Geum triflorum	F	--	0.962
	Lactuca oblongifolia	F	--	10.6
	Lithospermum canescens	F	--	0.962
	Ratibida columnifera	F	--	1.92
	Solidago mollis	F	--	0.962
	Viola pedata	F	--	0.962
24	*Agropyron caninum*	G	0.481	0.565
	Bromus inermis	G	20.2	11.3
	Poa pratensis	G	47.1	11.3
	Stipa spartea	G	3.37	1.69
	Anemone cylindrica	F	0.481	2.26
	Artemisia frigida	F	0.481	2.82
	Artemisia ludoviciana	F	1.92	7.91
	Galium boreale	F	6.25	9.04
	Helianthus rigidus	F	11.1	10.7
	Solidago canadensis	F	0.481	2.26
	Solidago mollis	F	0.962	3.39
	Amorpha canescens	S	1.44	--
	Symphiocarpos occidentalis	S	5.77	--
	Carex eleocharis	G	--	4.52
	Carex heliophila	G	--	4.52
	Stipa comata	G	--	0.565
	Achillea millefolium	F	--	0.565
	Androsace occidentalis	F	--	5.08
	Aster ericoides	F	--	6.21
	Astragalus flexuosus	F	--	3.39
	Comandra umbellata	F	--	5.08
	Solidago missouriensis	F	--	0.565
	Melilotus officinalis	F	--	1.69
	Potentilla hippiana	F	--	0.565
	Psoralea argophylla	F	--	3.95
29	*Agropyron caninum*	G	35. 8	31.3
	Poa pratensis	G	60.6	31.3
	Equisetum laevigatum	F	1.21	4.69
	Onosmodium molle	F	1.21	1.56
	Trifolium repens	F	1.21	3.13
	Carex spp.	G	--	1.56
	Oxalis stricta	F	--	14.1
	Euphorbia glyptosperma	F	--	10.9
	Artemisia ludoviciana	F	--	1.56

[1] F=forb, G=graminoid, S=shrub

Photo 3. ***Bouteloua gracilis-Stipa* spp. community at Camp Grafton South.**

shift in species composition early enough to avoid significant short-term and long-term environmental impacts on natural resources. Other sampling methods may be necessary to detect shifts in species composition towards a less desirable plant community or decreases in biodiversity that may result from heavy land-use.

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Initial beaked hazel growth responses following protection from ungulate browsing

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Abstract

Beaked hazel (*Corylus cornuta* Marsh) dominates the understory of many Boreal Mixedwood forests in central Alberta including those in Elk Island National Park, where this species demonstrates a high tolerance to browsing. This research quantified changes in beaked hazel stem morphology (total twig length and number) and leaf and twig biomass of current annual growth, both inside and outside 4 newly established exclosures during the growing seasons of 1999 and 2000. At 2 sites, leaf and twig current annual growth of beaked hazel shrubs recently protected from herbivory increased significantly ($P < 0.05$) by 85 to 114% relative to that of browsed shrubs. At another site, the removal of browsing changed the morphology of beaked hazel shrub growth ($P < 0.05$), with protected shrubs producing 26% more twigs that were shorter in aggregate length by 27%. The final site exhibited no significant ($P > 0.05$) changes in current annual growth at the individual shrub stem level, potentially due to intense intra-specific competition. These results indicate that at several locations in the Park, the recent history of intense browsing appears to be limiting the annual growth of beaked hazel, including browse production. Despite the general increase in growth of individual beaked hazel stems, however, no changes in production were evident at the community level ($P > 0.05$) with the removal of browsing after 2 years. Protection from browsing did increase average beaked hazel height by 40% over the same period.

Key Words: boreal forest, browsing release, *Corylus cornuta*, current annual growth, exclosures, shrub morphology

Resumen

El "Beaked hazel" (*Corylus cornuta* Marsh) domina el estrato arbustivo de muchos bosques Boreales Mixtos de la región central de Alberta, incluyendo los de Elk Island National Park, donde esta especie demuestra una alta tolerancia al ramoneo. Esta investigación cuantifico los cambios en la morfología de tallos (longitud total y número de ramas) y la biomasa de hojas y ramas del crecimiento anual actual del "Beaked hazel", tanto dentro como fuera de 4 exclusiones recientemente establecidas durante las estaciones de crecimiento de 1999 y 2000. En 2 sitios, el crecimiento anual actual de hojas y tallos de arbustos de "Beaked hazel" recién protegidos de la hervíboría se incremento significativamente ($P < 0.05$) de 85 a 114% en comparación con los arbustos ramoneados. En otro sitio, la remoción del ramoneo cambio la morfología de crecimiento del "Beaked hazel" ($P < 0.05$), los arbustos protegidos produjeron 26% más ramas que fueron 27% mas cortas en la longitud agregada. El sitio final no mostro cambios significativos ($P > 0.05$) en el crecimiento anual actual al nivel individual de tallo del arbusto, debido potencialmente a la intensa competencia intraespecifica. Esto resultados indican, que en varias localidades del Parque, la historia reciente de ramoneo intenso parece ser limitante del crecimiento anual del "Beaked hazel", incluyendo la producción de forraje para ramoneo. Sin embargo, a pesar del incremento general de crecimiento de los tallos individuales del "Beaked hazel", a nivel de comunidad, no hubo cambios evidentes en la producción ($P > 0.05$) 2 años después de la remoción del ramoneo. En el mismo periodo de tiempo la protección contra el ramoneo incremento en 40% la altura promedio del "Beaked hazel".

Beaked hazel (*Corylus cornuta* Marsh.) is a common understory shrub within the Lower Boreal Mixedwood (LBM) forests of western Canada, occurring mainly on moderately well-drained, moist sites (Willoughby 2000). Beaked hazel is a prolific shrub capable of producing vegetative clones via underground stems that produce new roots and aerial stems along their length (Tappeiner and John 1973). Clones are typically less than 2 m in diameter (Tappeiner 1971). As stands of beaked hazel age, the total phytomass and proportion of young stems in the population increases. However, beaked hazel density eventually declines as the tree overstory and shading increases (Kurmis and Sucoff 1989). Beaked hazel can influence forest ecology, with high densities inhibiting tree reproduction and reducing the abundance of more palatable browse species, as well as changing light intensity and the composition of litter in the understory (Tappeiner 1979, 1971).

Elk Island National Park (EINP) is located in east-central Alberta and has an understory dominated by dense stands of beaked hazel (Hardy Associates Ltd. 1986). Despite the abundance of beaked hazel and its role in providing the majority of

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available browse to native ungulates (Blyth et al. 1994), little information exists on the intra-specific response of this shrub to current levels of herbivory within the Park. Studies on other shrub species have found browsing may lead to reduced foraging opportunities for wildlife (e.g. Wambolt and Sherwood 1999, Bork et al. 1997a). Given that previous research has shown stem mortality may eventually lead to an increase in beaked hazel density (Tappeiner 1979), heavy browsing of this species may lead to unexpected increases in browse production.

This study assessed the effect of browsing on beaked hazel shrubs within EINP. To accomplish this, we employed the approach of Yokoyama and Shibata (1998) and quantified relative changes in the morphology and biomass of current annual growth within individual shrub stems for 2 successive years following the cessation of browsing. We hypothesized that if current levels of browsing suppress beaked hazel growth, stems recently protected from browsing would have greater current annual growth. Conversely, should intensive browsing facilitate beaked hazel current annual growth, individual stem growth would be lower in protected shrubs over the same period. A secondary objective was to compare beaked hazel growth at the population (i.e. per unit area) level with that at the individual stem (i.e. ramet) level, as previous growth responses have been found to differ depending on the biological scale of investigation (Tolvanen et al. 1992, Wambolt et al. 1998).

Methods

Study Site

Elk Island National Park is a 194 km^2 area situated 37 km east of Edmonton, Alberta (53°37'N, 112°58'W) within the Beaver Hills-Cooking Lake Moraine. The Park is elevated up to 60 m above the surrounding plains (710 to 760 m ASL), and is composed of knob and kettle topography, with slopes up to 20%. Upland soils are mostly well-drained Orthic Gray Luvisols under forest (Crown 1977), while Dark Gray Luvisols occupy open areas. Soil textures vary from loam to loamy sand.

Located in the cool continental climatic region, the Park receives about 450 mm of precipitation annually, with 75% falling as summer rain (Environment Canada 1993). Temperatures vary from –40° C in winter to 32° C in summer.

Uplands are dominated by aspen (*Populus tremuloides* Michx.) forests, which cover approximately 80% of the Park. The understory consists of a variety of herbs and shrubs, of which beaked hazel and marsh reedgrass (*Calamagrostis canadensis* (Michx.) Beauv.) are the most abundant (Bork et al. 1997a). These stands produce up to 1,700 kg ha^{-1} of total new growth in the understory, of which 47 to 68% is browse.

Elk Island is the only fenced national park in Canada and lacks major predators such as wolves. These conditions have resulted in high ungulate populations and intense use of vegetation. In 1999, aerial ungulate surveys estimated there were 3,493 large ungulates within the Park, including 340 moose, 1,870 elk, 1,043 bison, and 210 deer (Parks Canada 1999). Based on the year-long herbivore regime within the Park, these numbers are equivalent to an annual stocking rate of approximately 2 AUMs ha^{-1} (Best 2001).

Prescribed fire and herbivory are 2 of the main factors affecting vegetation within the Park (Parks Canada 1999, Bork et al. 1997a). Specifically, intense year-long herbivory over the past 80 years has reduced the abundance of preferred browse species such as aspen, chokecherry (*Prunus virginiana* L.), saskatoon (*Amelanchier alnifolia* Nutt.), as well as red-osier dogwood (*Cornus stolonifera* Michx.), and reduced the remaining shrubs to a hedged growth form (Parks Canada 1999, Bork et al. 1997a, 1997b). Aspen regeneration has also declined (Bork et al. 1997b). Although beaked hazel provides up to 75% of all browsed twigs, this species is the most abundant understory shrub (34% of all stems) and has been reported to be increasing in proportion to other understory species (Blyth et al. 1994). Specific utilization data for beaked hazel within the Park between 1991 and 1994 indicated annual winter twig use ranged from 40 to 55% (Blyth et al. 1994).

Experimental Design

In October 1998, 4 ungulate-proof exclosures, each 20 by 50 m in dimension and 2.2 m high, were constructed throughout the Park. Each exclosure was positioned locally to include a forest community, the understory of which consisted of beaked hazel along with various other shrubs. Plot pairs therefore consisted of an aspen-beaked hazel community divided by the exclosure fence, initially resulting in 2 areas of similar plant species composition and structure, as well as site characteristics (Table 1). Communities outside the exclosure were exposed to year-long, native ungulate herbivory, while enclosed communities were protected from browsing. Given that most browsing occurs during winter when alternative herbage is largely unavailable (Danell et al. 1994) and no evidence of summer browsing was apparent on the new growth of protected beaked hazel stems at the time of exclosure establishment (i.e. October), plants sampled the following summer were considered rested for 1 growing season.

Vegetation Sampling

Within each plant community inside and outside each exclosure, shrubs were sampled along a 15 m transect. At each of 20 sample points, 2 beaked hazel stems were systematically selected and tagged 0.75 m apart (n = 40 shrubs per community).

Table 1. Summary site descriptions for protected and unprotected forest communities at each of the 4 locations investigated.

Exclosure/ Site	Treatment	Slope	Aspect	1999 Rainfall	2000 Rainfall	Soil Texture[1]	Tree Density	Tree Cover
		(%)		(mm)	(mm)		(stem.ha^{-1})	(%)
Boreal	Protected	16	NE	141	178	L to SL	1,400	76
	Browsed	19	N	141	178	SL	1,350	82
Astotin	Protected	13	SW	330	264	L	275	7
	Browsed	13	W	330	264	L	100	11
Shirley	Protected	27	NW	172	175	C	925	55
	Browsed	20	NW	172	175	CL	500	30
Tawayik	Protected	0	n/a	193	227	L	1,975	66
	Browsed	0	n/a	193	227	L to SL	1,950	82

[1] L = loam, SL = sandy loam, C = clay, CL = clay loam.

Individual stems were defined as those free-standing at the soil surface. During August of 1999, one shrub stem at every point was sampled, with 20 shrubs harvested inside and 20 outside at each of the 4 exclosures (n = 160). The remaining 20 shrubs were sampled in each community during August 2000. Sampling in the first year was assumed to have a negligible effect on neighboring shrubs sampled in the second year, particularly given that sampling removed current annual growth only and affected a maximum of 0.3% of shrubs at any one location.

Parameters measured on each stem included the number of current annual growth (CAG) twigs per shrub and their total length, together with twig and leaf biomass. All new growth was clipped, sorted to twigs and leaves, dried at 50°C for 48 hours, and weighed. The samples were later pooled to the plant community level (i.e. the 20 shrubs) and analysed for crude protein (CP) and acid detergent fibre (ADF). Crude protein analysis was done using a Nitrogen Determinator (LECO Corporation, St. Joseph, Mich., USA) while ADF was measured using the filter bag technique (ANKOM Company 1993).

Community Attributes

In the second year, 2 additional 15 m transects were located in each of the 8 plant communities to measure overstory tree canopy cover and density, total shrub density and maximum shrub height, as well as beaked hazel cover, density, and current annual growth (CAG) per unit area at peak growth during August of 2000. Tree canopy cover was estimated using the line intercept method (Bonham 1989), while tree density was determined in a 20 by 20 m area overlying the transects. Beaked hazel cover (Daubenmire 1959) and density, along with total shrub density and maximum shrub height, were sampled at 2 m intervals along both transects within 1 m^2 quadrats (n = 16). Beaked hazel total leaf and twig CAG (per unit area) within the plant community was measured within 2, 0.25 m^2 quadrats harvested at systematic locations along each transect. All samples were oven-dried and weighed, with data from the 4 individual quadrats averaged to provide a value for the plant community.

Within each plant community, data were also collected on slope gradient, aspect, and soils, as well as growing season precipitation (May to August) within each year of the study (Table 1). Although winter precipitation is important for determining moisture recharge in boreal systems (Bork et al. 2001) and for regulating browsing intensity by herbivores during winter, local snow depth data for the exclosures were not available for the study period. Data from a central weather station within the Park, however, indicated winter (i.e. September through April) snowfall accumulations during 1998–99 and 1999–2000 were 111 and 105 cm, respectively, very similar to the 20-year mean for the area (107 cm) (Environment Canada, unpublished data). Four soil cores (0-15 cm) were randomly collected at each plant community in October 2000, bulked, and analysed for soil texture using the hydrometer method described by McKeague (1978).

Data Analysis

All shrub data were checked for normality and homogeneity of variances using Shapiro-Wilkes and Levenes statistics, respectively (SAS Institute Inc. 1991). Beaked hazel CAG at the plant community level was transformed using a log transformation, as were individual beaked hazel stem CAG twig counts, total twig length, and leaf and twig CAG.

In this investigation, plant communities were considered the primary experimental unit at each exclosure with sites treated as blocks because individual shrubs represented sub-samples, and thus, pseudoreplication (Hurlburt 1984). As a result, the interaction of site by herbivory was used as the primary error term for all main effects. Where significant interactions between herbivory and site were found on individual beaked hazel stem parameters, variation among sub-samples (i.e. individual stems) was used as the error term in a final step to more fully assess the nature of the interaction. Additionally, year was incorporated into the model as a split-plot to test for temporal differences in beaked hazel shrub recovery during the first and second years following protection from herbivory.

Total shrub density and maximum shrub height for each community were analysed using ANOVA procedures for a randomized complete block design (Steel et al. 1997), with the interaction of site and protection from herbivory as the error term. Beaked hazel cover, density, and production per unit area were analyzed using ANCOVA, where non-hazel shrub density was used as a covariate. In no case was the covariate significant ($P > 0.10$).

Individual beaked hazel stem current annual growth (CAG) parameters were analyzed similarly using ANOVA (leaf and twig CAG, as well as browse quality). Significant interaction effects were assessed in more detail using the variation provided by sub-sampled shrubs within each plant community. ANCOVA was used to assess morphological changes in shrub growth in order to account for uneven twig numbers and/or length among shrubs and isolate treatment effects. Twig numbers per shrub were adjusted for twig length, and vice versa in the ANCOVA, with significant covariate effects found in all cases ($P < 0.0001$). Incorporation of the covariate, however, did not alter the significance of any treatment effects. Post-hoc mean comparisons were conducted on all significant variables ($P < 0.05$) using Tukey's test, emphasizing those between protected and browsed areas.

Results and Discussion

Beaked Hazel Population Responses

The cover of beaked hazel varied among the exclosure sites ($P < 0.05$), but was similar between browsed and protected treatments in 2000 (Table 2). Among the 4 sites, Astotin had the greatest beaked hazel population, followed by the Shirley and Boreal sites, with Tawayik having relatively less. Although the greater abundance of beaked hazel at Astotin may be the result of increased summer rainfall during the 2 years of this study, a relatively open tree canopy may also account for this trend (Table 1). Open canopies are conducive to maintaining high beaked hazel densities (Kurmis and Sucoff 1989, Buckman 1964).

At least 1 other site (Tawayik) had a similar precipitation level (Table 1), but markedly less beaked hazel (Table 2). Unlike Astotin, the Tawayik site had a well-developed, relatively closed forest canopy (Table 1), indicating that light rather than moisture may regulate beaked hazel densities within the communities investigated. Regardless of the cause, the variation in density of beaked hazel among the 4 locations is important ecologically as it may influence other plants through inter-specific competition (Lauer and Glover 1999), as well as its own population through strong intra-specific competition, particularly at Astotin (Table 2).

The lone significant ($P < 0.01$) difference between browsed and protected treatments observed at the population level was an increase of 40% in the average maximum shrub height within the exclosures following the removal of herbivory (Table 2). The increase in shrub height might be expected as previous studies

Table 2. Effects of site (i.e. exclosure location) and protection from herbivory on mean beaked hazel population and plant community characteristics in 2000.

Factor	df	Beaked Hazel Cover[1]	Beaked Hazel Density[1]	Beaked Hazel CAG[1,2]	Maximum Shrub Height	Total Shrub Density
		(%)	(stems.m^{-2})	(kg.ha^{-1})	(cm)	(stems m^{-2})
Covariate	1	$P = 0.34$	$P = 0.65$	$P = 0.92$		
Site	3	**$P < 0.05$**	$P = 0.18$	$P = 0.26$	**$P < 0.05$**	$P = 0.07$
Astotin		80.4 a^{3}	31.0	1776	166.9a	40.8
Boreal		31.7 ab	8.0	442	111.7b	20.2
Shirley		38.8 ab	14.4	636	128.4 ab	23.0
Tawayik		3.8b	1.2	260	109.3b	12.7
Herbivory	1	$P = 0.26$	$P = 0.53$	$P = 0.69$	**$P < 0.01$**	$P = 0.67$
Browsed		41.2	12.3	822	108 a	23.1
Protected		36.2	15.0	735	150 b	25.2
SE		4.6	4.3	12	4.1	3.2
Site x Herbiv.[4]	2					

[1] Data analyzed using ANCOVA with non-hazel shrub density as a covariate.

[2] Current annual growth data transformed (log) prior to analysis. Original means presented for clarity.

[3] Within a factor, column means with different letters differ significantly ($P < 0.05$).

[4] Error term for Site and Herbivory.

have implicated herbivory within the Park as a cause of reduced structure in the understory (Bork et al. 1997b).

Individual Beaked Hazel Stem Growth

Initial analysis indicated there were significant ($P < 0.001$) site by herbivory interaction effects for all beaked hazel parameters assessed (Table 3). As a result, individual sites were further analysed separately using the variation among subsampled stems. This process was undertaken to provide a more detailed understanding of beaked hazel shrub responses to the presence or removal of herbivory. We also recognize, however, that although the paired (browsed and protected) plant communities were initially established on similar ecosites, the lack of complete independence among individual shrub stems within each community constitute pseudoreplication, and thus, inferences within each site must be tempered accordingly.

Examination of the individual beaked hazel growth responses among sites indicated that shrubs protected from browsing at both Boreal and Tawayik increased ($p < 0.05$) their leaf and twig growth relative to those outside the exclosure, ranging from 85 to 114% (Table 4). At Tawayik, this increase could be attributed, at least in part, to a significant increase ($P < 0.05$) in the length of new twig growth rather than the number of new twigs produced (Table 4).

Although year significantly ($P < 0.001$) affected both leaf current annual growth (CAG) and the number of twigs produced per shrub stem (Table 3), few interactions were evident between year and herbivory. Shrub growth was generally greater in 2000 than 1999, as leaf CAG increased from 4.92 g.stem^{-1} in 1999 to 5.69 g.stem^{-1} in 2000. Similarly, the mean number of twigs increased from 7.0 twigs.stem^{-1} to 9.3 over this same period. The increase over the 2 years may be due to more favorable growing conditions for beaked hazel, as well as the increases in beaked hazel growth described earlier within protected exclosures.

Table 3. Significance values of the effects of site (i.e. exclosure location), protection from herbivory, and their interaction, on individual hazel shrub stem CAG characteristics in 1999 and 2000.

Factor	df	Leaf CAG[1]	Twig CAG[1]	Total Twig Length per Shrub[1,2]	Number of Twigs per Shrub[1,2]
Covariate[3]	1			**$P < 0.0001$**	**$P < 0.0001$**
Site	3	$P = 0.51$	$P = 0.21$	$P = 0.20$	$P = 0.58$
Herbivory	1	$P = 0.28$	$P = 0.44$	$P = 0.95$	$P = 0.39$
Site x Herbivory[3]	3	**$P < 0.001$**	**$P < 0.0001$**	**$P < 0.0001$**	**$P < 0.001$**
Error 1	152				
Year	1	**$P < 0.001$**	$P = 0.17$	$P = 0.20$	**$P < 0.0001$**
Site x Year	3	$P = 0.10$	$P = 0.18$	$P = 0.20$	$P = 0.86$
Herbivory x Year	1	$P = 0.65$	$P = 0.31$	$P = 0.66$	$P = 0.57$
Site x Herbivory x Year[4]	3	$P = 0.16$	**$P < 0.05$**	$P = 0.31$	$P = 0.92$
Error 2	152				

[1] Data transformed prior to analysis using a log transformation.

[2] Data analyzed using ANCOVA, with twig numbers per shrub adjusted for twig length, and twig length adjusted for twig numbers.

[3] Error term for Site and Herbivory effects.

[4] Error term for Year and its interactions.

Twig CAG was also affected by a significant ($P < 0.05$) interaction between site, herbivory, and year (Table 3). Further examination of these results indicated this interaction was caused by variation in the year during which differences in twig growth were evident among sites. For example, at the Boreal exclosure the increase in twig growth within protected beaked hazel shrubs was evident in 1999, immediately following protection from herbivory. In contrast, newly protected shrubs at Tawayik did not generate an increase in twig growth until the second year. The delayed increase in CAG within protected beaked hazel shrubs at the latter site may be indicative of a more intense browsing history prior to exclosure establishment, which would have weakened shrubs by reducing photosynthetic capacity, plant carbohydrates and plant vigour (Briske and Richards 1995).

Beaked hazel shrubs at the Shirley site demonstrated no changes in leaf or twig current annual growth (CAG), but displayed evidence of changes in the morphology of new growth. In particular, protected beaked hazel shrubs produced a significantly ($P < 0.05$) greater number of new twigs, but which were shorter ($P < 0.05$) in aggregate length (Table 4). Although these changes did not coincide with significant differences in leaf or twig CAG (Table 4), they may signal future changes in growth as the recovery of protected beaked hazel shrubs progresses at this location.

Protected beaked hazel shrubs at several sites displayed either a non-significant or even weak trend towards reduced growth during the first year of recovery from browsing, before increasing more markedly during the second year (data not shown). We speculate that annual herbivory may stimulate individual beaked hazel growth by forcing stems to regenerate sufficient photosynthetic area to survive. Increases in the root:shoot ratio of plants immediately following defoliation is thought to account for positive responses in the above-ground growth of browsed shrubs (Bryant et al. 1991). With protection during the fall of 1998, beaked hazel shrubs may have reduced their above-ground growth the fol-

Table 4. Mean leaf and twig CAG, as well as total length and number of twigs, within individual beaked hazel shrub stems of plant communities protected and exposed to browsing at each of 4 sites in Elk Island National Park.

Site	Herbivory	Leaf CAG	Twig CAG	Total Twig Length	Twig Number
		(g DM stem^{-1})	(g DM stem^{-1})	(cm stem^{-1})	(no stem^{-1})
Astotin					
	Browsed	7.47 a[1]	2.43 a	110 a	5.5 a
	Protected	6.50 a	2.15 a	94 a	6.5 a
	SE	1.21	0.34	16	1.7
Boreal					
	Browsed	3.56 a	1.23 a	73 a	7.7 a
	Protected	7.46 b	2.27 b	72 a	10.2 a
	SE	1.16	0.32	15	2.1
Shirley					
	Browsed	3.59 a	1.10 a	64 a	8.6 a
	Protected	3.43 a	0.78 a	47 b	10.8 b
	SE	0.47	0.17	6	1.0
Tawayik					
	Browsed	3.60 a	0.81 a	62 a	9.0 a
	Protected	6.82 b	1.73 b	86 b	6.8 a
	SE	0.72	0.21	9	0.9
All Sites					
	Browsed	4.56	1.39	77	7.7
	Protected	6.06	1.73	75	8.6

[1] Within a parameter and column, means with different letters differ significantly at $P < 0.05$ using sub-samples as the experimental error term.

lowing summer because new growth produced the previous growing season remained intact. In turn, this would allow more photosynthates to be allocated to other important biological processes for plant recovery, including root development. As much as 39% of beaked hazel biomass is below-ground (Tappeiner and John 1973) and plays a key role in determining hazel survival.

The variable response between protected and browsed beaked hazel stems among the 4 sites may be attributable to several factors, including variability in precipitation, overstory cover, historical browsing pressure, or intra-specific competition. For example, high summer rainfall and an open tree canopy at Astotin (Table 1) may allow beaked hazel shrubs to more easily tolerate defoliation, leading to the absence of differences between protected and browsed shrubs at this site (Table 4). In addition, although shrubs at Astotin were clearly browsed (as evidenced by a well-defined hedge-line), they were considerably taller than shrubs at other sites (Table 2), which may allow them to restore leaf area more readily. Moreover, the unusually high density of beaked hazel at this site (Table 2) may maximize intra-specific competition. Beaked hazel plants compete very effectively with other shrub species by reducing light at the forest floor (Tappeiner 1979, Tappeiner and John 1973). The results observed here suggest beaked hazel stems may also compete with each other for resources and limit growth at high stand densities, thereby negating any potential growth response following the removal of browsing. Under these circumstances, removal of browsing may lead to stagnation and reduced growth of beaked hazel shrubs within the Astotin exclosure. There was also weak evidence of reductions in leaf and twig CAG within protected shrubs at this site (Table 4), which may continue to increase as shrub competition intensifies in the absence of browsing.

Beaked Hazel Browse Quality

Overall, there were few significant impacts of removing herbivory on the quality of beaked hazel growth in 2000. The lone significant effect ($P < 0.01$) was an interaction between exclosure site and protection from herbivory on leaf crude protein (CP), arising from a reduction ($P < 0.05$) in leaf CP at the Boreal and Shirley sites from 14.2 to 12.8%, and 11.2 to 9.8%, respectively, when protected from browsing. The decrease in leaf CP of protected beaked hazel shrubs within the Boreal exclosure coincided with an increase in leaf CAG (Table 4), thereby exemplifying the typical inverse relationship between forage quantity and quality (e.g.,Van der Wal et al. 2000).

Management Implications and Conclusion

At the scale of individual beaked hazel stems, responses to the removal of herbivory were evident at 3 of 4 sites over the 2-year sampling period within shrubs protected from browsing. These results indicate current levels of herbivory within Elk Island National Park tend to be impacting some stands of beaked hazel by either reducing twig and leaf current annual growth, or altering their morphology. The documented changes in individual beaked hazel shrub growth after protection indicates that although this shrub is relatively tolerant of defoliation, particularly in comparison with more palatable species (Bork et al.1997b), current levels of herbivory continue to affect, and in some cases reduce, beaked hazel growth. In contrast, other than an increase in maximum shrub height, no plant community or beaked hazel population characteristic changed following protection. It is also notable that despite the positive responses observed at the individual shrub level, these changes failed to translate into greater browse production at the population level (data not shown). Thus, factors other than shrub competition may be preventing individual stem responses from translating into increased browse production, at least within the 2-year period examined here. Further vegetation changes are also likely following the removal of herbivores and their associated action on ecosystem processes, as several studies indicate browsing affects soil chemistry and nutrient cycling (e.g., Kielland and Bryant 1998, Ruess et al. 1998).

In summary, the results of this research support the notion that the overall effect of intensive ungulate browsing in Elk Island is to reduce individual beaked hazel stem growth and production. The variable nature of the responses among sites indicates factors such as precipitation, microclimate, plant species composition and resulting competition, overstory characteristics, and previous disturbance may also regulate beaked hazel growth. Our results for beaked hazel also parallel the findings of Wambolt et al. (1998) for bitterbrush (*Purshia tridentata* Pursh) on the importance of scale (e.g., shrub stem vs population) in quantifying and interpreting the impact of defoliation, as several individual beaked hazel stem responses were observed in this study despite minimal changes within the plant community. In conclusion, year-long browsing by native ungulates has reduced the number and aggregate twig length, as well as leaf and twig biomass, of beaked hazel current annual growth at several sites throughout the Park. However, these changes also appear reversible with the cessation of browsing.

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Research observation: Hydrolyzable and condensed tannins in plants of northwest Spain forests

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Abstract

Tannins are secondary metabolites that may influence feeding by mammals on plants. We analyzed hydrolyzable and condensed tannins in 30 plant species consumed by livestock and deer, as a preliminary attempt to study their possible implications on browsing and grazing in forest ecosystems. Heathers (*Ericaceae*) and plants of the Rose (*Rosaceae*) family had tannins, while forbs, grasses and shrubs other than the heathers did not show astringency properties. We found the highest tannin content of all the species in *Rubus* sp., with the highest value around 180 mg TAE/g dry weight in spring. *Potentilla erecta, Alnus glutinosa* and *Quercus robur* were next with 57 to 44 mg TAE/g dw. Total tannins in heathers ranged from 22 to 36 mg TAE/g dw. Levels of condensed tannins were higher than hydrolyzable for most of the species. Only *Betula alba, Calluna vulgaris, Pteridium aquilinum* and *Vaccinium myrtillus* had 100% hydrolyzable tannins. Tannin content of the species changed seasonally with highest values during the growing season, corresponding to late winter or early spring, depending on the species.

Key Words: astringency, nutritional quality, Galicia

Resumen

Los taninos son metabolitos secundarios que pueden influir en la utilización de las plantas como alimento por los mamíferos. Analizamos los taninos condensados e hidrolizables de 30 especies de plantas consumidas por el ganado doméstico y el corzo, como un intento preliminar para estudiar sus posibles implicaciones en el ramoneo y pastoreo en ecosistemas forestales. Las rosáceas (*Rosaceae*) y los brezos (*Ericaceae*) tuvieron taninos, mientras que otros arbustos y las herbáceas no mostraron propiedades de astringencia. En *Rubus* sp., encontramos el más alto contenido de taninos de todas las especies, con el mayor valor en primavera (180 mg TAE/g de peso seco). *Potentilla erecta, Alnus glutinosa* y *Quercus robur* fueron los siguientes con más alto contenido de taninos, entre 57 y 44 mg TAE/g de peso seco. Los taninos totales en los brezos variaron de 26 a 36 mg TAE/g de peso seco. En la mayoría de las especies los niveles de taninos condensados fueron mayores que los de taninos hidrolizables. Sólo *Betula alba, Calluna vulgaris, Pteridium aquilinum y Vaccinium myrtillus* tuvieron el 100% de taninos hidrolizables. El contenido de taninos en las plantas cambió estacionalmente, presentándose los mayores valores durante la estación de crecimiento, correspondiendo a final del invierno o principio de la primavera, dependiendo de las especies.

Tannins are polyphenolic compounds that have become widely recognized as important factors influencing feeding by mammals on woody plants (Robbins et al. 1987, Happe et al. 1990, Bryant et al. 1992, Hagerman et al. 1992, McArthur et al. 1993, Haslam 1998). They are secondary metabolites that may inhibit digestion of protein and fiber or their characteristically astringent taste may cause flavor aversion and adversely affect feed intake (Provenza et al. 1990, Bryant et al. 1992, Hagerman et al. 1992).

Most studies of tannins have focussed on nontoxic effects on availability of protein. Condensed and hydrolizable tannins combine with protein to form tannin-protein complexes during mastication and digestion of forage (Hagerman et al. 1992). Formation of these stable complexes may reduce the amount of digestible protein available for herbivores and digestibility of forage may also be reduced if rumen microflora are negatively influenced by tannins.

In Galicia, the biomass of combustible plant material becomes very abundant. The use of vegetation by livestock and deer can be a useful tool to reduce forest fires, and silvopastoral systems have been reported as an alternative of socioeconomic and environment interest within the multiple use of forest (Silva-Pando and González-Hernández 1992, Silva-Pando et al. 1998, Rigueiro et al. 1999). The nutritional attributes of plants commonly found in Galician forests have been reported in previous research (González-Hernández and Silva-Pando 1999), but there is a lack of information about their content of antifeedant compounds like tannins.

The aim of this study was to analyze both the hydrolyzable and condensed tannin content of plants found in deer and livestock diets as a preliminary attempt to discuss their possible implications on browsing and grazing within forest ecosystems. We measured their astringency (capacity of tannins to form insoluble tannin-protein complexes) to determine their potential for reducing digestibility.

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Study Area

The study area is located in Galicia (northwest Spain, 43ºN, 8ºW) and included forest vegetation communities of this region such as deciduous oakwoods, conifer stands, and shrublands (broom, gorse, and heathlands). Oak forests constitute climax stage vegetation but are fragmented in most of the cases because of agriculture and other human uses in the past. Conifer, together with eucalyptus stands, come from reforestation, and their understory consists of seral succesional stages of plant communities between shrublands (broom-gorse-heatherlands) and the climax oak forests.

Climate is Atlantic with mild, wet winters at the coast, and colder inland. Continentality increases from the coast to inland areas where summers are dryer. Maximum temperatures increase and minimum decrease from northwest to southeast with annual mean temperatures varying from 7.3 to 14.2º C, and annual precipitation from 1,419 to 2,037 mm. Elevation ranged from 60 to 1,280 m. Soils in Galicia are mainly acid and the rock is granite, slate, or schists.

Table 1. Species analized and type of vegetation where they predominantly occur.

Life form	Species	Vegetation type
Trees		
	Alnus glutinosa(L.) Gaertner	(riparian areas)
	Betula alba L.	(riparian areas)
	Fagus sylvatica L.	(oakwood)
	Ilex aquifolium L.	(oakwood)
	Quercus robur L.	(oakwood)
	Salix atrocinerea Brot.	(riparian areas)
Shrubs		
	Calluna vulgaris (L.) Hull	(conifer, eucalyptus, shrubland)
	Cytisus multiflorus (L'Hér.) Sweet	(shrubland, oakwood)
	Cytisus striatus (Hill) Rothm.	(shrubland, oakwood)
	Daboecia cantabrica (Hudson) C. Koch	(conifer, heatherland, eucalyptus)
	Erica arborea L.	(oakwood , shrubland)
	Erica australis L.	(shrubland)
	Erica vagans L.	(shrubland)
	Erica umbellata L.	(conifer, eucalyptus, shrubland)
	Frangula alnus Miller	(oakwood)
	Genista florida L.	(oakwood, shrubland)
	Halimium lasianthum (Lam.) Spach	(conifer, shrubland)
	Hedera helix L.	(oakwood)
	Lonicera periclymenum L.	(oakwood)
	Pterospartum tridentatum (L.) Willk.	(conifer, eucalyptus, shrubland)
	Rubus sp.	(oakwood , conifer, shrubland)
	Ulex europaeus L.	(conifer, shrubland)
	Vaccinium myrtillus L.	(oakwood)
Ferns		
	Pteridium aquilinum (L.) Kuhn	(conifer, oakwood)
Forbs		
	Asphodelus albus Miller	(conifer, eucalyptus)
	Potentilla erecta (L.) Raüschel	(conifer, eucalyptus, shrublands)
Grasses		
	Agrostis curtisii Kerguélen	(conifer, oakwood)
	Pseudarrhenatherum longifolium (Thore) Rouy	(conifer, oakwood)

Material and Methods

Plants known as components of livestock and deer diets were considered for analysis of tannin content (Table 1). For each species, plant material with similar age and within homogenous site condition was clipped and combined into a single sample for analysis. Hand harvested plant parts were representative of plant parts that deer or livestock would select, corresponding to apical portions of shrubs no longer than 15 cm and less than 1 cm in twig diameter, and leaves from trees taken within browsing heights. Plants were harvested during their growing season, which for most of them occurred in spring. Perennials were harvested seasonally within the same year to study their tannin variation through the seasons. Plants of species analized seasonally were not sampled more than once.

Fresh plant material was transported immediately to the laboratory where it was lyophilized and stored frozen until analysis. Before analysis the samples were ground through a Wiley mill with 1 mm mesh screen.

Tannins were extracted with 70% acetone at room temperature. One gram of ground plant material was stirred with 10 ml of acetone for 15 minutes. The mixture was then centrifuged for 5 minutes in a clinical centrifuge (5000 g). The supernatant was saved and the sample extracted for 15 minutes again with fresh solvent. The process was repeated a total of 4 times. Acetone was evaporated from the supernatant with a rotary evaporator in a 30º C water bath. The remaining aqueous solution was rinsed twice with an equal quantity of ethyl ether to remove low molecular weight tannins (Broadhurst and Jones 1978). Remaining ethyl ether was evaporated with a rotary evaporator and distilled water was added to result in a total volume of 25 ml. Extracts were placed in sealed polypropylene test tubes and stored in a freezer at –10º C.

An index of protein precipitating capacity is commonly determined by the capacity of known amounts of plant extracts or tannins to precipitate bovine serum albumin (BSA). In this paper, astringency, or the capacity of tannins to precipitate proteins, was determined using the radial diffusion technique of Hagerman (1987), based on bovine serum albumin precipitation on agar plates. Selective determination of hydrolyzable and condensed tannins was made using the modified radial diffusion technique (Hagerman 1995) founded on the susceptibility of hydrolyzable tannins to degradation by hydroxylamine. With this method, samples containing only hydrolyzable tannins do not precipitate when radial diffusion is performed after addition of hydroxylamine since the tannin is decomposed. The estimation of condensed and hydrolyzable tannins was based on the difference between the area of the ring obtained before and after the reaction with hydroxylamine. Condensed tannins do not react to hydroxylamine and therefore the radial diffusion measurement is the same before and after hydroxylaminolysis. We used tannic acid as standard. All samples were analyzed in duplicate.

Results and Discussion

Tannins were present in many of the plants analyzed (Table 2), such as heathers (*Ericaceae*) and plants of the *Rosaceae* family. We found the highest tannin content in *Rubus* sp., *Potentilla erecta, Alnus glutinosa* and *Quercus robur*. Condensed tannins were predominant in most of these species. Concentrations of 75–100 g of condensed tannins/kg dry matter have depressed voluntary feed intake and rumen carbohydrate digestion as well as rates of body and wool growth in grazing sheep, while values of 30–40 g of condensed tannins/kg provided nutritional benefits (Barry and McNabb 1999). Based on these values, *Rubus* sp. could limit feed intake for some herbivores. In Galicia, only young sprouts of *Rubus* sp. are ocasionally browsed by horses and goats, and they have not been found to be part of cattle diets (Rigueiro et al. 1998). However, this species is very palatable for roe deer, mainly during fall and winter (Jackson 1980, Hosey 1981, Maizeret and Tran Manh Sung 1984, Costa Pérez 1992, Putnam 1996); these seasons correspond to the lowest levels of tannins we found in our study.

As opposed to the highest proportion of condensed tannins we found in *Rubus* sp., Starkey et al. (1999) have shown *Rubus spectabilis* in the Pacific Northwest have higher concentrations of hydrolyzable tannins than condensed. In our study, some plants such as *Betula alba, Calluna vulgaris, Vaccinium myrtillus* and *Pteridium aquilinum,* contained 100% hydrolyzable tannins.

There are apparently conflicting claims of beneficial and toxic effects caused by hydrolyzable tannins in various animal species (Jean-Blain 1998, Aerts et al. 1999, Clifford and Scalbert 2000) and the biological significance of different types of tannins, including their role in nutritional ecology. Some studies have reported the preference of deer for medium level hydrolyzable tannin pellets (3.8%) instead of control pellets without tannins, and have showed that daily consumption of pellets containing high level of tannins (9.1%) was lower than consumption of the control (Verheyden-Tixier and Duncan 2000). Studies of roe deer diets have found *Calluna vulgaris* and *Vaccinium myrtillus* appear in higher rates compared to other species of *Erica* in the same study area (Putnam 1996). We found most of plants in the *Ericaceae* family have predominantly condensed tannins except *Calluna vulgaris* and *Vaccinium myrtillus* with 100% hydrolyzable (Table 2).

Tannin content of the species changed seasonally. For those plants with tannins, the seasonal variation is showed in Figure 1. We obtained the highest values during the growing season, corresponding to late winter or early spring, depending on the species. There is a tendency of hydrolyzable tannins to be highest in the winter. *Halimium lasianthum* had 100% condensed tannins in the spring, but hydrolyzable tannins increased to 14% in winter

Table 2. Total, and percentages of hydrolyzable and condensed tannins in plants known as components of livestock and deer diets. Values correspond to spring. Total tannins are expressed in mg tannic acid eq/g dry weight. Percentages of crude protein (CP) are shown for some of the species (González-Hernández 1994). Species with absence of tannins are presented at the bottom of the table (–).

Life form	Species	Common name	Family	Total tannins	Hyd	Cond	CP
Trees				(mg TAE/g)	(%)	(%)	(%)
	Alnus glutinosa	alder	*Betulaceae*	57.11	30.1	69.9	
	Betula alba	galician birch	*Betulaceae*	12.85	100	0	
	Fagus sylvatica	beech	*Fagaceae*	24.36	27.0	73.0	7.8
	Quercus robur	oak	*Fagaceae*	43.87	10.2	89.8	9.0
	Salix atrocinerea	black willow	*Salicaceae*	40.43	28.1	71.9	
Shrubs							
	Halimium lasianthum	cistus	*Cistaceae*	32.70	0	100	7.3
	Erica vagans	heather	*Ericaceae*	22.36	24.9	75.1	
	Calluna vulgaris	heather	*Ericaceae*	25.37	100	0	6.1
	Erica australis	heather	*Ericaceae*	29.51	5.2	94.8	6.6
	Erica umbellata	heather	*Ericaceae*	31.63	24.9	75.1	6.7
	Vaccinium myrtillus	bilberry	*Ericaceae*	14.68	100	0	7.4
	Erica arborea	tree heather	*Ericaceae*	35.96	32.2	67.8	7.8
	Daboecia cantabrica	heather	*Ericaceae*	33.78	10.3	89.7	8.5
	Rubus sp.	bramble	*Rosaceae*	181.60	25.5	74.5	10.4
Forbs							
	Potentilla erecta	tormentila	*Rosaceae*	46.20	2.6	97.4	9.8
Ferns							
	Pteridium aquilinum	bracken fern	*Hypolepidaceae*	4.16	100	0	13.0
Trees							
	Ilex aquifolium	holly	*Aquifoliaceae*	–			8.3
Shrubs							
	Hedera helix	ivy	*Araliaceae*	–			9.3
	Lonicera periclymenum	honeysuckle	*Caprifoliaceae*	–			9.7
	Pterospartum tridentatum	carqueixa	*Fabaceae*	–			7.3
	Ulex gallii	gorse	*Fabaceae*	–			9.3
	Cytisus multiflorus	broom	*Fabaceae*	–			12.3
	Ulex europaeus	gorse	*Fabaceae*	–			8.7
	Cytisus striatus	broom	*Fabaceae*	–			15.3
	Genista florida	broom	*Fabaceae*	–			18.0
	Frangula alnus	black dogwood	*Rhamnaceae*	–			11.7
Forbs							
	Asphodelus albus	white asphodel	*Liliaceae*	–			17.4
Grasses							
	Agrostis curtisii	bent-grass	*Poaceae*	–			9.3
	Pseudarrhenatherum longifolium	grass	*Poaceae*	–			8.6
	Dactylis glomerata	orchardgrass	*Poaceae*	–			17.4

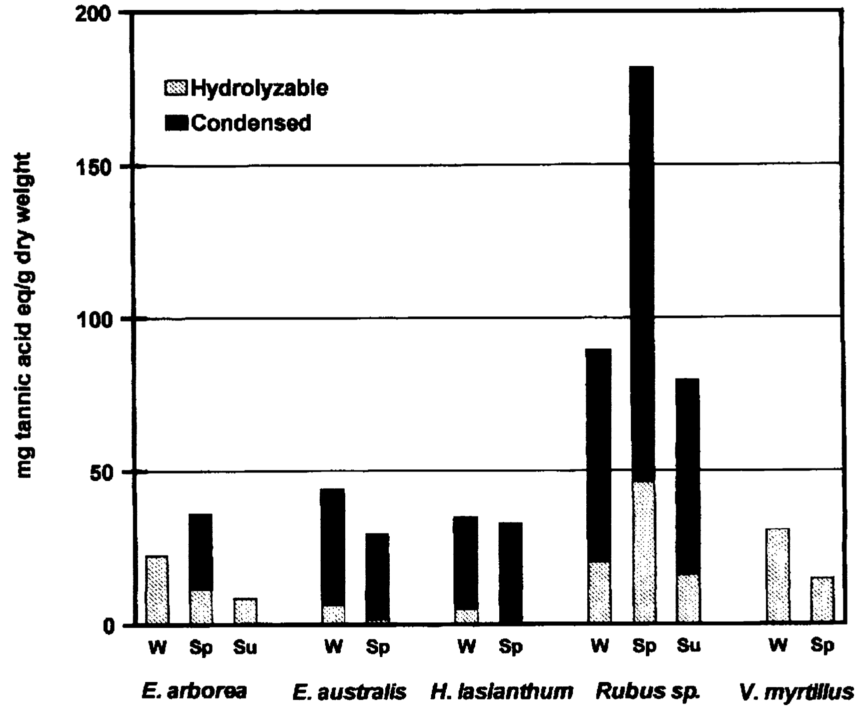

Fig. 1. Winter, spring and summer concentrations of hydrolyzable and condensed tannins (mg tannic acid eq/g dry weight).

(Fig. 1). *Erica arborea* tannin concentrations increased in spring, and the ratio of tannins changed from 67.8% condensed in spring to 100% hydrolyzable during the summer and winter.

We reported in previous studies the low digestibility of plants of Galician woodlands as an important limiting factor in livestock production (González-Hernández and Silva-Pando 1999). Digestible protein can be a significant limiting factor for some deer and elk populations because the tannin content in the plants limit its availability (Starkey et al. 1999). Available protein, rather than total protein content, has been reported as the physiologically important parameter relative to animal requirements and metabolic capabilities (Robbins et al. 1987)

Other plants analyzed in our study such as leguminose shrubs and grasses did not contain tannins (Table 1). Neither did other plants such as holly (*Ilex aquifolium*), ivy (*Hedera helix*), honeysuckle (*Lonicera periclymenum*) and black dogwood (*Frangula alnus*); all of them are considered of high preference in herbivore diets and with good nutritional attributes (Costa 1992, Fandos et al. 1987, Clutton-Brock and Albon 1989, Putnam 1996, González-Hernández and Silva-Pando 1999).

Hervibores may ameliorate the effects of certain tannins in natural forages on protein digestibility through physiological and behavioural adaptations, and some animals are able to deal with them better than others. As plants have developed the enzymatic means to synthesize defensive chemicals, animals have evolved detoxification mechanisms to overcome the plant defenses. Browsing animals are better able than grazers to resist adverse effects of dietary tannins and phenolic compounds, which are common constituents of shrubs and trees. Browsers like deer have salivary tannin-binding proteins that counteract the astringent effects of tannins but these salivary proteins are absent in sheep and cattle (Austin et al. 1989).

Conclusions

In Galician forests, many forage species contain significant levels of astringent tannins with the potential to greatly reduce the availability of protein for livestock and deer. Digestible protein is likely to be a significant limiting factor in forest communities containing predominantely plants of the *Ericaceae* family, especially if grasses or forbs are not available. Understory of conifer and eucalyptus stands, as well as some shrublands, consist mainly of heathers, and could be more limited in the digestible protein available for deer and livestock than oakwoods and other shrublands containing predominantely gorse or broom.

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Observation: Leafy spurge control in western prairie fringed orchid habitat

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Abstract

The western prairie fringed orchid (*Platanthera praeclara* Sheviak and Bowles) is a threatened species of the tallgrass prairie. Invasion by leafy spurge (*Euphorbia esula* L.) is a serious threat to western prairie fringed orchid habitat. The objectives of this study were to develop a herbicide treatment to control leafy spurge while sustaining western prairie fringed orchid populations and to evaluate the soil seedbank composition of leafy spurge-infested sites to guide long-term management strategies. Quinclorac (3,7-dichloro-8-quinolinecarboxylic acid), imazapic {(±)-2-[4,5-dihydro-4-methyl-4-(1-methylethyl)-5-oxo-1*H*-imidazol-2=yl]-5-methyl-3-pyridinecarboxylic acid}, and glyphosate [N-(phosphonomethyl)glycine] plus 2,4-D (2,4-dichlorophenoxy acetic acid) were applied in the fall for 2 consecutive years, and changes in leafy spurge cover, density, yield, and herbaceous yield were assessed. In a separate study, quinclorac, imazapic, and glyphosate plus 2,4-D were each fall-applied to 12 western prairie fringed orchids and assessed for reoccurrence and density of orchids 1-year after treatment. Quinclorac and imazapic, but not glyphosate plus 2,4-D, reduced leafy spurge cover, density, and yield without causing deleterious effects to associated native herbaceous cover and yields. Western prairie fringed orchid reoccurrence and density were unaffected by any herbicide 1 year after treatment. Soil cores were removed in spring and fall following the first year herbicide treatment, washed and placed in trays. Seedlings were allowed to germinate for 16 weeks in the greenhouse. Over 50 plant species were identified in the soil seedbank, of which approximately 60% were early seral species indicative of disturbance. Given the dominance of leafy spurge in the seed bank, a long-term management program to control this noxious species is warranted. Although these results are promising, longer-term studies need be conducted to ensure that repeated herbicide treatments do not harm the western prairie fringed orchid.

Key Words: invasive species, herbicides, range improvement, soil seedbank

Resumen

"Western prairie fringed orchid" (*Platanthera praeclara* Sheviak and Bowles) es una especie amenazada en los pastizales altos. La invasión de "Leafy spurge" (*Euphorbia esula* L.) Es una seria amenaza para el hábitat del "Western prairie fringed orchid". Los objetivos de este estudio fueron desarrollar un tratamiento de herbicida para controlar el "Leafy spurge" mientras se mantienen poblaciones de "Western prairie fringed orchid" y evaluar la composición del banco de semillas del suelo de sitios infestados con "Leafy spurge" para guiar estrategias de manejo a largo plazo. En el otoño de 2 años consecutivos se aplicaron los siguientes herbicidas: Quinclorac (ácido 3,7-dicloro-8-quinolinecarboxilico), Imazapic {(±)-2-[ácido 4,5-dihidro-4-metil-4-(I-metiletil)-5-oxo-I*H*-imidazo1-2=y1]-5-metil-3-piridinecarboxilico} y Glifosato [N-(Fosfonometil)glicine] mas 2,4-D (ácido 2,4- diclorofenoxiacético) y se evaluaron los cambios de cobertura, densidad, rendimiento de "Leafy spurge" y el rendimiento de herbáceas. En un estudio separado el Quinclorac, Imazapic, and Glifosato mas 2,4-D fueron aplicados cada otoño a 12 "Western prairie fringed orchids" y se evaluó la reocurrencia y densidad de las orquídeas 1 año después de aplicar el tratamiento. El Quinclorac e imazapic, pero no el glifosato mas 2,4-D, redujeron la cobertura, densidad y rendimiento del "Leafy spurge" sin causar efectos perjudiciales en la cobertura y rendimiento de las herbáceas nativas asociadas. Después de 1 año de aplicados los tratamientos ninguno de ellos afectó la reocurrencia y densidad de "Western prairie fringed orchid". Muestras de suelo fueron removidas en la primavera y otoño siguientes del primer año de tratamiento de herbicida y fueron lavadas y colocadas en charolas. Se permitió que las plántulas germinaran en el invernadero durante un periodo de 16 semanas. Mas de 50 especies de plantas se identificaron en el banco de semilla del suelo, de las cuales aproximadamente el 60% fueron especies serales indicativas de disturbio. Dada la dominancia de "Leafy spurge" en el banco de semilla, se garantiza un programa de manejo a largo plazo para controlar esta especie nociva. Aunque estos resultados son promisorios, se necesita conducir estudios a largo plazo para asegurar que los tratamientos repetidos de herbicidas no dañan el "Western prairie fringed orchid".

Leafy spurge (*Euphorbia esula* L.) invasion in southeastern North Dakota is a threat to the western prairie fringed orchid (*Platanthera praeclara* Sheviak and Bowles), a federally listed threatened plant species (U.S. Fish and Wildlife Service 1989, Wolken et al. 2001). Leafy spurge is an introduced perennial noxious weed that infests approximately 0.5 million ha in North Dakota (Lym et al. 2000). It is a long-lived plant native to Europe and Asia that spreads prolifically by seed and adventitious buds on roots and crowns (Dunn 1979). Leafy spurge can tolerate a variety of environmental conditions and habitats from rocky

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buttes to sandy shorelines and is difficult to control. Plant communities where leafy spurge dominates often have reduced frequency and density of associated native herbaceous species (Selleck et al. 1962). Leafy spurge has been detected in habitats supporting the western prairie fringed orchid in North Dakota (Sieg and Bjugstad 1994) and Minnesota (Winter 1994), and continued expansion of this invasive species could present a serious threat to the western prairie fringed orchid (U.S. Fish and Wildlife Service 1996).

The original range of the western prairie fringed orchid extended from Manitoba, Canada through North Dakota and Minnesota to Oklahoma and Missouri (Bowles 1983). Western prairie fringed orchid populations, once widespread throughout tallgrass prairies, are now limited to isolated prairie remnants due to habitat loss. One of the largest populations remaining occurs on the Sheyenne National Grassland, a 28,750 ha federally managed tallgrass prairie in southeastern North Dakota. Leafy spurge infests approximately 15 to 20% of the Sheyenne National Grassland. If leafy spurge is allowed to continue to spread into western prairie fringed orchid habitat, it could outcompete the western prairie fringed orchid; yet, non-selective control methods also pose a potential threat to the western prairie fringed orchid (U.S. Fish and Wildlife Service 1996).

Leafy spurge has been controlled with a variety of herbicides (Lym 1998). However, herbicides cannot be used in areas where the western prairie fringed orchid is located due to its status as a threatened species. The biological control agent *Aphthona* spp. flea beetles have become widely established and can greatly reduce leafy spurge infestations, but *Aphthona* spp. generally do not survive well in the sandy, mesic habitat of the western prairie fringed orchid (Lym 1998, Mundal et al. 2002).

Traditionally treatments of picloram (4-amino-3,5,6-trichloro-2-pyridinecarboxylic acid) plus 2,4-D (2,4-dichlorophenoxy acetic acid) either spring or fall applied have been used to control leafy spurge in the region (Lym 1998). However, picloram cannot be used in areas with a high water table, which often includes habitats that support the western prairie fringed orchid. Herbicides that have potential to control leafy spurge without harming the western prairie fringed orchid include imazapic {(±)-2-[4,5-dihydro-4-methyl-4-(1-methylethyl)-5-oxo-1*H*-imidazol-2=yl]-5-methyl-3-pyridinecarboxylic acid} and quinclorac (3,7-dichloro-8-quinolinecarboxylic acid), which provide good to excellent leafy spurge control with little or no injury to other desirable broadleaf and grass species (Kuehl and Lym 1997, Markle and Lym 2001). Also, glyphosate [N-(phosphonomethyl)glycine] plus 2,4-D can be used for leafy spurge control in areas with a high water table such as the Sheyenne National Grassland, and has no soil residual (Lym 1998).

A herbicide demonstration trial on the Sheyenne National Grassland in the early 1990's indicated that herbicides could be used to control leafy spurge and allow the western prairie fringed orchid to reestablish; however, after 2 years the trial had to be discontinued because the threatened western prairie fringed orchid appeared in some plots treated with fall-applied herbicides. Therefore, the present study was initiated with the objectives of 1) evaluate 3 fall-applied herbicides for leafy spurge control, 2) assess the impact of these herbicides on reappearance and density of the western prairie fringed orchid and production of other species, and 3) quantify the soil seedbank composition to determine what plant species are present to revegetate the site following control of leafy spurge.

Materials and Methods

Study Area

The study was conducted on the Sheyenne National Grassland (46° 28' N latitude, 97° 16' W longitude) approximately 80 km southwest of Fargo, N.D. The Sheyenne National Grassland is part of a geologic unit known as the Sheyenne River Delta formed approximately 10,000 to 12,000 years ago. The Sheyenne National Grassland consists of stabilized sandy dune-like topography with well drained hummocks (uplands) and subirrigated swales (lowlands). The soils of the study were Serden (Mixed, frigid typic Udipsamments) and Maddock-Hecla (Sandy, mixed, frigid Entic Hapludolls-Sandy, mixed, frigid Oxyaquic Hapludolls) loamy fine sands, which are well drained and susceptible to wind erosion.

Average annual precipitation for the area is 48 cm with approximately 70% received during the growing season May–September. Precipitation received during this study (1997 and 1998) was 60 and 78 cm, respectively, which was above the long-term average.

The vegetation of the Sheyenne National Grassland is complex consisting of at least 12 distinct plant communities (Seiler and Barker 1985). The major plant communities present on the study site were sedge meadow, tallgrass prairie and mixed grass prairie. The sedge meadow was dominated by various sedges (*Carex* spp.), bluegrasses (*Poa* spp.), reed grasses (*Calamogrostis* spp.), switchgrass (*Panicum virgatum* L.), and willows (*Salix* spp.), which invaded the site. The tallgrass prairie was dominated by big bluestem (*Andropogon gerardii* Vitman), little bluestem (*Schizachyrium scoparium* Michx.), switchgrass, and Kentucky bluegrass (*Poa pratensis* L.). The mixed grass prairie was dominated by needlegrass (*Stipa* spp.), blue grama [*Bouteloua gracilis* (H.B.K.) Lag ex. Griffiths], Kentucky bluegrass, and the introduced leafy spurge.

Leafy Spurge Herbicide Trial

Fall-applied herbicides that generally control leafy spurge and can be used in the mesic habitat that supports the western prairie fringed orchid were evaluated. Treatments included glyphosate plus 2,4-D at 220 plus 330 and 440 plus 670 g ae ha^{-1}, imazapic at 70 and 140 g ae ha^{-1} plus methylated seed oil[1] at 2.3 liters ha^{-1} plus urea-ammonium nitrate fertilizer (28% N) at 2.3 liters ha^{-1}, and quinclorac at 880 and 1100 g ae ha^{-1} plus methylated seed oil[2] at 2.3 liters ha^{-1}. Herbicides were applied with a hand-held CO$_2$-pressurized sprayer with four, 8001 flat-fan nozzles[3] delivering 80 liters ha^{-1} at 280 kPa. The treatments were applied 2 consecutive years in mid-September in 1997 and 1998, to mature leafy spurge with 3 to 10 cm of fall regrowth on stems and branches. The experimental design was a randomized complete block, replicated 4 times, with 3- by 9.1-m plots.

Vegetation cover and density were estimated using 6, randomly placed 0.1-m^2 quadrats (Daubenmire 1959) in the summer of 1998, 10 months after the first treatment, with the final evaluations made in 1999, 22 months after the first treatment. Percent canopy cover was visually estimated for litter, leafy spurge, forb, grass, shrub, and bare ground. Individual plants were identified and counted by species to determine density in each treatment.

Herbaceous yield was estimated in August 1999 (23 months after the first

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[1] Methylated seed oil was SUN-IT II by AGSCO, 1160 12th St. NE, Grand Forks, N.D. 58201.

[2] Methylated seed oil was SCOIL by AGSCO, 1160 12th St. NE, Grand Forks, N.D. 58201.

[3] TeeJet, Spraying Systems Co., P.O. Box 7900 Wheaton Ill. 60189.

treatment) by clipping five, 0.25-m^2 quadrats and hand separating to leafy spurge, grass, grass-like, native forb, and other categories. Quadrats were randomly located on transects placed centrally through the length of each plot. Yield samples from each plot were placed in individual bags, dried at 45° C for 7 days, and weighed.

Herbicide efficacy was tested using the general factorial analysis of variance (ANOVA) for a randomized complete block design. Herbicide control of leafy spurge was evaluated along with injury to other species (SPSS 1994). Means were separated using the Duncan's Multiple Range Test and considered significant at $P < 0.05$.

Herbicide Effect on Western Prairie Fringed Orchid Reoccurrence

Authorization to treat up to 96 western prairie fringed orchids [permit PRT-704930 (subpermit sp 98-41.99] was obtained from the U.S. Fish and Wildlife Service. Herbicides were the same as described in the first study, except only the highest use rate for each treatment was included. Herbicides were applied as previously described except a 2 nozzle handheld sprayer boom was used since the treated area was a 1-m^2 quadrat centered on each western prairie fringed orchid. Each of the 4 treatments was randomly assigned to 12 flowering (replicates) western prairie fringed orchids for a total of 48 western prairie fringed orchids in the study. The herbicides were applied in mid-September 1998. This timing was optimal for leafy spurge control with these herbicides and allowed the western prairie fringed orchid to complete its life cycle; most of the treated western prairie fringed orchids had disseminated their seeds and were senescent.

Western prairie fringed orchid counts were conducted during peak flowering in July 1999. A 1-m^2 quadrat was centered on each permanently marked western prairie fringed orchid. Western prairie fringed orchids inside the quadrat were counted and recorded. Herbicide treatment effects on western prairie fringed orchids were tested using ANOVA for a completely random experimental design (SPSS 1994). Means were separated using Duncan's Multiple Range Test and considered significant at $P < 0.05$.

Above-average precipitation during the study and plentiful rainfall throughout the 1999 growing season resulted in a high water table. Study western prairie fringed orchids were under water in September 1999 at the time that second-year herbicide treatments were to be applied; consequently the study was terminated.

Soil Seedbank Study

Soil cores for seedbank analysis were taken from the herbicide efficacy plots in May and October 1998. Each plot was subdivided into 2, 1.5- by 9.1-m subsections with 5 soil cores sampled centrally at 1.5-m intervals down the long axis of each subsection. Soil cores were taken to a depth of 2.5 cm using a standard golf-cup cutter (10 cm diameter). Soils were composited by subsection, dried at 35° C for 7 days and placed in a refrigerator at 3° C prior to germination.

Greenhouse germination procedures followed those outlined by Ter Heerdt et al. (1996). The soil cores were washed through coarse (4 mm) and fine (2 mm) sieves to remove roots, pebbles, sand, clay, etc. Each concentrated sample was then spread from 3 to 5 mm thick in 28- by 56-cm trays on a mixture of steam-sterilized soil and commercial potting mix topped by a 4-mm thick layer of sterile silica sand. Trays were watered daily, temperature was maintained between 20 and 28° C, and natural and supplemental light at 450 :μ Em^{-2} second^{-1} resulted in 16 hours of available light. Following germination, seedlings were identified, counted, and removed. Seedlings that could not be identified were transplanted to larger pots for continuation of growth until a positive identification could be made. Trays were evaluated until no seedlings emerged for at least 1 week, resulting in an approximately 16-week germination period.

Scientific names of plants germinated from soil cores follow that of the Flora of the Great Plains (Great Plains Flora Association 1986). Coefficients of conservatism were assigned to plant species based on an assessment provided by the Northern Great Plains Floristic Quality Assessment Panel (2001). Coefficients of Conservatism range from a value of 0 for plant species that flourish in highly disturbed habitats to 10 for species indicative of undisturbed, natural habitats.

Soil seedbank composition was analyzed using the ANOVA procedure for a randomized complete block design replicated 4 times (SPSS 1994). Means were separated using Duncan's Multiple Range Test and considered significant at $P < 0.05$.

Results and Discussion

Leafy Spurge Herbicide Trial

Foliar canopy cover of leafy spurge 10 and 22 months after first treatment was reduced by quinclorac and imazapic following 2 annual fall-applied treatments regardless of application rate (Table 1). Glyphosate plus 2,4-D did not consistently reduce leafy spurge canopy cover. Grass canopy cover 10 months after first treatment increased where imazapic at 70 g ae

Table 1. Percent canopy cover following 2 annual fall-applied herbicide treatments for leafy spurge control on the Sheyenne National Grassland, North Dakota.

		Plant class[2]					
		10 MAFT[3]			22 MAFT[3]		
Treatment[1]	Rate	Leafy spurge	Graminoids	Native forbs	Leafy spurge	Graminoids	Native forbs
	(g ae ha^{-1})	(%)			(%)		
Control		13 cd	31 ab	16 ab	18 b	33 b	4 a
Glyphosate +2,4-D	220 + 330	8 bc	33 abc	8 a	7 a	50 c	4 a
Glyphosate +2,4,-D	440 + 670	18 d	23 a	9 a	19 b	18 a	6 a
Imazapic + MSO[3] + 28%N[3]	70	4 ab	48 d	9 a	4 a	51 c	6 a
Imazapic + MSO[3] + 28%N[3]	140	2 a	39 bcd	13 ab	2 a	48 c	6 a
Quinclorac + MSO[3]	880	2 ab	45 cd	20 ab	3 a	60 d	5 a
Quinclorac + MSO[3]	1100	1 a	31 ab	23 b	1 a	64 d	5 a

[1] Applied in mid-September in 1997 and 1998 to the same plots.

[2] Means in columns followed by a different letter differ ($P < 0.05$).

[3] Abbreviations: MAFT, months after first treatment; MSO, methylated seed oil at 2.3 liters ha^{-1}; 28% N, urea-ammonium nitrate fertilizer at 2.3 liters ha^{-1}.

ha^{-1} and quinclorac at 880 g ae ha^{-1} were applied. Grass foliar cover 22 months after first treatment increased compared to the control for all treatments evaluated, except glyphosate plus 2,4-D at 440 plus 670 g ha^{-1}. The reduced grass cover from the high rate glyphosate plus 2,4-D treatment was due to herbicide injury, which has been documented in prior studies in the northern Great Plains (Lym and Kirby 1991, Lym et al. 1991). Native forb cover 10 and 22 months after first treatment was not altered regardless of treatment.

Table 2. Leafy spurge stem density following 2 annual fall-applied herbicide treatments on the Sheyenne National Grassland, North Dakota.

Treatment[1]	Rate	10 MAFT[2,3]	22 MAFT[2,3]
	-- (g ae ha^{-1}) --	------------- (no. m^{-2})	--------------
Control		40 c	79 b
Glyphosate + 2,4-D	220 + 330	35 c	75 b
Glyphosate + 2,4-D	440 + 670	20 b	74 b
Imazapic + MSO[3] + 28%N[3]	70	2 a	19 a
Imazapic + MSO[3] + 28%N[3]	140	0 a	6 a
Quinclorac + MSO[3]	880	3 a	16 a
Quinclorac + MSO[3]	1100	0 a	5 a

[1] Applied in mid-September in 1997 and 1998 to the same plots.

[2] Means in columns followed by a different letter differ ($P < 0.05$).

[3] Abbreviations: MAFT, months after first treatment; MSO, methylated seed oil at 2.3 liters ha^{-1}; 28% N, urea-ammonium nitrate fertilizer at 2.3 liters ha^{-1}.

Leafy spurge stem density was reduced following single and repeated quinclorac and imazapic treatments at both rates evaluated (Table 2). Leafy spurge stem density 10 months after first treatment averaged 0 to 3 stems m^{-2} for quinclorac and imazapic treatments compared to 40 stems m^{-2} in the untreated control. Leafy spurge stem density 22 months after first treatment increased slightly to 5 and 19 stems m^{-2}, but the stem count nearly doubled in the untreated control to 79 stems m^{-2}. Generally, glyphosate plus 2,4-D did not reduce leafy spurge stem density compared to the control.

Leafy spurge yield 23 months after first treatment was reduced following 2 annual treatments of quinclorac and imazapic, regardless of application rate (Table 3). In contrast, grass yield following 2 annual treatments of quinclorac and imazapic significantly increased compared to the untreated control but not with glyphosate plus 2,4-D. Yields of grass-likes, forbs and other plant species did not differ from the untreated control.

The response of leafy spurge and grass to herbicides was similar to previous reports. Kuehl and Lym (1997) and Masters et al. (1998) reported good leafy spurge control with fall-applied quinclorac treatments without adverse affects on forage yields. Masters et al. (1998) and Markle and Lym (2001) reported similar control of leafy spurge with imazapic to the present study with little to no loss in herbage production. However, imazapic has been injurious to grasses when a fall treatment was followed by a spring treatment compared to a single fall treatment (Masters et al. 1998).

Herbicide Effect on Western Prairie Fringed Orchid Reoccurrence

Three fall-applied herbicide treatments did not reduce reoccurrence of western prairie fringed orchid the first year following treatment (Fig. 1). Western prairie fringed orchids reoccurred in 83% of the plots treated with quinclorac, 60% for both the imazapic and glyphosate plus 2,4-D treatments, and 50% of the untreated plots. These levels of reoccurrence of untreated western prairie fringed orchid are similar to the previous report that 55% of permanently marked flowering western prairie fringed orchid in grazed and ungrazed pastures on the Sheyenne National Grassland reappeared the year following marking (Sieg and King 1995). Similarly, western prairie fringed orchid densities 1 year after treatment were not reduced on treated plots relative to control plots (Fig. 2). Western prairie fringed orchid densities averaged 1.9, 1.3, and 0.9 plants m^{-2} in the plots treated with quinclorac, glyphosate plus 2,4-D and imazapic, respectively, compared to 1.1 western prairie fringed orchids m^{-2} in the untreated plots.

We attribute these results mostly to the timing of herbicide treatments relative to the phenology of the western prairie fringed orchid. The western prairie fringed orchids had completed their life cycles and were senescent when the herbicides were applied, so little imazapic and quinchlorac absorption and translocation into the western prairie fringed orchid roots was expected. Also some evidence suggests that quinclorac and imazapic are more likely to damage dicots such as leafy spurge than they are to damage monocots such as the western prairie fringed orchid (Lym et al. 1991, Kuehl and Lym 1997, Masters et al. 1998, Markle and Lym 2001). Cover of grasses was reduced by most of the herbicide treatments relative to the control, but grass production 23 months after first treatment in the imazapic and quinclorac treatments was higher compared to the untreated plots (Table 3). In contrast, this study and others (Lym and Kirby 1991, Lym et al. 1991) document that glyphosate treatments may reduce grass production.

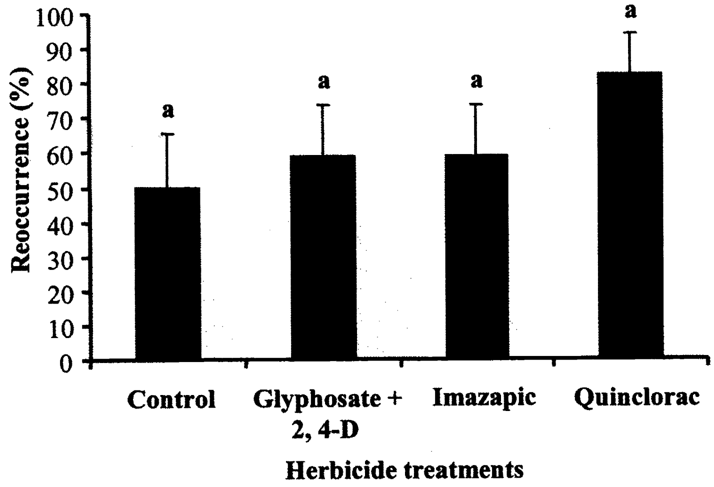

Fig. 1. Effect of fall-applied herbicides on reoccurrence of western prairie fringed orchids the season following treatment on the Sheyenne National Grassland, N.D. Herbicide rates were glyphosate plus 2,4-D at 440 plus 670 g ae ha^{-1}, imazapic at 150 g ae ha^{-1} plus methylated seed oil at 2.3 liters ha^{-1}, and quinchlorac at 1100 g ae ha^{-1} plus methylated seed oil at 2.3 liters ha^{-1}. Percent reoccurrence did not differ ($P > 0.05$) among treatments.

Table 3. Herbaceous yields in August 1999, 23 months after the first treatment, following 2 annual fall-applied herbicide treatments for leafy spurge control on the Sheyenne National Grassland, North Dakota.

		Plant class[2]				
Treatment[1]	Rate	Leafy spurge	Grass	Grass-like	Native forbs	Other
	(g ae ha^{-1})			(g m^{-2})		
Control		101 b	120 a	9 ab	38 ab	63±6.4 a
Glyphosate + 2,4-D	220 + 330	75 b	86 a	3 a	47 b	34±2.4 a
Glyphosate + 2,4-D	440 + 670	70 b	79 a	5 a	30 ab	65±6.9 a
Imazapic + MSO[3] + 28%N[3]	70	9 a	172 c	9 ab	26 ab	56±6.0 a
Imazapic + MSO[3] + 28%N[3]	140	2 a	224 d	1 a	34 ab	29±4.9 a
Quinclorac + MSO[3]	880	13 a	160 bc	25 b	10 a	30±3.7 a
Quinclorac + MSO[3]	1100	4 a	200 cd	15 ab	33 ab	29±2.4 a

[1] Applied in mid-September in 1997 and 1998 to the same plots.

[2] Means in columns followed by a different letter differ ($P < 0.05$).

[3] Abbreviations: MSO, methylated seed oil at 2.3 liters ha^{-1}; 28% N, urea-ammonium nitrate fertilizer at 2.3 liters ha^{-1}.

Finally, some evidence exists that herbicides may reduce interspecific competition, and thus may encourage the western prairie fringed orchid to germinate and develop when adequate soil moisture is present. Several studies have documented episodic flowering and seed production in the western prairie fringed orchid that is associated with adequate soil moisture (Sieg and King 1995), and others have speculated on the importance of disturbances such as fire or grazing for stimulating western prairie fringed orchid growth (Bowles 1983).

Soil Seedbank Study

A total of 53 genera or species were identified in spring and fall soil seedbank cores (Table 4). Of these, 60% were considered early seral species indicative of disturbed tallgrass prairie. Grasses that germinated, which are indicative of disturbance were the annual species, common witchgrass (*Panicum capillare* L.) and yellow foxtail (*Setaria glauca* (L.) Beauv.), and perennial species, redtop (*Agrostis stolonifera* L.) and Kentucky bluegrass (*Poa pratensis* L.). Thirty-six genera or species of forbs were identified, of which less than 50% were perennial and nearly 33% were introduced species. Introduced species included common lambsquarters (*Chenopodium album* L.), Canada thistle (*Cirsium arvense* (L.) scop.), leafy spurge, kochia (*Kochia scoparia* (L.) Schrad.), prickly lettuce (*Lactuca serriola* L.), black medic (*Medicago lupulina* L.), sweetclover (*Melilotus* spp.), field thistle (*Sonchus arvensis* L.) and field pennycress (*Thlapsi arvense* L.).

Fourteen grass genera or species were present, of which approximately 80% were perennial and native species of the tallgrass prairie (Table 4). Native tallgrass prairie species germinating from soil cores included big bluestem, sideoats grama (*Bouteloua curtipendula* (Michx) Torr.), prairie junegrass (*Koeleria pyramidata* (Lam.) Beauv.), little bluestem, sand dropseed (*Sporobolus cryptandrus* (Torr.) A. Gray), needleandthread (*Stipa comata* Trin. & Rupr.) and green needlegrass (*Stipa viridula* Trin.). *Carex, Juncus* and *Typha* species were also identified in soil cores.

There was an abundance of viable seed in the soil seedbank of the study area (Table 5). The average seedling density to a 2.5 cm depth ranged from 1570 to 2090 seedlings m^{-2}. Of this, 38% to over 50% were leafy spurge seedlings. Perennial grasses only comprised an average of 4% of total seedlings in the samples. Total native perennial species, i.e., grasses, forbs and *Carex* spp., averaged 18%, while early seral and invasive species such as leafy spurge, introduced grasses, *Poa* spp., forbs and others totaled 82% of all seedlings in the samples. Thus, for every square meter of soil surface, approximately 1400 early seral and invasive species seeds and propagules could potentially germinate and cover the site. Based on these findings, a sustained weed management program would be needed to successfully revegetate the site upon which this study was conducted following control of leafy spurge.

Conclusions

Quinclorac and imazapic applied in consecutive falls decreased leafy spurge foliar cover, density and yield. Herbaceous yields, other than leafy spurge, were not reduced and generally were stimulated following quinclorac and imazapic treatment. Fall-applied glyphosate plus 2,4-D did not control leafy spurge or result in increased herbaceous yield.

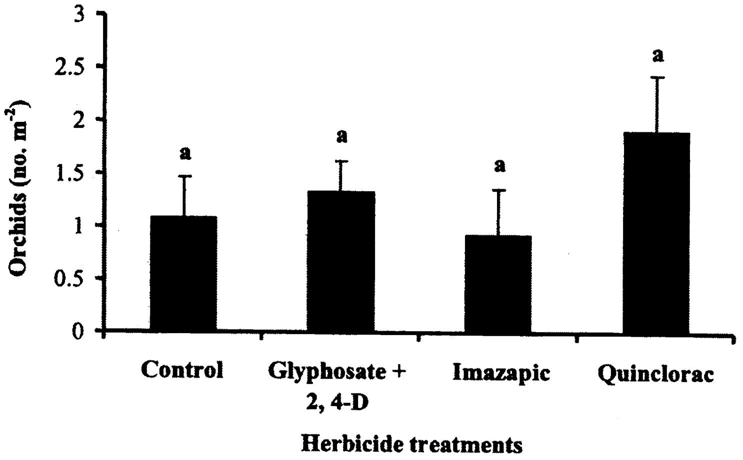

Fig. 2. Average density of western prairie fringed orchids reappearing in herbicide-treated areas the season following treatment on the Sheyenne National Grassland, N.D. Herbicide rates were glyphosate plus 2,4-D at 440 plus 670 g ae ha^{-1}, imazapic at 140 g ae ha^{-1} plus methylated seed oil at 2.3 liters ha^{-1}, and quinchlorac at 1100 g ae ha^{-1} plus methylated seed oil at 2.3 liters ha^{-1}. Densities did not differ ($P > 0.05$) among treatments.

Table 4. Scientific name, common name, season encountered, life form, origin, and coefficient of conservatism of plant species identified on herbicide treatments for leafy spurge control in southeastern North Dakota.

Scientific name[1]	Common name	Season[2]	Life form[3]	Origin[4]	Coefficient of conservatism[5]
Forb species					
Amaranthus retroflexus L.	Rough pigweed	Both	A	N	0
Ambrosia artemisiifolia L.	Common ragweed	Fall	A	N	0
Ambrosia psilostachya DC	Western ragweed	Spring	P	N	2
Artemisia dracunculus L.	Green sagewort	Both	P	N	4
Artemisia frigida Willd.	Fringed sage	Both	P	N	4
Artemisia ludoviciana Nutt.	Gray sage, pasture sage	Both	P	N	3
Aster ericoides L.	White aster	Spring	P	N	2
Chenopodium album L.	Common lambsquarters	Spring	A	I	0
Cirsium arvense (L.) Scop.	Canada thistle	Both	P	I	0
Conyza canadensis (L.) Cronq.	Horseweed	Both	A	N	0
Epilobium ciliatum Ref.	Willow herb	Spring	P	N	3
Erigeron philadelphicus L.	Philadelphia fleabane	Spring	B	N	2
Erigeron strigosus Muhl. ex Willd.	Daisy fleabane	Spring	A	N	3
Erysimum asperum (Nutt.) DC	Western wallflower	Both	B	N	3
Euphorbia esula L.	Leafy spurge	Both	P	I	0
Euphorbia glyptosperma Englem.	Ridge seeded spurge	Both	A	N	0
Fragaria virginiana Duchn.	Wild strawberry	Both	P	N	4
Geranium spp.	Geranium spp.	Both	A, P	I, N	-
Kochia scoparia (L.) Schrad.	Kochia	Fall	A	I	0
Lactuca serriola L.	Prickly lettuce	Fall	A	I	0
Lepidium densiflorum Schrad.	Peppergrass	Both	A	N	0
Liatris spp.	Liatris spp.	Spring	P	N	-
Lycopus asper Greene	Rough bugleweed	Both	P	N	4
Medicago lupulina L.	Black medic	Both	A	I	0
Melilotus spp.	Sweetclover	Both	B	I	0
Oenothera biennis L.	Common evening primrose	Both	B	N	0
Oxalis stricta L.	Yellow wood sorrel	Both	P	N	0
Physalis virginiana P. Mill.	Virginia groundcherry	Fall	P	N	4
Rudbeckia hirta L.	Black eyed susan	Both	B	N	5
Salsola iberica Senn. & Pau	Russian thistle	Spring	A	I	0
Solanum ptycanthum Dun. ex CD	Black nightshade	Both	A	N	0
Solidago gigantea Ait.	Late goldenrod	Fall	P	N	4
Solidago missouriensis Nutt.	Prairie goldenrod	Spring	P	N	5
Sonchus arvensis L.	Field thistle	Both	P	I	0
Thlaspi arvense L.	Field pennycress	Both	A	I	0
Urtica dioica L.	Stinging nettle	Fall	P	N	0
Grass species					
Agrostis stolonifera L.	Redtop	Both	P	I	0
Andropogon gerardii Vitman	Big bluestem	Both	P	N	5
Bouteloua curtipendula (Michx) Torr.	Sideoats grama	Spring	P	N	5
Dichanthelium wilcoxianum (Vasey) Freckmann	Wilcox dichanthelium	Both	P	N	8
Koeleria pyramidata (Lam.) Beauv.	Prairie junegrass	Spring	P	N	7
Muhlenbergia racemosa (Michx.) B.S.P.	Marsh muhly	Spring	P	N	4
Panicum capillare L.	Common witchgrass	Both	A	N	0
Poa compressa L.	Canada bluegrass	Spring	P	I	0
Poa pratensis L.	Kentucky bluegrass	Fall	P	I	0
Schizarchyrium scoparium (Michx.) Nash	Little bluestem	Both	P	N	6
Setaria glauca (L.) Beauv.	Yellow foxtail	Spring	A	I	0
Sporobolus cryptandrus (Torr.) A. Gray	Sand dropseed	Spring	P	N	6
Stipa comata Trin. & Rupr.	Needleandthread	Spring	P	N	6
Stipa viridula Trin.	Green needlegrass	Spring	P	N	5
Other					
Carex spp.	Sedge spp.	Both	P	N	-
Juncus spp.	Rush spp.	Both	P	N	-
Typha spp.	Cattail spp.	Both	P	I, N	-

[1] Scientific names follow the nomenclature of the Flora of the Great Plains (Great Plains Flora Association 1986).

[2] Indicates if the seedlings were encountered in the spring, fall, or both sample periods.

[3] Life-form - P, perennial; A, annual; B, biennial.

[4] Origin - N, native; I, introduced.

[5] A coefficient value of 0 is indicative of species that flourish in highly disturbed habitats, while higher values (to 10) are assigned to species from undisturbed, natural areas (The Northern Great Plains Floristic Quality Assessment Panel 2001).

Table 5. Combined spring and fall soil seedbank composition for 6 herbicide treatments for leafy spurge control in southeastern North Dakota.

			Class[3]							
Treatment[1]	Rate	Seedling density[2]	Leafy spurge	Perennial native grasses	*Poa* spp.	Native forbs	Introduced forbs	Other	Total native perennial species[4]	Total introduced species[5]
	(g ae ha^{-1})	(no. m^{-2})	(%)							
Control		2090	37.6 a	4.7 ab	21.3 a	10.2 b	17.1 b	9.1 a	14.9 a	38.5 a
Glyphosate + 2,4-D	220 + 330	1590	45.4ab	4.8 ab	28.0 a	7.2 ab	7.0 a	7.6 a	12.0 a	35.3 a
Glyphosate + 2,4-D	440 + 670	1620	51.9 b	2.7 a	22.7 a	6.3 ab	7.5 a	8.9 a	9.1 a	30.3 a
Imazapic + MSO[6] + 28%N[6]	70	1430	46.7ab	3.5 ab	23.0 a	6.4 ab	8.5 a	11.9 a	9.9 a	31.6 a
Imazapic + MSO[6] + 28%N[6]	140	1770	45.7ab	3.5 ab	24.9 a	5.4 a	9.4 a	11.1 a	8.9 a	34.5 a
Quinclorac + MSO[6]	880	1710	50.0ab	5.9 b	23.6 a	5.3 a	7.5 a	7.7 a	11.3 a	31.2 a
Quinclorac + MSO[6]	1100	1770	42.9ab	3.9 ab	21.7 a	8.7 ab	13.3 ab	9.5 a	12.6 a	35.2 a

[1] Applied in mid-September in 1997 and 1998 to the same plots.
[2] Average number of seedlings m^{-2} in soil sampled to a 2.5 cm depth.
[3] Means in a column followed by a different letter differ ($P < 0.05$).
[4] Includes perennial and native grasses and forbs.
[5] Leafy spurge and Other category are not included in total percentage of introduced species.
[6] MSO, methylated seed oil at 2.3 $liters^{-1}$; 28% N, urea-ammonium nitrate fertilizer at 2.3 liters ha^{-1}.

Single season data on the impact of these herbicides on the western prairie fringed orchid demonstrated no reductions in western prairie fringed orchid reoccurrence or density in treated plots. This result can most likely be attributed to the timing of the herbicide application. In this study, western prairie fringed orchids were sprayed after they were senescent, thus reducing potential translocation in western prairie fringed orchid. Also following senescence, reduction of herbicide absorption into the roots would be expected. Longer term data are needed to fully assess the impact of herbicide treatments on western prairie fringed orchid regrowth, flowering, and seed production.

A total of 53 genera or species were identified in the soil seedbank, of which 60% were considered early seral species indicative of disturbance. Approximately 1500 to over 2000 seedlings m^{-2} of soil surface to a 2.5 cm depth, from seeds and propagules were present in soils from the study site. Over 80% of the seedlings were early seral species and invasive species including leafy spurge, which comprised over half of these seedlings. Thus, a long-term weed management program will be necessary to successfully revegetate this site even after leafy spurge is controlled. Questions concerning the effect of repeated fall-applied herbicide treatments on the western prairie fringed orchid in a long-term weed management program remain to be answered.

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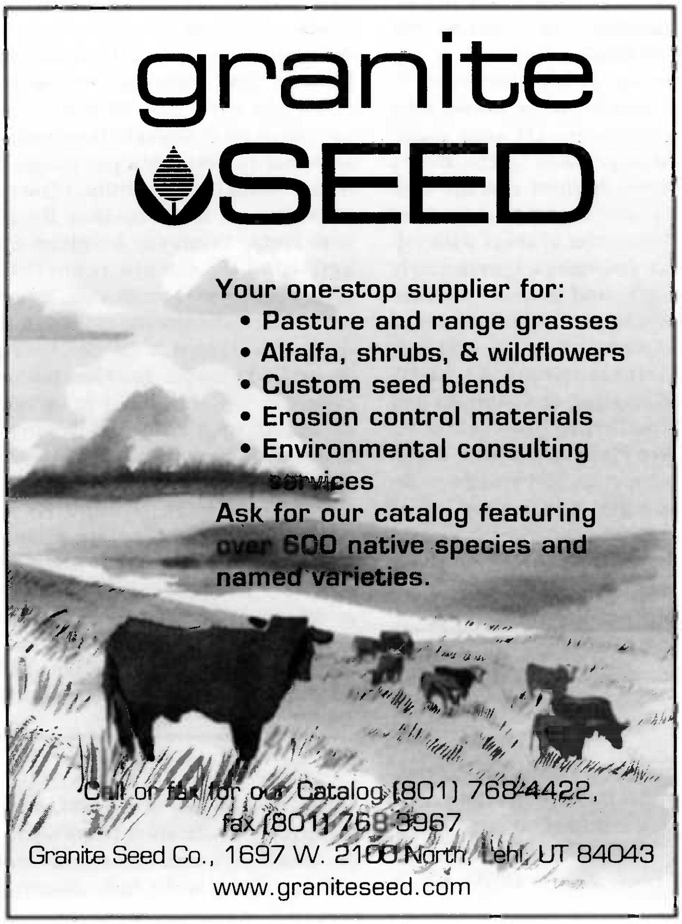

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Characterization of diversity among 3 squirreltail taxa

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Abstract

Squirreltail (*Elymus elymoides, E. multisetus*) is a complex of 5 taxa whose systematic interrelationships are uncertain. Our objectives were to determine whether the 3 taxa studied here, *Elymus elymoides* ssp. *elymoides, E. elymoides* ssp. *brevifolius*, and *E. multisetus*, can be distinguished by several ecological and physiological traits and whether geographical origin is correlated with these traits across accessions within taxa. A multivariate principal component analysis of materials collected in the 10 contiguous western states successfully distinguished taxa, but no pair of the 3 taxa appeared to be more ecologically similar than any other pair. *Elymus elymoides* ssp. *elymoides*, which prevails in the semi-arid cold desert, was shortest and exhibited the lowest total plant dry-matter, earliest phenology, and lowest seed mass. *Elymus elymoides* ssp. *brevifolius*, which prevails in the Rocky Mountains, exhibited slowest emergence, highest specific root length, lowest nitrate reductase activity, and lowest root-to-shoot ratio. *Elymus multisetus*, which is most common in areas with relatively warm springs, exhibited fastest emergence (particularly from deep seeding), greatest root length, and greatest root-to-shoot ratio. *Elymus elymoides* ssp. *brevifolius* accessions clustered into 3 groups: late-maturing high-seed mass accessions originating in Colorado, New Mexico, and Arizona (Group A), early-maturing low-seed mass accessions originating in Colorado and Utah (Group B), and intermediate-maturing low-seed mass accessions originating in the Snake River Plain of southern Idaho (Group C). The ecologically distinct subspecies and groups within ssp. *brevifolius* are indicative of the highly ecotypic nature of the squirreltails, suggesting that restoration practitioners should match site with genetically and ecologically appropriate plant material for these species.

Key Words: *Elymus elymoides*, genetic variation, plant autecology, *Sitanion hystrix*

Resumen

"Squirreltail (*Elymus elymoides*, *E. multisetus*) es un complejo de 5 taxas cuyas interrelaciones sistemáticas son inciertas. Nuestros objetivos fueron determinar si las 3 taxas estudiadas aquí *Elymus elymoides* ssp. *elymoides*, *E. elymoides* ssp. *brevifolius*, y *E. multisetus*, pueden ser distinguidas por varias características ecológicas y fisiológicas y si el origen geográfico esta correlacionado con estas características a través de las accesiones dentro de la taxa. Un análisis multivariado de componentes principales de los materiales colectados en los 10 estados contiguos del oeste distinguió en forma exitosa la taxa, pero ningún par de las tres taxas pareció ser mas ecológicamente similar que cualquier otro par. *Elymus elymoides* ssp. *elymoides*, el cual prevalece en el desierto frío semiárido, fue el más corto y mostró la menor materia seca por planta, la fisiología más temprana y la menor biomasa de semilla. *Elymus elymoides* ssp. *brevifolius*, que prevalece en las Montañas Rocallosas presento la emergencia mas lenta, la mayor longitud especifica de raíz, la mas baja actividad de nitrato reductasa y la relación más baja de tallo:raíz. *Elymus multisetus*, que es mas común en áreas con primaveras relativamente calientes, mostró la emergencia más rápida (particularmente en siembras profundas), la mayor longitud de raíz y la mayor relación tallo:raíz. Las accesiones de *Elymus elymoides* ssp. *brevifolius* se agruparon en tres grupos: accesiones de madurez tardía-alta biomasa de semilla originarias de Colorado, New Mexico y Arizona (Grupo A), accesiones de madurez temprana -baja biomasa de semilla originarias de Colorado y Utah (Grupo B) y un grupo de accesiones de madurez intermedia-baja biomasa de semilla originarias del Snake River Plain del sudeste de Idaho (Group C). Las subespecies y grupos ecológicamente distintos dentro de ssp. *brevifolius* son indicativos de la naturaleza altamente ecotípica de los "Squirreltails, sugiriendo que los que practican la restauración de pastizales deben aparejar el sitio con un el material vegetal genética y ecológicamente apropiado de estas especies.

The squirreltails (*Elymus elymoides* [Raf.] Swezey and *E. multisetus* [J.G. Smith] Burtt-Davy) are increasingly important grasses for restoring rangeland communities on disturbed sites in the Intermountain Region of western North America. Systematists generally recognize up to 5 squirreltail taxa (Wilson 1963), which we refer to in this paper as *elymoides, brevifolius, californicus, hordeoides*, and *multisetus*. These taxa have been recognized in both *Sitanion* and in *Elymus*, with the latter being the currently preferred classification (Barkworth et al. 1983). However, rank of the taxa varies with taxonomic treatment.

There seems to be little dissension regarding the retention of 2 taxa in *E. elymoides*, namely ssp. *elymoides* and ssp. *californicus*. Wilson (1963) mentioned the marked similarity of their karyotypes. Also, M.E. Barkworth and J.J.N. Campbell (pers. comm. 2000) noted that they appear to hybridize when sympatric.

Taxonomic treatments have varied in their handling of specimens keying to *brevifolius* and *hordeoides* in Wilson's (1963)

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treatment. *Brevifolius* was treated as a separate species by Wilson (1963) (*S. longifolium* J.G. Smith), reluctantly treated as a separate species by Holmgren and Holmgren (1977), treated as a subspecies of *E. elymoides* (ssp. *brevifolius*) by M.E. Barkworth and J.J.N. Campbell (2000 pers. comm.), and unrecognized as a separate taxon by Hitchcock (1950) and Arnow (1993). *Hordeoides* has been treated as a separate species by Wilson (1963) (*S. hordeoides* Suksdorf) or as part of a species including *elymoides, californicus*, and *brevifolius* by Holmgren and Holmgren (1977) and by M.E. Barkworth and J.J.N. Campbell (pers. comm.).

Some systematists readily recognize *multisetus* as worthy of specific rank (*E. multisetus* [J.G. Smith] Burtt-Davy = *S. jubatum* J.G. Smith) (Hitchcock 1950, Wilson 1963, Barkworth et al. 1983), while others do so only reluctantly (Holmgren and Holmgren 1977). Wilson (1963) noted that the karyotype of *multisetus* was the most distinctive of the 5 squirreltail taxa. He reported extensive introgressive hybridization between *multisetus* and *elymoides* in southeastern California and southern Nevada, though not in other locales where these 2 taxa are sympatric. Holmgren and Holmgren (1977) suggested that a reasonable approach would be amalgamation of all 5 taxa into a single species.

Wilson (1963) provides a reliable key that easily separates the 5 taxa based on floral appendages. We have used it to identify over 100 accessions in our collection, which includes representatives of all taxa except *hordeoides*. Our objective was to determine how 3 taxa, *multisetus, brevifolius,* and *elymoides*, compare for traits relating to seedling establishment, leaf and root morphology, and phenology because such traits may be correlated with adaptation to particular range sites. We also wished to determine the degree of separation or overlap between the taxa based on these traits and to gather any insights from the relationship between performance and geographical origin of the accessions.

Materials and Methods

Data set 1

Twenty-one of the 27 accessions (Tables 1, 2) in data set 1 originated from USDA-NRCS Plant Materials Centers in Aberdeen, Ida. and Bridger, Mont., or the Upper Colorado Environmental Plant Center in Meeker, Colo.. Two accessions

Table 1. Means for 1 *californicus*, 17 *elymoides*, 5 *brevifolius*, and 4 *multisetus* squirreltail accessions in data set 1 for 8 traits in a 25-day greenhouse trial.

Accession	Collection location	Days to emergence	Leaf length (10 days post-plant)	Total plant dry-matter	Root-to-shoot ratio	Leaf area	Specific leaf area	Root length	Specific root length
		(no.)	(mm)	(mg plant^{-1})	(mg mg^{-1})	(mm^2 plant^{-1})	(mm^2 mg^{-1})	(mm plant^{-1})	(mm mg^{-1})
californicus									
PI 531604	Toe Jam Creek, Elko Co., Nev.	6.0	73	10.46	0.389	174	31.3	914	324
elymoides									
Acc:1107	sec 32 T22N R22E, Lemhi Co., Ida.	5.4	65	9.56	0.424	148	29.1	916	317
Acc:1108	sec 36 T4N R26E, Butte Co., Ida.	6.3	61	9.57	0.315	168	29.4	698	316
Acc:1109	sec 11 T4N R26E, Butte Co., Ida.	6.0	58	9.26	0.306	182	31.9	652	324
Acc:1110	sec 26 T4N R26E, Butte Co., Ida.	5.8	58	6.98	0.516	110	31.0	687	289
Acc:1111	sec 11 T4N R26E, Butte Co., Ida.	6.2	58	8.38	0.442	158	33.5	853	337
Acc:1112	sec 11 T4N R27E, Butte Co., Ida.	5.1	67	9.79	0.365	175	31.0	838	330
Acc:1113	1737 m, Custer Co., Ida.	5.3	74	8.85	0.423	157	31.3	1057	410
Acc:1114	Morse Creek, Custer Co., Ida.	6.2	54	7.14	0.291	116	27.7	641	410
Acc:1115	Leaton Gulch, Custer Co., Ida.	6.2	62	9.57	0.405	167	32.6	717	270
Acc:1116	Bradbury Flat, Custer Co., Ida.	6.0	64	9.56	0.335	178	33.8	668	275
Acc:1117	Round Valley, Custer Co., Ida.	5.6	62	10.18	0.354	182	32.9	814	322
Acc:1124	Squaw Butte, Harney Co., Ore.	6.1	60	10.27	0.359	150	25.2	960	368
PI 619489	Whitehall, Mont.	5.4	63	8.86	0.427	142	29.0	830	323
PI 619491	Big Piney, Wyo.	5.6	60	10.33	0.352	191	32.1	711	273
PI 619555	Warren, Mont.	6.2	57	9.36	0.285	174	31.7	629	298
PI 619561	Big Piney, Wyo.	5.8	60	9.69	0.436	167	32.0	821	306
9019219	btwn Worland & Ten Sleep, Wyo.	5.8	64	10.15	0.325	214	35.2	667	284
mean		**5.8 b$^{\#}$**	**62 b**	**9.26 c**	**0.374 b**	**163 b**	**31.1 a**	**774 b**	**321 a**
brevifolius									
Acc:1123	btwn Prairie City & Dixie Pass, Ore.	5.7	70	12.44	0.358	197	27.6	1017	343
Acc:1130	Savageton, Wyo.	6.4	71	9.35	0.280	157	28.0	700	376
PI 531605	btwn N. LaVeta Pass & Gardner, Colo.	7.0	56	10.50	0.267	154	23.8	794	368
9040187	Wet Mountains, Custer Co., Colo.	7.4	49	10.75	0.305	158	25.0	836	361
9040189	Buford, Rio Blanco Co., Colo.	6.3	65	12.10	0.333	210	29.7	943	332
mean		**6.6 a**	**62 b**	**11.03 b**	**0.309 c**	**175 b**	**26.8 b**	**858 b**	**356 a**
multisetus									
Acc:1132	Paradise Valley, Nev.	4.8	85	16.60	0.483	269	31.2	1434	268
PI 531603	Lake Tahoe, Nev.	4.4	85	18.48	0.483	303	31.0	1980	335
PI 531606	Central Ferry, Wash.	4.8	82	13.89	0.392	245	32.3	1520	393
PI 619466	Redlands, Lassen Co., Cal.	5.5	84	15.45	0.429	262	31.2	1161	278
mean		**4.9 c**	**84 a**	**16.11 a**	**0.447 a**	**270 a**	**31.4 a**	**1524 a**	**319 a**

$^{\#}$taxa means followed by different letters in the same column are significantly different at $P < 0.05$.

Table 2. Means for 1 *californicus*, 17 *elymoides*, 5 *brevifolius*, and 4 *multisetus* squirreltail accessions in data set 1 for 5 traits in field and greenhouse trials.

Accession	Heading date	Seed mass	Emergence index		Nitrate reductase activity
	(days after 30/4/95)	(mg seed^{-1})	(20 mm)	(60 mm)	(per mg protein)
californicus					
PI 531604	29	4.14	6.36	3.64	7.66
elymoides					
Acc:1107	15	3.27	6.71	3.01	7.83
Acc:1108	27	2.67	6.54	2.01	7.34
Acc:1109	15	2.71	6.62	3.03	7.01
Acc:1110	31	2.95	6.51	2.34	5.38
Acc:1111	19	3.02	6.31	2.80	7.17
Acc:1112	24	2.47	6.74	2.90	6.52
Acc:1113	31	2.94	7.21	3.38	6.03
Acc:1114	17	3.07	6.36	3.50	7.50
Acc:1115	33	3.43	6.67	4.36	8.48
Acc:1116	33	3.49	6.83	4.40	9.46
Acc:1117	36	3.33	7.43	4.80	9.13
Acc:1124	36	3.44	6.64	2.93	6.68
PI 619489	31	3.26	5.71	1.14	7.34
PI 619491	29	3.48	6.44	3.40	8.48
PI 619555	33	3.00	6.60	2.82	7.83
PI 619561	27	2.86	6.56	3.41	8.64
9019219	29	4.07	6.18	4.32	8.64
mean	**27 b**[#]	**3.14 b**	**6.59 a**	**3.21 ab**	**7.62 a**
brevifolius					
Acc:1123	47	3.94	5.67	3.73	3.91
Acc:1130	29	3.98	5.92	3.94	6.85
PI 531605	46	6.83	5.05	3.40	4.57
9040187	59	6.32	5.62	3.43	5.54
9040189	45	5.51	5.46	2.94	5.87
mean	**45 a**	**5.32 a**	**5.54 b**	**3.49 b**	**5.35 b**
multisetus					
Acc:1132	42	5.29	6.58	4.03	9.62
PI 531603	50	6.33	6.10	4.24	8.64
PI 531606	47	4.89	7.30	4.25	8.15
PI 619466	33	4.69	7.25	3.63	8.15
mean	**43 a**	**5.30 a**	**6.81 a**	**4.04 a**	**8.64 a**

[#] taxa means followed by different letters in the same column are significantly different at $P < 0.05$.

were obtained from USDA-ARS, i.e., W6 22031 (David C. Ganskopp, Burns, Ore.) and W6 20963 (James A. Young, Reno, Nev.). The 4 remaining accessions (PI 531603 through PI 532606), obtained from the National Plant Germplasm System, were originally from the collection of the late D.R. Dewey of our laboratory. We determined the taxon of each accession using the dichotomous key provided by Wilson (1963) that distinguishes the taxa based on number and bifurcation of awns. Seed samples of these accessions are deposited in the National Plant Germplasm System at the USDA-ARS Western Regional Plant Introduction Station in Pullman, Wash. (http://www.ars_grin.gov/npgs).

Data were collected from evaluations in the field and 4 greenhouse trials. The field evaluation was established on 2–3 Sept. 1993 at Greenville Farm, North Logan, Ut. (41°45'59" N, 111°48"34"W) on a Millville silt loam (coarse-silty, carbonatic, mesic Typic Rendolls; 2–4% slope). Accessions were established as field transplants on 0.5-m centers in a 7 x 7 plant block. Each block was filled with 49 plants unless fewer were available. Because the blocks were not replicated, data collected from this trial were only for 2 traits of high heritability, which were heading date (the number of days after 30 Apr. 1995 that the majority of the plants in a plot had at least 1 spike emerge from the boot) and seed mass (mg seed^{-1} averaged across 1994 and 1995 harvests). Seed harvested from these blocks was used to conduct a seedling growth trial in the greenhouse, 2 depth-of-seeding trials, and a nitrate reductase activity assay in the greenhouse. Because outcrossing in squirreltail is negligible (Jensen et al. 1990), seed harvested from such a block may be presumed to be genetically representative of the original collection.

The seedling growth trial was planted in a greenhouse maintained at 20 ± 5°C on 8 Jan. 1996 in a soil consisting of 3 parts Kidman fine sandy loam (coarse-loamy, mixed, mesic Calcic Haploxerolls): 1 part peat moss. Five seeds of an accession were planted 5 mm deep in 65 X 255-mm cone-containers. Accessions were assigned to 10 replications in a randomized complete block design. The third seedling to emerge was retained, days-to-emergence was recorded, and the other seedlings were removed. Water was supplied daily with a 32% Rorison nutrient solution (Arredondo et al. 1998). Length of the first leaf was measured on day 10. Plants were harvested on day 25 and divided into shoots and roots. Leaf area was determined with a leaf-area meter (LI-3000, LI-COR, Lincoln, Neb.). Roots were recovered by gentle washing with a slow-moving stream of water. Root length was measured on fresh tissue with 'Branching' software (version 1.52β) (Berntson 1992). Shoots and roots were then oven-dried at 70°C for 48 hours before weighing. Specific leaf area was calculated as leaf area/shoot mass, and specific root length was calculated as root length/root mass.

To measure seedling emergence, 2 greenhouse trials were conducted at 20 ± 5° C at depths of 20 mm and 60 mm. Both trials were planted in above-ground beds filled with the greenhouse soil described above. This was underlain by a gravel layer for drainage. The beds were 1.067-m wide and furrows were 50.8-mm apart. Fifty seeds of an accession were planted per half-length of each furrow. Another randomized accession was planted in the opposite half. Accessions were planted in a randomized complete block design with 6 replications. The 20-mm trial was planted on 9 to 10 Dec. 1996 and seedling emergence was tallied daily. Emergence index was calculated as $\sum[(g_n-g_{(n-1)})/n]$, where $(g_n-g(_{n-1}))$ is the number of seedlings germinating since the previous day and n is the number of days since the germination trial began (Maguire 1962). Therefore, large numbers indicate fast emergence and small numbers indicate slow emergence, the opposite direction of the days-to-emergence variable in the above-mentioned seedling growth trial. The 60-mm trial was planted on 4 Feb. 1997 and conducted similarly.

High nitrate reductase activity may facilitate higher assimilation of soil nitrogen, thereby promoting seedling establishment. For the nitrate reductase assay, the 27 accessions were grown in a 20 ± 5°C greenhouse as seedlings in the same soil as the depth-of-seeding evaluations. Fresh samples of leaf tissue were harvested 2 to

4 hours after sunrise, placed directly into liquid N_2, and stored at –80°C until use. Frozen tissue was powdered in liquid N_2 and extracts were made by grinding in 5 to 10 vol. of 50 mM MOPS buffer (pH 7.5) containing 10 mM $MgCl_2$,1 mM EDTA, 0.1% Triton X-100, 2.5 mM DTT, 1 mM PMSF, 10 µM leupeptin, and 10 µM chymostatin. After centrifugation of the extracts at 12,000 g for 4 min, the supernatant was transferred to a fresh tube and used immediately to assay total NADH:nitrate reductase activity according to Redinbaugh et al. (1996). Assays were performed in a 200-µl volume containing 50 mM MOPS, 10 mM K-phosphate buffer (pH 7.5) containing 13 mM KNO_3, 500 µM NADH, and 10 µM FAD. Soluble protein in the extracts was determined using a dye-binding assay (Redinbaugh and Campbell 1985).

Data set 2

For the second data set, data were collected from a field evaluation and a greenhouse seedling growth trial. Forty-seven accessions (Table 3) were established as field transplants on 3–4 Sept. 1996 at Evans Farm, Millville, Ut. (41°41'39"N 111°49'58"W) on a Nibley silty clay loam (fine, mixed mesic Aquic Argiustolls; 0-3% slope). All 47 accessions were collected from their native sites in 1995. The planting design was similar to data set 1. Heading date (the mean number of days after 30 Apr. 1997/1998 that the majority of the plants in a plot had at least 1 spike emerge from the boot), seed mass (the mean mg seed^{-1} across 1997/1998), and plant height (mean across 1997/1998) were measured on these plots. Seed harvested from these blocks was used to conduct a seedling growth trial in the greenhouse as for data set 1.

The seedling growth trial was planted in a greenhouse maintained at 20 ± 5°C on 12 Mar. 1999 in the same design and soil as used in data set 1. Water was supplied without nutrient solution. Days-to-emergence of the third seedling was recorded and its leaf length was measured 17 days after planting. The plants were harvested 14 Apr. (replications 1 to 3), 15 Apr. (replications 4 to 8), and 16 Apr. (replications 9 to 10) and divided into shoots and roots. For data set 2, we used a Comair root length scanner (Commonwealth Aircraft Corp. Ltd., Melbourne, Australia) to measure root length of fresh tissue that had been stored in refrigerated vials of water. This greatly expedited the process compared to the technique used for data set 1. After scanning, shoots and roots were oven-dried at 70°C for 48 hours before weighing. Specific root length was calculated as root length/root mass.

Statistical analysis

For each trait, differences between means of any 2 taxa were tested for deviation from zero using a t-test at $\alpha = 0.05$. Values for all accessions were standardized to unit variance for each trait before multivariate analysis. Thirteen and 9 orthogonal principal components, the number of variables in each data set, were generated for data sets 1 and 2, respectively (Morrison 1976). Because a large proportion of the total variance was accounted for by the first 2 principal components for both data sets, only the first 2 were retained. These 2 principal components were each defined by a vector of scalars, each representing a trait. These are termed the principal component loadings for Principal Component 1 and Principal Component 2, respectively. Principal Component 1 loadings are the single set of numbers, 13 in the case of data set 1 and 9 in the case of data set 2, that best circumscribes the data set. Likewise, the Principal Component 2 loadings are the second single set of numbers that best circumscribes the variation remaining after Principal Component 1 variation is removed. We rotated principal component loadings using an orthogonal varimax rotation in PROC FACTOR (SAS Institute, Cary, NC) to maximize the amount of information included in the 2 retained principal components (Kaiser 1958). Principal component scores were calculated for each accession for each of the 2 principal components by multiplying the vector of standardized means by the vector of rotated principal component loadings. Accessions were plotted in 2 dimensions based on Principal Component 1 and Principal Component 2 scores. Because 2 of the 13 traits measured in data set 1 and 3 of the 9 traits measured in data set 2 were taken from unreplicated plots, comparisons were made only between taxa rather than between individual accessions. The individual accessions provided replication for their respective taxa.

Table 3. Loadings for the first 2 principal components in data sets 1 (13 traits) and 2 (9 traits).

	Principal component	
Trait	1	2
Data set 1		
Days to emergence	-0.563	-0.635
Leaf length	0.818	0.339
Total plant dry-matter	0.968	0.018
Root-to-shoot ratio	0.437	0.526
Leaf area	0.903	0.227
Specific leaf area	0.055	0.854
Root length	0.924	0.059
Specific root length	-0.040	-0.517
Heading date	0.655	-0.552
Seed mass	0.702	-0.593
Germination index (20 mm)	0.028	0.791
Germination index (60 mm)	0.477	0.163
Nitrate reductase activity	0.222	0.749
Data set 2		
Days to emergence	0.353	-0.882
Leaf length	0.082	0.921
Total plant dry-matter	0.512	0.824
Root-to-shoot ratio	-0.754	0.395
Root length	0.441	0.788
Specific root length	0.302	-0.654
Heading date	0.912	0.008
Plant height	0.905	0.001
Seed mass	0.902	0.291

Results and Discussion

Data set 1

In the 25-day greenhouse trial, *multisetus* accessions emerged faster, had longer leaves at 10 days, and had greater total plant dry-matter at harvest than the other 2 taxa (Table 1). The faster seedling development of *multisetus* may relate to its prevalence in regions with relatively warm springs like the Columbia and Snake River Plains. *Brevifolius* emerged slowest, which may be because of the cooler springs and late freezes of the Rocky Mountains, a region where this taxon predominates. *Elymoides* had the least total plant dry-matter of the 3 taxa, probably because it is most common in the semi-arid cold desert, a stressful environment where conservative growth is probably advantageous. Root-to-shoot ratio was least for *brevifolius* and greatest for *elymoides*. Evaporative demand, necessitating a greater root-to-shoot ratio, is typically greater in the semi-arid cold desert, where *elymoides* predominates, than in the Rocky Mountains, where *brevifolius* predominates. *Brevifolius* and *elymoides* were similar for leaf area and root length and lower than *multisetus*, which again may relate to the latter's prevalence in warmer regions. *Brevifolius* had lower specific leaf area, i.e., thicker leaves, than the other 2 taxa, but no differences among taxa were observed for specific root length. Likewise, Arredondo et al. (1998) found that 4 *brevifolius* accessions had lower specific leaf area than the *multisetus*, Sand Hollow. Low specific leaf area is associated with high carbon investment and long leaf life-span (Reich 1997), a characteristic of perennials relative to cheatgrass (Arredondo et al. 1998). We are uncertain as to whether *brevifolius* plants have greater longevity in their environments than do *multisetus* or *elymoides* plants.

In the field trial, *elymoides* headed earlier and produced seed with lower mass than the other taxa (Table 2), suggesting that it is adapted to regions lacking the summer precipitation that is found in the Rocky Mountains, for example. In the greenhouse depth-of-emergence trials, *multisetus* emerged significantly faster than *brevifolius* at both 20 and 60-mm depths. The 25-day greenhouse trial also demonstrated the slow germination rate of *brevifolius*, based on emergence from a shallow 5-mm depth. *Elymoides* emergence was similar to *multisetus* and faster than *brevifolius* at 20 mm, but lagged behind with *brevifolius* at 60 mm. The low seed mass of *elymoides* accessions may have been a disadvantage at the deeper 60-mm planting depth, while the high seed mass of *brevifolius* may have compensated for its inherently slow germinability at this depth. Correlations between seed mass and emergence index were negative ($r = -0.50$; $P < 0.01$) at 20 mm and positive ($r = 0.34$; $P < 0.10$) at 60 mm. Thus, larger-seeded accessions emerged faster at 60 mm, while the reverse was true at 20 mm. Emergence indices at the 2 depths were uncorrelated across accessions ($P > 0.10$).

Nitrate reductase activities were lower for *brevifolius* than the other 2 taxa (Table 2). In agronomic crops, high leaf nitrate reductase activity was correlated with increased plant growth and grain yield, especially at low (<10 mM) external nitrate concentrations (Johnson et al. 1976, Feil et al. 1993). In addition, barley mutants with low nitrate reductase activity grew slower in the cool early-season and matured later than wild-type plants (Blackwood and Hallam, 1979). Measured nitrate reductase activity is the result of a complex interaction of nitrate, carbohydrate availability, plant development, and light. But plant materials with higher nitrate reductase activity, e.g., *elymoides* and *multisetus*, that can more effectively assimilate and compete for soil nitrogen may grow or become established faster than those with lower nitrate reductase activity, e.g., *brevifolius*. Indeed, the slow emergence of *brevifolius* from a 5-mm planting depth relative to *elymoides* and *multisetus* was noted above. Principal component loadings for days to emergence and nitrate reductase activity were negatively correlated for both principal components 1 and 2, but the relationship was stronger for principal component 2 (Table 3).

Principal Components 1 and 2 explained 38 and 29% of the variation, respectively, among accessions for the 13 traits. Loadings for Principal Component 1 indicate that accessions with higher Principal Component 1 scores had generally more rapid emergence at a 5-mm planting depth, greater day-10 leaf length, and greater total plant dry-matter, root-to-shoot ratio, leaf area, and root length at harvest in the greenhouse trial; later heading date and greater seed mass in the field; and more rapid emergence from a 60-mm planting depth (Table 3). Principal Component 1 separated *multisetus* (high scores) from *elymoides* (low scores). *Brevifolius* was intermediate between these 2, but closer to *elymoides* (Fig. 1). Loadings for Principal Component 2 indicate that accessions with higher Principal Component 2 scores had generally more rapid emergence at a 5-mm planting depth; greater root-to-shoot ratio, greater specific leaf area (thinner leaves), and lower specific root length (thicker roots) at harvest in the greenhouse trial; earlier heading date and lower seed mass in the field; more rapid emergence from a 20-mm planting depth; and higher nitrate reductase activity. Principal Component 2 separated *elymoides* and *multisetus* (high scores) from *brevifolius* (low scores). Overlap among the 3 taxa was absent in the 2-dimensional scatter plot, but beyond that, accessions did not appear to be organized in any geographical manner.

Values for the lone *californicus* accession, PI 531604, were within the range of *elymoides* accessions for all traits except total plant dry-matter in the greenhouse and seed mass in the field, where PI 531604 had slightly greater values (Tables 1, 2). Accession PI 531604 was clearly more similar to *elymoides* than to *brevifolius* or *multisetus*, supporting a close tax-

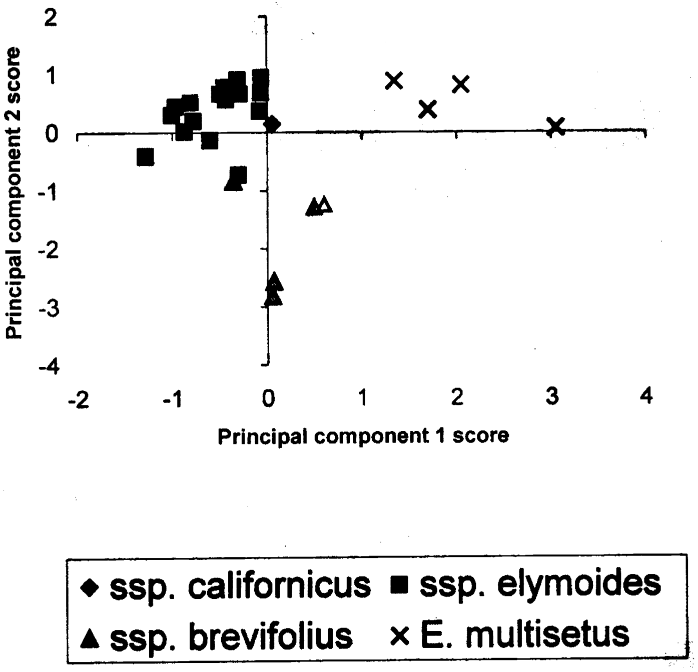

Fig. 1. Plot of the first 2 principal component scores for 27 *Elymus elymoides* and *E. multisetus* squirreltail accessions in data set 1.

Table 4 Means for 10 *elymoides*, 21 *brevifolius*, and 16 *multisetus* squirreltail accessions in data set 2 for 6 traits in a 34-day greenhouse trial.

Taxon/ Accession	Collection location	Elevation	Days to emergence	Leaf length (17 days post-plant)	Total plant dry-matter	Root-to-shoot ratio	Root length	Specific root length
		(m)	(no.)	(mm)	(mg plant^{-1})	(mg mg^{-1})	(mm plant^{-1})	(mm mg^{-1})
elymoides								
T-1173	east of Mountain Home, Ida.	1050	5.7	38	4.09	1.28	640	278
T-1174	west of Mountain Home, Ida.	950	4.4	38	5.18	1.27	860	297
T-1175	Ditto Creek, Elmore Co., Ida.	1000	4.6	42	4.58	1.01	720	313
T-1191	County Rd 10, Moffat Co., Colo.	2150	5.0	41	5.36	1.16	870	302
T-1192	Point of Rocks, Sweetwater Co., Wyo.	2200	4.7	47	5.69	1.39	1090	329
T-1193	Superior, Wyo.	2200	5.9	37	4.04	1.68	730	289
T-1198	btwn Sage Junction & Laketown, Ut.	2200	5.0	42	4.47	1.27	840	336
T-1223	Fish Creek, Carey, Ida.	1450	4.3	49	5.94	1.09	870	281
T-1224	Atomic City, Bingham Co., Ida.	1500	4.5	49	5.26	1.35	770	255
PI 619553	Shoshone, Ida.	1300	4.8	38	5.29	1.20	780	270
mean		**1633**	**4.9 b**[#]	**42 b**	**4.99 c**	**1.27 a**	**817 c**	**295 b**
brevifolius								
group A								
T-1180	northeast of Wagonmound, N.M.	2000	7.4	30	5.52	0.84	710	282
T-1233	north of Hermosa, Colo.	2000	5.8	44	9.53	0.61	1210	335
T-1238	east of Chimney Rock, Colo.	2050	5.8	44	8.89	0.50	970	327
T-1239	northeast of Pagosa Springs, Colo.	2350	6.4	39	7.33	0.85	1160	345
T-1242	north of Lake City, Colo.	2450	6.4	37	6.16	0.88	1060	367
T-1249	west of Sargents, Colo.	2600	6.8	35	7.68	0.65	1080	356
T-1260	south of Westcliffe, Colo.	2450	6.6	42	6.61	0.76	1060	372
T-1264	north of Colmor, N.M.	1850	7.0	35	5.33	0.74	800	354
T-1265	north of Wagonmound, N.M.	1900	7.1	37	5.56	0.82	980	392
T-1271	southwest of Ocate, N.M.	2300	6.3	45	6.86	0.81	1050	342
T-1272	La Cueva, N.M.	2200	6.4	43	5.46	0.92	850	326
T-1277	Tres Piedras, N.M.	2350	6.6	44	5.70	0.91	1030	380
T-1299	north of Flagstaff, Ariz.	2150	6.2	47	8.44	0.76	1500	411
(mean)		(2204)	(6.5)	(40)	(6.85)	(0.77)	(1035)	(353)
group B								
T-1228	Colton, Ut.	2150	6.5	37	3.70	1.31	910	433
T-1243	north of Powderhorn, Colo.	2750	6.3	39	5.10	1.07	1070	405
T-1308	northwest of Almont, Colo.	2500	5.7	39	4.37	1.07	980	434
(mean)		(2467)	(6.2)	(38)	(4.39)	(1.15)	(987)	(424)
group C								
T-1202	hwy 75 X 20, Blaine Co., Ida.	1350	5.4	42	4.71	1.26	720	274
T-1203	east of Fairfield, Ida.	1500	5.4	52	6.28	0.84	1060	369
T-1204	east of Hill City, Ida.	1550	5.8	43	6.55	1.17	1010	286
T-1205	west of Hill City, Ida.	1600	4.2	44	5.92	1.26	1080	327
T-1206	east of Dixie, Elmore Co., Ida.	1600	5.0	45	5.92	1.18	1080	336
(mean)		(1520)	(5.2)	(45)	(5.88)	(1.14)	(990)	(319)
mean		**2100**	**6.1 a**	**41 b**	**6.27 b**	**0.91 b**	**1018 b**	**355 a**
multisetus								
PI 619454	A-line canal, Gem Co., Ida.	950	3.9	61	10.49	1.14	1660	297
PI 619456	Cartwright Rd., Ada Co., Ida.	1000	4.1	49	9.00	1.17	1560	321
PI 619457	Little Land & Livestock, Canyon Co., Ida.	800	3.8	64	9.91	1.22	1360	250
PI 619458	northwest of Mayfield, Elmore Co., Ida.	1100	4.0	51	9.92	1.31	1470	262
PI 619459	Boise, Ida.	1000	3.9	55	9.21	1.20	1530	305
PI 619460	Bogus Basin Rd., Ada Co., Ida.	1000	4.3	53	9.05	1.16	1510	311
PI 619461	Barber, Ida.	950	3.9	51	9.24	1.16	1390	280
PI 619462	southeast of Mayfield, Elmore Co., Ida.	1100	3.7	58	8.74	1.39	1360	267
PI 619463	Ditto Creek, Elmore Co., Ida.	1000	3.9	55	9.17	1.34	1490	284
PI 619464	Lower Hatley, Canyon Co., Ida.	800	3.8	56	9.61	0.99	1280	268
PI 619465	Seaman's Gulch Rd., Ada Co., Ida.	1000	4.4	53	9.87	1.23	1510	278
PI 619467	Middle Hatley, Gem Co., Ida.	800	4.3	52	8.25	1.07	1160	272
PI 619564	Ditto Creek, Elmore Co., Ida.	1100	4.9	44	7.38	1.04	1030	273
T-1165	King Hill, Ida.	850	4.3	63	10.87	1.25	1610	267
T-1183	Mountain Home, Ida.	1000	4.2	65	10.26	0.99	1380	270
T-1214	Black's Creek, Ada Co., Ida.	1100	4.2	49	7.99	1.04	1200	294
mean		**950**	**4.1 c**	**55 a**	**9.31 a**	**1.17 a**	**1406 a**	**281 b**

[#] taxa means followed by different letters in the same column are significantly different at $P < 0.05$.

onomic relationship between *californicus* and *elymoides*, as favored by Wilson (1963).

Data set 2

In the greenhouse trial, *multisetus* emerged faster, had longer leaves at 17 days, and had greater total plant dry-matter at harvest than the other 2 taxa (Table 4). *Brevifolius* emerged most slowly from a 5-mm planting depth and *elymoides* had the least total plant dry-matter. Root-to-shoot ratio was least for *brevifolius* and greater for *multisetus* and *elymoides*. Specific root length was greater for *brevifolius* (thin roots), especially group B (see below), than for *multisetus* or *elymoides*. *Multisetus* had the greatest root length with *brevifolius* intermediate and *elymoides* least. In the field trial (Table 5), *elymoides* had the earliest heading date, the lowest seed mass, and the shortest height. *Brevifolius* and *multisetus* did not differ from one another for these traits.

The first 2 principal components explained 41 and 40% of the variation, respectively, among accessions for the 9 traits. Loadings for Principal Component 1 indicate that accessions with high Principal Component 1 scores had generally greater total plant dry-matter, lower root-to-shoot ratio, and greater root length at harvest in the greenhouse trial; and later heading date, greater height, and greater seed mass in the field (Table 3). Principal Component 1 separated *brevifolius* and *multisetus* (high scores) from *elymoides* (low scores) (Fig. 2). Loadings for Principal Component 2 indicate that accessions with higher Principal Component 2 scores had generally more rapid emergence at a 5-mm planting depth; greater leaf length on day 17 and greater total plant dry-matter, greater root length, and lower specific root length (thicker roots) at harvest in the greenhouse trial. Principal Component 2 separated *multisetus* (high scores) from *elymoides* and *brevifolius* (low scores). This separation resulted in plots that oriented the 3 taxa in a similar manner to data set 1 (Fig. 1). Variation among accessions was greater for *brevifolius* than the other 2 taxa; this was reflected mostly by Principal Component 1 scores.

Together, Principal Components 1 and 2 separated *brevifolius* accessions into 3 groups (Fig. 2). "Group A" accessions were late-maturing with high-seed mass and originated from medium to high elevations (1850 to 2600 m) in Colorado, New Mexico, and Arizona. "Group B" accessions were early-maturing (as early as *elymoides*) with low-seed mass and originated from high elevations (2150 to 2750 m) in Colorado and Utah. "Group C" accessions were intermediate-maturing with low-seed mass and originated from low to medium elevations (1350 to 1600 m) in southern Idaho. Amplified fragment length polymorphisms (AFLP), a DNA marker technique, have verified that these 3 groups are genetically distinct (Larson et al. 2003).

In the greenhouse (Table 4), days to emergence were generally lesser for Group C accessions and more similar to *elymoides* than were Group A or B accessions. Total plant dry-matter was generally greatest for Group A accessions, least for Group B accessions, and intermediate for Group C accessions. Root-to-shoot ratio

Table 5. Means for 10 elymoides, 21 *brevifolius*, and 16 *multisetus* squirreltail accessions in data set 2 for 6 traits in a 2-year field trial.

Taxon/ Accession	Heading date	Plant height	Seed mass
	(days after 4/30)	(m)	(mg seed^{-1})
elymoides			
T-1173	21	0.28	2.21
T-1174	21	0.32	2.37
T-1175	22	0.31	2.16
T-1191	18	0.28	3.29
T-1192	20	0.27	2.83
T-1193	15	0.38	2.36
T-1198	20	0.48	2.91
T-1223	26	0.42	3.01
T-1224	24	0.42	2.73
PI 619553	23	0.38	3.05
mean	**21 b**	**0.35 b**	**2.69 b**
multisetus			
PI 619454	44	0.53	4.88
PI 619456	42	0.58	5.50
PI 619457	42	0.58	4.72
PI 619458	42	0.68	5.83
PI 619459	41	0.53	5.05
PI 619460	42	0.58	5.01
PI 619461	41	0.64	5.18
PI 619462	45	0.65	5.07
PI 619463	45	0.57	4.72
PI 619464	44	0.63	4.87
PI 619465	42	0.61	5.14
PI 619467	42	0.56	4.62
PI 619564	42	0.66	4.87
T-1165	33	0.53	4.15
T-1183	41	0.62	5.39
T-1214	41	0.60	5.49
mean	**42 a**	**0.59 a**	**5.03 a**
brevifolius			
group A			
T-1180	60	0.66	4.81
T-1233	62	0.64	4.51
T-1238	47	0.75	5.10
T-1239	49	0.75	5.34
T-1242	42	0.77	5.36
T-1249	46	0.68	5.71
T-1260	51	0.53	4.58
T-1264	65	0.71	4.86
T-1265	60	0.71	5.02
T-1271	57	0.72	5.23
T-1272	57	0.72	5.48
T-1277	53	0.63	4.51
T-1299	63	0.66	6.16
(mean)	(55)	(0.68)	(5.13)
group B			
T-1228	23	0.51	3.39
T-1243	24	0.53	3.77
T-1245	17	0.58	3.37
(mean)	(21)	(0.54)	(3.51)
group C			
T-1202	34	0.50	3.75
T-1203	32	0.54	3.74
T-1204	34	0.58	4.61
T-1205	38	0.62	3.47
T-1206	38	0.60	3.27
(mean)	(35)	(0.57)	(3.77)
mean	**45 a**	**0.64 a**	**4.57 a**

#taxa means followed by different letters in the same column are significantly different at $P < 0.05$.

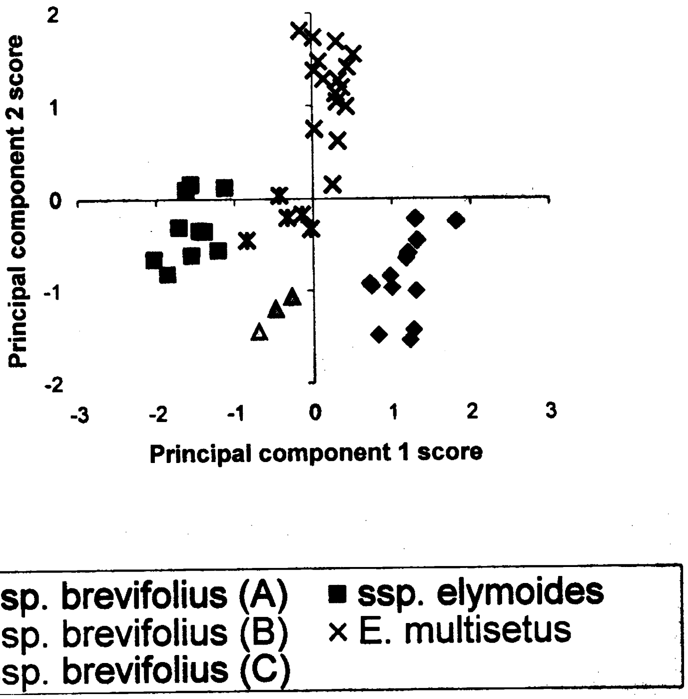

Fig. 2. Plot of the first 2 principal component scores for 47 *Elymus elymoides* and *E. multisetus* squirreltail accessions in data set 2.

was generally lower for Group A accessions than Group B or C accessions, which were more similar to *elymoides* and *multisetus*. Specific root length was generally greater for Group B accessions than Group A or C accessions, which were more similar to *elymoides* and *multisetus*. In the field trial (Table 5), seed mass was generally greater for Group A accessions, which were more similar to *multisetus*, than Group B or C accessions, which were more similar to *elymoides*. Plant height was generally greater for Group A accessions than Group B or C accessions, which were more similar to *multisetus*, which in turn was greater than *elymoides*.

While the geographical range of Group C is clearly separate from Groups A and B, Groups A and B themselves are overlapping and may occur as biotypes at the same site. Accession T-1245, a group B accession originating northwest of Almont, Colo., was collected at the same site as T-1308, which was not included in data set 2, but has been confirmed as a Group A accession based on its AFLP profile (Larson et al. 2003). Likewise, T-1264, a Group A accession originating north of Colmor, N.M., was collected from the same site as T-1309, also not included in data set 2. Based on its early maturity (unpublished data), however, T-1309 is likely a Group B accession.

Relative to Group A, Group B is earlier in maturity, is shorter, and has greater root-to-shoot ratio, greater specific root length (thinner roots), lower total plant dry-matter, and lower seed mass. We wonder whether some or all of these traits may be associated with adaptation to higher elevations. In fact, T-1243 (Powderhorn, Colorado), a Group B accession, was collected at 2,750 m, the highest elevation of any accession. While our elevation data (Table 4) do not directly support this speculation, we may have missed a trend by failing to collect at higher elevations than we did.

Conclusions

In both data sets, the 3 squirreltail taxa were easily separated by the traits examined. Data set 1 had 13 traits and data set 2 had 9 traits. The 8 traits in common to both data sets were days to emergence from 5 mm; leaf length (at 10 days in data set 1 and 17 days in data set 2), total plant dry-matter, root-to-shoot ratio, root length, and specific root length at harvest; heading date; and seed mass. In addition to the 8 traits in common, data set 1 included leaf area, specific leaf area, days to emergence from 20 mm, days to emergence from 60 mm, and nitrate reductase activity. In addition to the 8 traits in common, data set 2 included plant height. With 1 exception (root-to-shoot ratio) the 2 data sets ranked the taxa in the same order for all 8 common traits. However, for 3 of these traits (root-to-shoot ratio, root length, and specific root length), significant differences among taxon means were slightly different. For root-to-shoot ratio, data set 1 grouped middle-ranking *elymoides* with lowest-ranking *breviolius*, while data set 2 grouped highest-ranking *elymoides* with middle-ranking *multisetus*. For root length, data set 1 grouped lowest-ranking *elymoides* with middle-ranking *brevifolius*, while data set 2 grouped lowest-ranking *elymoides* apart from middle-ranking *brevifolius*. For specific root length, data set 1 grouped all 3 taxa together, while data set 2 separated highest-ranking *brevifolius* apart from *elymoides* and *multisetus*.

Of all taxa, *elymoides* was the earliest, shortest, and had the lowest seed mass, seedling dry-matter, and root length. *Brevifolius* had the lowest root-to-shoot ratio, specific leaf area, and nitrate reductase activity, the highest specific root length, and generally the slowest emergence from a normal planting depth. Low specific leaf area is associated with high carbon investment and great leaf life-span (Reich 1997). *Multisetus* had the fastest emergence from a normal planting depth, longest leaf length at 10 days (data set 1) or 17 days (data set 2) post-plant, and greatest seedling dry-matter, leaf area, and root length.

Wilson (1963) stated that *brevifolius* displays the greatest ecological diversity of the 5 squirreltail taxa, being found in desert to montane habitats from 600 to 3000 m elevation and with extreme variation in size. Variation among accessions was similar for the 3 taxa in data set 1, but *brevifolius* had the greatest variation in data set 2, perhaps because these *brevifolius* accessions represented a wider geographical distribution than the other 2 taxa. Nevertheless, we found a greater degree of discontinuity, e.g., Groups A, B, and C, within *brevifolius* than within *multisetus* or *elymoides*. In data set 2, accessions that plotted near the convergence of the 3 taxa were from the environs of southern Idaho, a region with ample representation of all 3 taxa. Overall, Group C accessions were more similar to *elymoides* and *multisetus* than were Group A or B accessions (Fig. 2).

Five *brevifolius* accessions in data set 1 can be reinterpreted based on findings of data set 2 and subsequent AFLP analysis (Larson et al. 2003). Three late-maturing, high seed-mass accessions, 9040189, 904187, and PI 531605, qualify as Group A, according to AFLP data. While no AFLP data have been collected on the fourth accession, Acc:1123, it appears to be a member of Group C based on its Oregon origin, fast emergence (Table 1) and low seed mass (Table 2). It should be noted, however, that its heading date is similar to the 3 Group A accessions. The fifth accession, Acc:1130 (Savageton, Wyo.), is unique in this study. Based on AFLP results, it belongs to "Group D", accessions of which we have collected on the High Plains from Alberta to Colorado.

Our data support the recognition of *elymoides, brevifolius,* and *multisetus* taxa, but they do not provide direction as to whether each merits specific or subspecific rank. From an ecological perspective, these data do not support the suggestion that any one pair of *elymoides, multisetus,* and *brevifolius* is more similar than any other pair. Furthermore, these results provide guidance as to which specific commercially available plant materials should be planted in which locations. For example, the 3 distinct groups of *brevifolius* accessions, as well as the different taxa, are ecologically distinct and are likely adapted to regions in which their particular group is found in nature. These results reflect the highly ecotypic nature of the squirreltails.

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Nitrogen and row spacing on *Digitaria eriantha* production and digestibility

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Abstract

Research on the effects of the rate and method of fertilizer application or row spacing on dry matter yield and digestibility of perennial forage crops either is scarce or has produced contradictory results. The objective of this study was to determine the effects of various rates of N fertilization, method of fertilizer application and row spacing on dry matter yields and in vitro dry matter digestibility (IVDMD) in the cultivated, perennial forage grass *Digitaria eriantha* Steud. subsp. *eriantha* cv. Irene. Field studies were conducted on a petrocalcic Ustipsament, sandy loam soil. The total annual N fertilizer (0, 50 or 100 kg ha^{-1}) was applied once (in early spring) or split (half in early spring, half in early summer) on rows 0.3 or 0.5 m apart. Plants were clipped, leaving 50 mm of stubble, whenever they reached 260–280 mm height during the 1998–1999 and 1999–2000 growing seasons. All fertilized treatments produced higher ($P < 0.05$) dry matter yields than unfertilized controls. Averaged across both seasons, annual dry matter yields were 3.5, 5.2, and 6.0 Mg ha^{-1} for 0, 50, and 100 kg ha^{-1} N treatments, respectively. Dry matter yields during summer were greater ($P < 0.05$) under split than single application. Row spacing did not affect dry matter yield. Although small, increases in IVDMD due to fertilization were significant ($P < 0.05$). Mean IVDMD was 602, 633, and 656 g kg^{-1} for N fertilization rates of 0, 50, and 100 kg ha^{-1}. It is suggested that N application should be between 50 and 100 kg ha^{-1} for *D. eriantha*, and that this application should be split rather than applied at one time in early spring.

Key Words: forage yield and quality, perennial forage grasses, semiarid Argentina, fertilization

Resumen

Las investigaciones sobre los efectos de la forma de aplicación de fertilizantes o espaciamiento entre hileras en la producción y digestibilidad de la materia seca en especies forrajeras cultivadas perennes son escasas o han producido resultados contradictorios. El objetivo de este estudio fue determinar los efectos de varias tasas de fertilización nitrogenada, forma de aplicación del fertilizante y espaciamiento entre hileras en los rendimientos de materia seca y en la digestibilidad in vitro de la materia seca (DIVMS) en la gramínea forrajera cultivada perenne *Digitaria eriantha* Steud. subsp. eriantha cv. Irene. Los estudios fueron conducidos a campo en un suelo perteneciente al subgrupo Ustipsament petrocálcico. La fertilización total anual de N (0, 50, ó 100 kg ha^{-1}) fue aplicada de una sola vez a principios de primavera o dividida, la mitad a principios de primavera y la otra mitad a principios del verano, en hileras separadas 0.3 ó 0.5 m entre sí. Las plantas fueron cortadas a 50 mm desde el nivel del suelo toda vez que alcanzaron 260–280 mm de altura durante las estaciones de crecimiento de 1998–1999 y 1999–2000. Todos los tratamientos fertilizados mostraron una mayor ($P < 0.05$) producción de materia seca que los controles no fertilizados. Los rendimientos de materia seca anuales fueron 3.5, 5.2, y 6.0 Mg ha-1 en los tratamientos no fertilizados y en aquellos que recibieron 50 y 100 kg ha^{-1}, respectivamente en promedio para ambas estaciones. Los rendimientos de materia seca durante el verano fueron mayores ($P < 0.05$) cuando la aplicación del fertilizante fue dividida que cuando se efectuó de una sola vez. El espaciamiento entre hileras no afectó los rendimientos de materia seca. Aunque pequeños, los incrementos en la DIVMS debidos a la fertilización fueron significativos ($P < 0.05$). La DIVMS promedio fue de 602, 633, y 656 g kg^{-1} para tasas de fertilización nitrogenada de 0, 50 y 100 kg ha^{-1}. Se sugiere que la fertilización con N en *D. eriantha* debería oscilar entre 50 y 100 kg ha^{-1} y que la aplicación fuera preferiblemente dividida en vez de una sola vez a principios de primavera.

Digitaria eriantha Steud. subsp. *eriantha* cv. Irene is of the warm-season perennial forage grasses utilized in livestock production systems of semiarid environments. This species, native to South Africa (Rethman et al. 1997), has a great adaptive capacity, a high production potential and a clear, positive response to N fertilization (Rethman 1987, Dannhauser 1991, Pieterse and Rethman 1995). It has not, however, always produced satisfactory responses in terms of animal production. While Grunow et al. (1984) reported improved individual and per hectare weight gains in cattle, production increases were scarce in sheep (Van Vuuren et al. 1997). In Argentina, promising responses in terms of forage production have been obtained for this species in the Provinces of La Pampa and San Luis (Stritzler et al. 1986, Veneciano and Terenti 1997), while in Buenos Aires Province experimental information has become available only in the last few years (Gargano et al. 2001a, 2001b). These responses in forage yields are due to an improved management of *D. eriantha.*

The method of N fertilization of *D. eriantha* has produced some contradictory results on dry matter yields. Rethman (1987) rec-

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ommended split N fertilization for this species to adjust rates of N fertilizer to precipitation regimes. Other authors have fertilized *D. eriantha* by applying 127 kg ha^{-1} N in 3 unequal amounts during November through February based upon the phenology of this species (Veneciano and Terenti 1997). However, Pieterse and Rethman (1995) suggested that N fertilization of *D. eriantha* should be made once during the growing season. Their suggestion was based on the observation that split fertilization did not increase productivity in *D. eriantha*. Given that the method of N fertilization has produced such contradictory results, we decided to test whether split or at once application of N during the growing season would improve dry matter yields in *D. eriantha.*

Another factor which may influence dry matter yields in the field is row spacing of plants. Although most research evaluating the effects of row spacing on dry matter yields has been conducted on row crops (Natr 1976, Farnham 2001), some studies have been conducted on perennial forage grasses (Kruger and Smit 1974, Muir et al. 2001). Depending on the plant establishment phase, results reported in these studies range from no effect to increases or decreases in dry matter yields as spacing among rows becomes narrower (Muir et al. 2001). Thus, determination of row spacing in productivity of perennial forage crops is important since dry matter yields can be affected. While the effects of N fertilizer have been partially addressed in *D. eriantha* (i.e. Rethman et al. 1987, Pieterse and Rethman 1995), row spacing and quality have not in this species, which makes our study unique in this regard.

The objective of this study was to determine the effects of different rates of N fertilization, method of fertilizer application and row spacing on *D. eriantha* forage production and quality. These studies will advance the knowledge of this species' performance under varying management conditions.

Materials and Methods

Study Area

Field experiments were conducted over 2 years (1998–1999 and 1999–2000) at the Universidad Nacional del Sur research facility in Bahía Blanca (38° 48'S, 62° 13'W), Argentina. Soil belongs to the subgroup petrocalcic Ustipsament (USDA 1999). It has a sandy-loam texture, and is low in organic matter and highly susceptible to wind erosion (Sánchez and Kruger 1981). A meteorological station located at the study site provided rainfall and temperature data. During the 7-month growing period (September through March), rainfall was 448 mm in 1998–1999 and 469 mm in 1999–2000. Average annual rainfall during the last 10 years is 483 mm for the same period (Servicio Meteorológico Nacional 2000).

Experimental Procedures

Experimental plots were disked in June 1997, harrowed in mid-October, and the seed bed was then hand-smoothed using a rake. Plots were seeded on 23 Oct. 1997 using a manual monofurrow machine which allowed control of seeding depth, and had a wheel to produce compaction of the row. Pelleted seeds with 60% cultural value (% seed purity x % germination) were seeded at a depth of 0.015 m and rate of 4 kg ha^{-1}. From seedling emergence onward, weeds were controlled by hoeing.

Experimental Design and Treatments

The experiment was a split-plot in a randomized complete block design with row spacing and N fertilization rates as main plots and method of fertilization as subplots. Nitrogen was applied at 0, 50, and 100 kg ha^{-1} during each season on row spacings of 0.3 or 0.5 m. The total amount of N was applied as urea (46-0-0) either all at once in early spring (22 September in 1998/1999; 23 September in 1999/2000) or split applied: half in early spring and the other half in early summer (22 December in both years). Timing of urea applications were made to coincide with a rainfall or irrigation event equivalent to 3-4 mm to allow for its disolution and penetration in the soil. Blocks were 5 m apart one from another. Each of the 3 blocks was composed of 6 main plots: 3 plots were 4.5 x 1.2 m each with row spacings of 0.3 m, and the other 3 plots were 4.5 x 2.0 m each with row spacings of 0.5 m.

The experimental design in spring used blocks with unequal number of replicates because N application was fractionated (Table 1). We used a 2-way ANOVA to analyze this information. There were 8 treatments as a result of combining 4 rates of N fertilizer (0, 25, 50, and 100 kg ha^{-1} N) and 2 row spacings (Table 1). The 25 kg ha^{-1} N rate was the result of spring and summer split application of 50 kg ha^{-1} N. As a result, each row spacing had 2 subplots (replicates) of the 0 and 50 kg ha^{-1} N and 1 subplot (replicate) of the 25 and 100 kg ha^{-1} N within each block (see Table 1). The experimental design during summer and that resulting from applying N all at once in early spring was split blocks; each block remaining was divided into 12 subplots, 1 per treatment. We thus used a 3-way ANOVA for studying summer and total results (3 rates of N fertilizer x 2 row spacings x 2 methods of fertilizer application). There were 3 replicates, 1 per block, for each treatment combination.

Table 1. Total annual amount of N fertilization, and rate of N application when the fertilizer was applied split or all at once at row spacings of either 30 or 50 cm.

Total annual amount of N	Split		At once
	Spring (Sp)	Summer (Su)	Spring (Sp)
	------ (kg ha^{-1}) ------		
0	0	0	0
50	25	25	50
100	50	50	100

Measurements and Analytical Procedures

Forage grown during 1997-1998 was clipped to 50-mm stubble height during mid- winter (August) and removed from the plots, prior to spring regrowth in 1998. Thus, only current-year growth was included in each season. Subsequently, plants were clipped to 50 mm stubble whenever they reached 260–280 mm height during the growing season. Spring or summer dry matter yields include all clippings made from September to mid-December or mid-December to early April, respectively. Total annual dry matter yield was calculated by summing up yields of spring plus summer. The first clipping took place on 25 October in 1998 and 16 November in 1999. The average number of spring harvests was 3.5 in 1998 and 2.0 in 1999. Total number of harvests ranged from 7 to 9 during 1998-1999 and 4 to 5 during 1999–2000 (see Fig. 1). All plant material clipped within each plot at a distance of 0.5 m from its periphery was discarded. The remaining forage within each plot was used for dry matter determinations. Dry matter yield and IVDMD were measured on forage harvested in spring or summer. Harvested forage was dried at 60° C and weighed. Forage samples coming from either spring or summer harvests were combined for each subplot within each season and ground to pass a 1 mm-mesh screen for analysis of IVDMD following Barnes (1966). In vitro dry matter digestibility of total annual dry matter yield was calculated from spring and summer determinations. Digestible dry matter yields were calculated by multiplying dry matter yields and IVDMD.

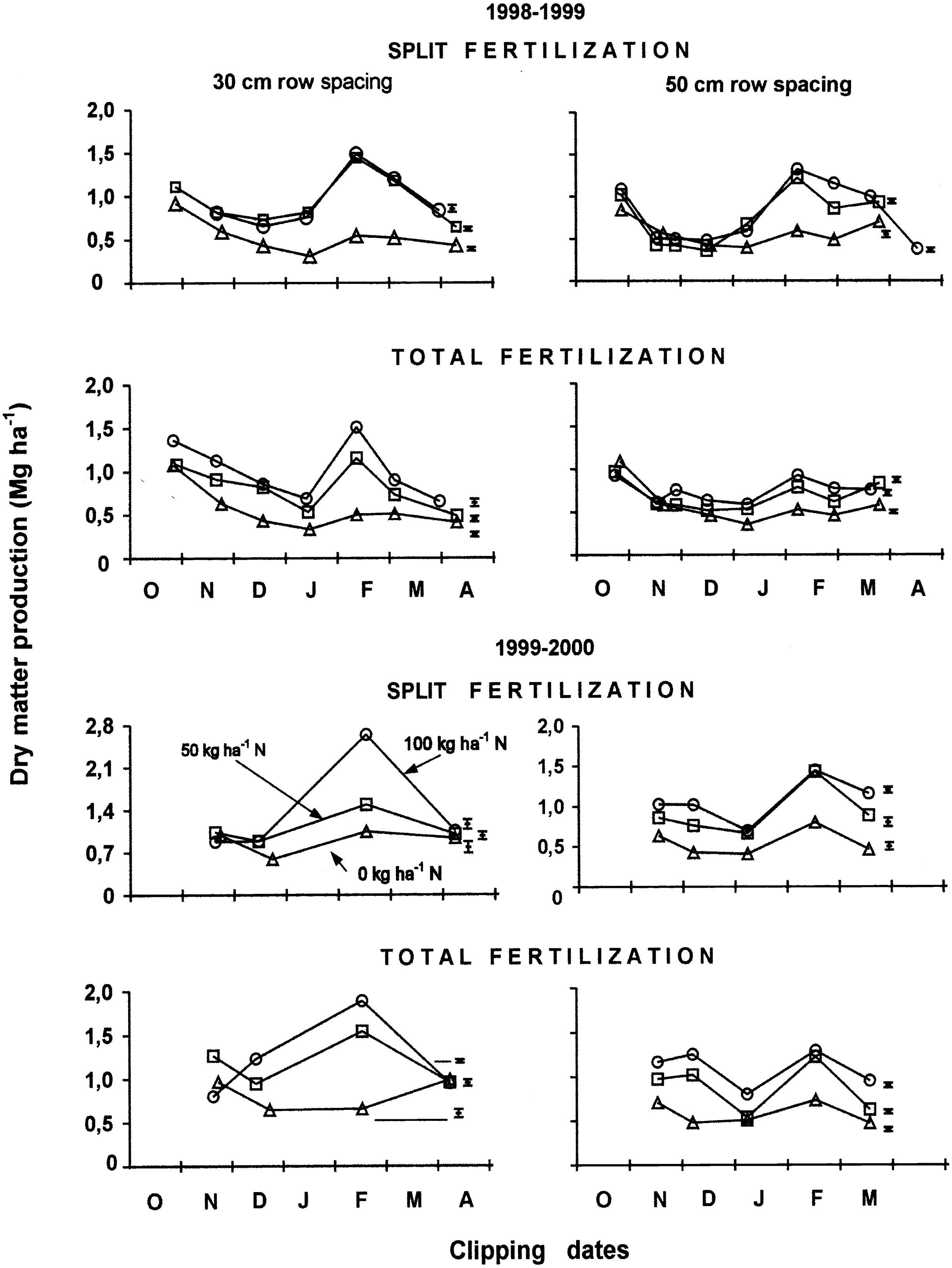

Fig. 1. Dry matter yields at each clipping date as affected by row spacing and method and rate of N fertilization during 1998-99 and 1999-00. Each value is an average of n = 3. Vertical bars indicate 2x the average SE of the means for each N fertilization rate. Note the change of scale in 1999-00 under split fertilization and 0.3 m row spacing.

Statistical Analysis

Spring determinations were analyzed using 2-way ANOVA with unbalanced blocks but proportional replicates. A 3-way ANOVA with split blocks was used to analyze summer and total annual yields and IVDMD. When interactions occurred, multiple comparisons were conducted using the combined mean square error which was obtained from the formula of Satterthwaite (Steel and Torrie 1988). Yield and IVDMD differences were determined using the least significant difference test, although a t test was used when average dry matter yields under split fertilization were compared with those under single fertilization.

Results and Discussion

Dry Matter Yields

Spring and summer were analyzed separately since treatments interacted significantly ($P < 0.05$) with seasons for spring, summer or total annual dry matter yields. A significant ($P < 0.05$) interaction was also found between rate of N fertilizer and row spacing in the spring of 1998–1999 and 1999–2000 (Table 2). Except at 0.3 m row spacing, for which N fertilization rates of 25 and 50 kg ha^{-1} did not differ ($P > 0.05$), spring dry matter yields increased ($P < 0.05$) as fertilization rates increased in both row spacings during 1998–1999 (Table 2). Yield increase with increased N fertilization is a frequent response in cultivated perennial grass species, although plant responses to fertilization are highly dependent on subsequent precipitation levels (Hernández 1991, Pieterse and Rethman 1995, Jacobsen et al. 1996, Veneciano and Terenti 1997). Total spring yields at 0.3 m row spacing were similar or greater, but not lower, than those at 0.5 m (Table 2). Muir et al. (2001) reported that biomass decreased as row spacing increased during plant establishment years in *Panicum virgatum*. These authors suggested that it may be advantageous to plant *P. virgatum* in narrow rows (aproximately 0.25 m) to maximize production during establishment. Narrow row spacing, however, may decrease biomass production during some years after establishment in this species (Muir et al. 2001). The advantage of narrow row spacing during the establishment years, nevertheless, may outweight disadvantages in later years.

In spring, dry matter yields were lower in 1999–2000 than in 1998–1999 (Table 2). This may be due to a couple of reasons. First, plants clipped in spring 1999 had been clipped in the previous spring. Several studies have shown that repeated clipping of the same plants over consecutive years will reduce dry matter yields of perennial grasses (Stout et al. 1981, Becker et al. 1997). Second, there was a wider range between temperature extremes in October during the second than the first season. Even though October is often a temperate month (Servicio Meteorológico Nacional 2000), absolute maximum temperatures reached 35° C and absolute minimum temperatures fell below freezing in October 1999. As a result, the first clipping was delayed and the total number of spring clippings was lower (Fig. 1) in 1999 than in 1998. Similar results of increased dry matter yields with increased N fertilization were obtained in 1999–2000 for both row spacings (Table 2). Except at the highest rate of N fertilization, 1999–2000 spring yields were similar or greater at 0.3 than 0.5 m row spacing (Table 2). Narrower row spacings on herbaceous crop and perennial grass species may lead to less competitive, reduced detrimental effects from weeds on dry matter production, and contribute to greater soil cover which in turn may reduce soil erosion (Young 1956, Akobundu and Ahissou 1985, Muir et al. 2001).

Table 2. Spring dry matter yields as influenced by row spacing and N fertilization rates in 1998–99 and 1999–00. Values are means ± 1 standard error.

	Row	N fertilization rates (kg ha^{-1})			
Season	spacing	0	25	50	100
	(m)	(Mg ha^{-1})			
1998–99	0.3	2.0 ± 0.04 ab†	2.7 ± 0.05 c	2.6 ± 0.06 c	3.3 ± 0.12 e
	0.5	2.0 ± 0.02 a	2.2 ± 0.06 b	2.6 ± 0.02 c	2.9 ± 0.06 d
1999–00	0.3	1.6 ± 0.04 b	1.9 ± 0.03 c	2.0 ± 0.02 c	2.0 ± 0.02 c
	0.5	1.1 ± 0.02 a	1.6 ± 0.06 b	2.0 ± 0.03 c	2.4 ± 0.06 d

†Within each season, means followed by a different letter are significantly different ($P < 0.05$) according to the Least Significant Difference Test.

During summer, fertilization rate and row spacing interacted significantly ($P < 0.05$) within each method of fertilization and season. In 1998–1999, dry matter yields were greater ($P < 0.05$) on fertilized than on unfertilized plots for all treatments (Table 3). Except at 50 kg ha^{-1} under split fertilization and 0.3 m row spacing ($P > 0.05$), highest ($P < 0.05$) dry matter yields were obtained when applying 100 kg ha^{-1} N (Table 3). Increases in average dry matter yields were greater ($P < 0.05$) under split than single fertilization (Table 3). Similar to spring, summer dry matter yields were similar or greater, but not lower, during the 1998–1999 than the 1999–2000 season (Table 3). This was due, at least partially, to the drier summer in the second season. No rainfall occurred for 38 days from 16 December 1999. In addition, number of clippings were lower in summer 1999–2000 than in the previous growing season. Dry matter yields also increased ($P < 0.05$) with increasing rates of fertilization in all treatments during 1999–2000 (Table 3). During this period, average dry matter yield was more than 13% greater ($P < 0.05$) with split than single fertilization (Table 3). Dry matter yields were 71% greater under split or 60% greater under single fertilization compared with unfertilized controls.

Table 3. Summer dry matter yields as influenced by row spacing, and method and N fertilization rates in 1998–99 and 1999–00. Values are means ± 1 standard error.

	Method of N	Row	N fertilization rates (kg ha^{-1})		
Season	fertilization	spacing	0	50	100
		(m)	(Mg ha^{-1})		
1998–99	Split	0.3	1.8 ± 0.03 a†	4.1 ± 0.07 d	4.3 ± 0.12 de
		0.5	2.2 ± 0.07 b	3.7 ± 0.07 c	4.4 ± 0.06 e
	Single	0.3	1.8 ± 0.06 a	2.9 ± 0.07 bc	3.8 ± 0.07 d
		0.5	1.9 ± 0.04 a	2.8 ± 0.09 b	3.0 ± 0.05 c
1999–00	Split	0.3	2.0 ± 0.14 b	2.5 ± 0.06 c	3.7 ± 0.10 f
		0.5	1.7 ± 0.06 a	3.0 ± 0.03 d	3.3 ± 0.05 e
	Single	0.3	1.6 ± 0.09 a	2.5 ± 0.04 b	2.8 ± 0.05 c
		0.5	1.7 ± 0.03 a	2.4 ± 0.01 b	3.0 ± 0.03 d

†Within each method of N fertilization and season, means followed by a different letter are significantly different ($P < 0.05$) according to the Least Significant Difference Test.

Results obtained regarding the method of fertilization of *D. eriantha* have been contradictory (Rethman 1987, Pieterse and Rethman 1995, Veneciano and Terenti 1997). Present study demonstrated that dry matter yields of this species were greater when N application was split than when it was applied at once, which may be associated with better fertilizer utilization efficiency. It is likely that fertilizer fractioning during the growing season diminishes N losses through ammonia volatilization and/or leaching (Vlek et al. 1981, Garwood 1988, Mazzarino et al. 1998). Application costs, however, double when the same amount of fertilizer is applied at 2 different times rather than at once during the growing season. This study also showed that there was not a clear effect of row spacing on dry matter yield (e.g., in 1998–1999: Table 3).

Fertilization increased ($P < 0.05$) total annual dry matter yields in all treatments during both seasons, although differences between 50 and 100 kg ha^{-1} were not always significant (Table 4). Increased dry matter production in *D. eriantha* after N fertilization has been observed under different environmental conditions, using various sources and rates of N fertilizer, and after fertilizing at different times during its growing season (Pieterse and Rethman 1995, Veneciano and Terenti 1997, Gargano et al. 2001a). In fact, N application appears necessary to obtain dry matter yields greater than those found on unfertilized controls (mean = 3.5 Mg ha^{-1}). In a recent 4-year study, Gargano et al. (2001b) reported an average dry matter yield of 3.6 Mg ha^{-1} at the same experimental site when no N was applied. Some studies have reported on N fertilization rates which are economically feasible for this species (Grunow and Rabie 1985, Rethman 1987). Similar N rates to those used in our study increased dry matter yields in *Eragrostis curvula*, another perennial tussock grass species in semiarid Argentina (Hernández 1991). Average dry matter yields were sufficiently greater under split than single N fertilization during the 1998–1999 summer as to obtain greater ($P < 0.05$) total annual dry matter yields (Table 4). During the second season, however, average dry matter yield differences among fertilization methods were not as great so that total yields were similar ($P > 0.05$).

In Vitro Dry Matter Digestibility

There was no interaction ($P > 0.05$) between season and treatment for spring, summer or mean annual IVDMD. As a result, average values for both seasons are reported. Spring IVDMD differed ($P < 0.05$) with fertilization rates but not with row spacings (Table 5). Unfertilized controls showed a lower ($P < 0.05$) IVDMD than any of the fertilized treatments. The highest value was obtained when applying 100 kg ha^{-1} N but it was only 25 g kg^{-1} greater than the average of the other 2 rates of N fertilizer.

During summer, only the main effects rate of N fertilizer and row spacing were significant ($P < 0.05$). Row spacing only differed ($P < 0.05$) when N was applied once. Differences among average values of summer IVDMD under 0, 50, and 100 kg ha^{-1} N (Table 6) followed the same pattern as observed for spring (Table 5). Other workers have reported a small or even no response of IVDMD to fertilization under rates of N fertilizer, similar or greater than those used in our study, applied on forage at different phenological stages (Grunow and Rabie 1985, Veneciano and Terenti 1997) or on deferred pastures (Gargano et al. 2001a).

Nitrogen fertilization rates and row spacing interacted significantly ($P < 0.05$) within each method of fertilization for mean annual IVDMD (Table 7). As verified for spring and summer sampling, IVDMD increased as N fertilization rates increased (Table 7). Under split fertilization, erratic responses were obtained when comparing row spacings (Table 7). When fertilizer was applied at one time, however, IVDMD was greater ($P < 0.05$) at 0.5 than at 0.3 m row spacing only in the 0 and 100 kg ha^{-1} N treatments (Table 7).

Effects of treatments on digestible dry matter yields are not presented because they were practically identical to those reported for dry matter yields.

Table 4. Total dry matter yields as influenced by row spacing, and method and N fertilization rates in 1998–99 and 1999–00. Values are means ± 1 standard error.

Season	Method of N fertilization	Row spacing	N fertilization rates (kg ha^{-1}) 0	50	100
		(m)	-(Mg ha^{-1})-		
1998–99	Split	0.3	3.8 ± 0.07 a†	6.7 ± 0.11 d	6.7 ± 0.04 d
		0.5	4.0 ± 0.02 b	5.9 ± 0.09 c	7.0 ± 0.07 e
	Single	0.3	3.9 ± 0.06 a	5.7 ± 0.11 c	7.1 ± 0.08 e
		0.5	4.0 ± 0.08 a	5.4 ± 0.09 b	6.0 ± 0.08 d
1999–00	Split	0.3	3.6 ± 0.09 b	4.4 ± 0.08 c	5.5 ± 0.12 d
		0.5	2.7 ± 0.10 a	4.6 ± 0.04 c	5.3 ± 0.09 d
	Single	0.3	3.3 ± 0.07 b	4.7 ± 0.05 d	4.9 ± 0.04 d
		0.5	2.9 ± 0.02 a	4.4 ± 0.04 c	5.5 ± 0.03 e

†Within each method of N fertilization and season, means followed by a different letter are significantly different ($P < 0.05$) according to the Least Significant Difference Test.

Table 5. In vitro dry matter digestibility in spring as influenced by row spacing and N fertilization rates. Within each row spacing, values are averaged from both seasons. Values are means ± 11 standard error.

Row spacing	N fertilization rates (kg ha^{-1}) 0	25	50	100
(m)	(g kg^{-1})			
0.3	590 ± 2.2	634 ± 2.0	644 ± 2.3	664 ± 2.5
0.5	613 ± 2.9	640 ± 1.8	646 ± 2.1	669 ± 2.4
Average	602 ± 2.6 a†	637 ± 1.9 b	645 ± 2.2 b	666 ± 2.4 c

†Means followed by a different letter are significantly different ($P < 0.05$) according to the Least Significant Difference Test.

Table 6. In vitro dry matter digestibility in summer as influenced by row spacing and N fertilization rates within each method of N fertilization. Values are averaged from both seasons. Values are means ± 1 standard error.

Season	Method of N fertilization	Row spacing	N fertilization rates (kg ha^{-1}) 0	50	100
	(m)	-(g kg^{-1})-			
Split	0.3	602 ± 2.8	634 ± 4.1	665 ± 7.7	634 ± 5.0 a†
	0.5	609 ± 1.5	628 ± 6.9	648 ± 3.3	628 ± 4.4 a
Single	0.3	586 ± 4.9	620 ± 4.1	636 ± 2.0	614 ± 5.1 a
	0.5	614 ± 2.0	632 ± 4.5	662 ± 6.9	636 ± 3.8 b
Average			603 ± 2.5 a ‡	624 ± 3.0 b	653 ± 3.1 c

†Within each method of N fertilization, row (†) and column (‡) means followed by a different letter are significantly dif-

Table 7. **Mean annual in vitro dry matter digestibility as influenced by row spacing and N fertilization rates within each method of N fertilization. Values are averaged from both seasons. Values are means ± 1 standard error.**

Seaason	Method of N fertilization	Row spacing	N fertilization rates (kg ha^{-1}) 0	50	100
		(m)-	-(g kg^{-1})-		
	Split	0.3	597 ± 2.9 a †	634 ± 2.3 c	661 ± 6.4 e
		0.5	610 ± 2.3 b	632 ± 3.5 c	648 ± 1.7 d
	Single	0.3	588 ± 4.0 a	627 ± 1.7 c	648 ± 1.8 d
		0.5	615 ± 2.9 b	638 ± 4.6 cd	665 ± 6.9 e

†Within each method of N fertilization, row (†) and column (‡) means followed by a different letter are significantly different ($P < 0.05$) according to the Least Significant Difference Test.

Conclusions

Dry matter yields increased when *D. eriantha* was fertilized with N. Results suggest use of a N fertilization rate between 50 and 100 kg ha^{-1}. Greater dry matter yields were obtained when N fertilization was split than when it was applied at 1-time. Row spacing did not affect dry matter yield. This encourages seeding of *D. eriantha* in 0.3 rather than 0.5 m inter-row spacing which would contribute to reduced competition from weeds and increased soil cover. In vitro dry matter digestibility increased with N fertilization but these increases were of a small magnitude which makes doubtful its biological and/or economical relevance.

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Clubmoss effects on plant water status and standing crop

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Abstract

Clubmoss (*Selaginella densa* Rydb.), a low growing, vascular cryptogam forms carpet-like mats that cover up to 80% of the ground in the Northern Mixed Prairie. Many range managers believe clubmoss competes with grasses for water or intercepts precipitation and negatively affects plant water relations and productivity. The objective of these studies was to test the hypothesis that precipitation has greater effects on leaf xylem water potentials (Leaf$_{xwp}$) and plant productivity than clubmoss. Studies examined the effects of clubmoss on Leaf$_{xwp}$ of Junegrass (*Koeleria cristata* Pers.) and blue grama (*Bouteloua gracilis* [HBK.] Lag.), and productivity of forbs and graminoids by: 1) irrigating or reducing precipitation relative to natural precipitation; 2) removing clubmoss relative to clubmoss present, and; 3) irrigating with 0.0 to 25 mm of water when clubmoss was present or removed. Leaf$_{xwp}$ of Junegrass and blue grama were unaffected by clubmoss through the growing season (P = 0.33), but Leaf$_{xwp}$ were lowest (P $\leq$ 0.05) when precipitation was reduced relative to the control and when irrigating. Standing crop of forbs was similar in the control and clubmoss removal treatment (P = 0.22) and among precipitation treatments (P = 0.13), averaging 28 g m^{-2} (SE = 2.2). Graminoid standing crop was unaffected by clubmoss (P = 0.35) and was greatest (P = 0.02) when irrigated (74 g m^{-2}), intermediate in the control (53 g m^{-2}), and least (36 g m^{-2}) with reduced precipitation (SE = 8.7). Clubmoss did not affect (P = 0.70) total standing crop; total standing crop declined from 102 g m^{-2} when irrigated to 76 g m^{-2} in the control, and 69 g m^{-2} (SE = 9.0) with reduced precipitation. Clubmoss had no influence (P = 0.06) on Leaf$_{xwp}$ when irrigated with 0 to 25 mm of water. The decline in Leaf$_{xwp}$ from 1 to 7 days after irrigation was the product of the interacting effects of the amount of water applied and days after irrigation (P = 0.03). More than 10 mm of irrigation water were required to impart a significant increase (P $\leq$ 0.05) in Leaf$_{xwp}$. The hypothesis that clubmoss reduces productivity of associated plants in the Northern Mixed Prairie by increasing water stress is rejected. Similarly clubmoss does not reduce plant water stress or increase production. Precipitation amounts overshadow any effects clubmoss has on Leaf$_{xwp}$ and plant production. Range managers in the Northern Mixed Prairie may want to consider maximizing the effectiveness of precipitation in this water-limited environment instead of focusing on reducing or attempting to eliminate clubmoss.

Resumen

"Clubmoss" (*Selaginella densa* Rydb.) Es una planta criptógama vascular de bajo crecimiento que forma manchones de plantas semejantes a una alfombra que cubren hasta el 80% del suelo de las Praderas Mixtas del Norte. Muchos manejadores de pastizales creen que el "Clubmoss" compite con los zacates por agua o intercepta la precipitación y afecta negativamente las relaciones hídricas y productividad de los zacates. El objetivo de estos estudios fue probar la hipótesis de que la precipitación tiene mayores efectos en los potenciales hídricos del xilema de la hoja (Hoja$_{xwp}$) y la productividad de la planta que el "Clubmoss" . Los estudios examinaron los efectos del "Clubmoss" en el Hojaxwp de los zacates "Junegrass" (*Koeleria cristata* Pers.) y "Blue grama" (*Bouteloua gracilis* [HBK.] Lag.) y la productividad de hierbas y graminoides mediante: 1) irrigación o reduciendo la precipitación en relación a la precipitación normal; 2) removiendo el "Clubmoss" en relación al presencia del "Clubmoss" y 3) irrigando de 0.0 a 25 mm de agua cuando el "Clubmoss" estaba presente o ausente por remoción. A lo largo de la estación de crecimiento el Hoja$_{xwp}$ del "Junegrass" y el "Blue grama" no fue afectado por la presencia del el "Clubmoss" (P = 0.33), pero los Hojaxwp fueron los mas bajos (P $\leq$ 0.05) cuando la precipitación se redujo en relación al control y cuando fueron irrigados. La biomasa en pie de las hierbas fue similar en los tratamientos control y con remoción de "Clubmoss" (P = 0.22) y entre tratamientos de precipitación (P = 0.13), promediando 28 g m^{-2} (ES = 2.2). La biomasa en pie de las graminoides no fue afectada por el "Clubmoss" (P = 0.35) y fue mayor (P = 0.02) cuando se aplico riego (74 g^{-2}), intermedia en el control (53 g^{-2}) y la mas baja (36 g m^{-2}) con la precipitación reducida (ES = 8.7). El "Clubmoss" no afecto la biomasa total en pie (P = 0.70), la biomasa total en pie disminuyo de 102 g m^{-2} con irrigación a 76 g m^{-2} en el control y 69 g m^{-2} (ES = 9.0) con precipitación reducida. El "Clubmoss" no tuvo influencia (P = 0.06) en el Hoja$_{xwp}$ cuando se aplico riego de 0 a 25 mm. La disminución del Hoja$_{xwp}$ del día 1 al 7 después del riego fue producto de los efectos interactuantes de la cantidad de agua aplicada y los días después del riego (P = 0.03). Mas de 10 mm de agua irrigada fueron requeridos para producir un aumento significativo (P $\leq$ 0.05) en el Hoja$_{xwp}$. Se rechazó la hipótesis de que el "Clubmoss" reduce la productividad de las plantas asociadas en las Praderas Mixtas del Norte al aumentar el estrés hídrico. Igualmente, el "Clubmoss" no reduce el estrés hídrico de las plantas o incrementa la producción. Las cantidades de precipitación sobreponen cualquier efecto que el "Clubmoss" tiene sobre el Hoja$_{xwp}$ y la producción de planta. Los manejadores de pastizales del las Praderas Mixtas del Norte pueden querer considerar el maximizar la efectividad de la precipitación en este ambiente de precipitación limitada en lugar de enfocarse en reducir o intentar eliminar el "Clubmoss" .

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Key Words: *Bouteloua gracilis, cryptogams, Koeleria cristata,* leaf xylem water potentials, microphytic crust, Northern Mixed Prairie, *Selaginella densa*

Clubmoss (*Selaginella densa* Rydb.), a low growing (5–20 mm), non-flowering, and vascular cryptogam grows in carpet-like mats that provide up to 80% ground cover in many plant communities in the Northern Mixed Prairie (Coupland 1950, Heady 1952, Van Dyne and Vogel 1967, Dolan and Taylor 1972). Low water-use requirements enable clubmoss to grow in areas where precipitation is insufficient for sustaining extensive cover of forbs and graminoids (Webster and Steeves 1964). Clubmoss grows over a wide range of sites with low water availability (Van Dyne and Vogel 1967) and in plant communities disturbed by excessive grazing or severe drought (Clarke et al. 1943, Heady 1952). This diminutive perennial generally increases with grazing (Campbell et al. 1962, Smoliak 1965, Van Dyne and Vogel 1967, Smoliak et al. 1972, Abouguendia 1990), but it can decrease when grazing and trampling are intense (Coupland 1950, Van Dyne and Vogel 1967).

The fine roots of clubmoss form an extensive network 2 to 5 cm below the soil surface (Coupland and Johnson 1964). Majorowicz (1963) concluded that clubmoss competes with grasses by absorbing water like a "sponge". Clubmoss may also reduce water availability by intercepting precipitation, with greatest water losses occurring after small precipitation events (Couturier and Ripley 1973). Extensive cover and the dense rooting of clubmoss have led some people to assume that this plant competes with grasses and negatively affects plant water relations and thus productivity, particularly during drought and in environments dominated by small precipitation events (Dolan 1966, Wagner 1966, Taylor 1967, Dolan and Taylor 1972). On the other hand, cover afforded by clubmoss may reduce runoff and erosion, modify soil temperatures, and increase soil organic matter, water infiltration, effectiveness of precipitation, and water availability (Van Dyne and Vogel 1967, Dolan and Taylor 1972, Naeth et al. 1991a, Shay et al. 2000), which may lead to increased plant production.

The objectives of our studies were to determine if clubmoss influences water relations of grasses and plant productivity. We tested the hypothesis that precipitation has greater affects on plant water relations as indicated by leaf xylem water potentials (Leaf_{xwp}) and plant productivity than clubmoss. Studies were designed to contrast the effects on Leaf_{xwp} and productivity by: 1) supplementing precipitation through irrigation or reducing precipitation relative to natural precipitation; 2) removing clubmoss relative to clubmoss present; 3) observing the interactions between 1 and 2 above, and; 4) measuring Leaf_{xwp} following irrigation with 0 to 25 mm of water.

Material and Methods

Study Site Descriptions

Research was conducted at 2 sites, Dundurn and Rudy, about 60 km south of Saskatoon, Saskatchewan in the Dundurn Sandhills (51°31'N, 106° 48'W; 525 m elevation) during the summers of 1997 and 1998. The Dundurn Sandhills formed along the south shore of glacial lake Saskatchewan 11,000 to 14,000 years ago (Christiansen 1979). Both study sites are Sandy Range Sites (Abouguendia 1990) with Dark Brown Chernozemic soils of the Asquith association (Ellis et al. 1970). This soil developed on sandy, glacio-fluvial and lacustrine deposits, and is moderately coarse-textured. Hulett et al. (1966) described the plant communities in this area.

Annual precipitation ranges from 313 to 423 mm in the Northern Mixed Prairie of southern Saskatchewan and Alberta (Table 1). From April through September about 41 to 58% of the daily precipitation events are ≤2.5 mm, and about 84 to 89% of daily precipitation events are ≤10 mm. Annual precipitation at the study sites averages 315 mm, with about 65% received from late-April through September (Environment Canada 1982). Most of this precipitation is received in May and June.

Precipitation totaled 187 mm from September 1996 through April 1997, 10 mm in May, 92 mm in June, 7 mm in July, and 78 mm in August 1997 for a total of 374 mm (Table 2). About 63 mm of precipitation were received from September 1997 through April 1998, with an additional 13 mm received in May, 67 mm in June, 69 mm in July, and 30 mm in August 1998 for a total of 242 mm. Temperatures in this area range from an average of –17° C in January to 19° C in July (Environment Canada 1982). The first month of the year with mean monthly temperatures above 0° C was April in 1997 and 1998; July and August were the warmest months in both years.

Cattle-proof exclosures, about 2 ha in size, were established immediately before applying treatments at each site. Although detailed records of use are not available, cattle had grazed the study sites in late summer to early autumn for many years before our studies were initiated. Annual

Table 1. Annual precipitation and probabilities of daily precipitation events of different sizes during April-September in the Northern Mixed Prairie at 7 locations in Saskatchewan and 4 locations in Alberta. Data are for the period of 1966-1995 (Environment Canada). Column totals may not equal exactly 100% because of rounding errors.

	Location										
Precipitation variable (mm)	Saskatchewan							Alberta			
	Assiniboia	Estevan	Kindersley	Regina	Saskatoon	Swift Current	Val Marie	Brooks	Craigmyle	Lethbridge	Medicine Hat
	Annual precipitation (mm)										
Annual precipitation	398	423	320	379	354	341	329	313	415	402	337
Daily precipitation	Probability of daily precipitation event (%)										
>0-2.5	52.9	54.5	58.3	55.4	56.1	57.6	55.4	40.7	40.7	51.0	54.3
>2.5-5.0	17.9	15.2	17.6	16.6	16.7	17.0	17.7	21.3	19.7	16.6	16.7
>5.0-10.0	14.9	14.3	12.0	14.8	14.9	14.0	14.1	21.2	20.3	16.5	16.5
>10.0-15.0	6.6	7.1	6.3	5.9	5.2	4.7	5.7	7.3	8.6	6.2	6.0
>15.0-20.0	2.2	3.4	2.6	2.3	3.2	3.5	3.7	4.3	4.2	3.9	2.7
>20.0-25.0	2.4	2.0	1.4	1.9	1.4	1.8	1.5	1.9	2.6	2.6	1.6
>25.0-50.0	2.3	3.1	1.5	2.8	2.4	1.4	1.7	3.3	3.4	2.5	1.9
>50.0	0.5	0.3	0.3	0.4	0.2	0.2	0.3	0.1	0.4	0.7	0.4

Table 2. Precipitation (mm) received at Dundurn and Rudy during the study from May through August 1997 and 1998.

Month	Time (days of month)	Precipitation treatment					
		Natural precipitation		Precipitation reduced		Irrigation	
		1997	1998	1997	1998	1997	1998
May	1-5	—[1]	—	—	—	—	—
	6–10	—	—	—	—	—	—
						(40)[2]	(40)
	11–15	0	0	—	0	0	0
	16–20	5	11	—	0	5	11
	21–25	5	0	2	0	5	0
	26–31	0	2	0	0	0	2
June	1-5	0	9	0	0	0	9
	6–10	33	0	0	0	33 (40)	0 (40)
	16–20	15	0	0	0	15	0
	21–25	32	0	0	0	32	0
	26–30	11	58	0	0	11	58
July	1-5	1	59	0	0	1	59
	6–10	4	10	0	0	4 (40)	10 (40)
	11–15	0	0	0	0	0	0
	16–20	0	0	0	0	0	0
	21–25	2	0	0	0	2	0
	26–31	0	0	0	0	0	0
August	1-5	0	0	0	0	0	0
	6–10	7	0	0	0	7 (40)	0 (40)
	11–15	69	12	0	0	69	12
	16–20	0	0	0	0	0	0
	21–25	2	18	0	0	2	18
	26–31	0	0	0	0	0	0
Total		186	179	2	0	346	339

[1] —Data missing.

[2] 40 mm of additional water were supplied by irrigation during this period.

utilization of graminoids was estimated at 70 to 80% (Romo, pers. observ.). Range condition (Abouguendia 1990) was poor (range condition score = 20%) at Dundurn and fair (range condition score = 30%) at Rudy.

Experiment 1—Effects of precipitation and clubmoss on Leaf$_{xwp}$ and standing crop

Two clubmoss treatments, the control and clubmoss removed, were factorially applied in combination with 3 precipitation treatments including natural precipitation, monthly precipitation augmented by irrigation with a single application of 40 mm of water, and precipitation reduced with rainout shelters. These treatments were intended to create a gradient of precipitation to determine if clubmoss or precipitation had greater effects on plant water status. The experimental design was a randomized-complete-block with 4 replications. Clubmoss and precipitation treatments were applied to 3- by 3-m plots with 2-m buffer zones between plots. All measurements were restricted to a 2- by 2-m area centered in each plot.

Plots were established at Dundurn in 1997, and a second set of plots was established in 1998 at Rudy, about 2 km away. Clubmoss treatments were applied once in April 1997 at Dundurn and once in April 1998 at Rudy; cool-season plants were initiating growth at these times. A stiff-toothed garden rake was used to uproot and remove clubmoss. In some areas a small, 3-pronged, hand-held weeding tool was used to remove small patches of clubmoss without disturbing other plants. Standing crop of clubmoss from one, 50- by 50-cm quadrat in each clubmoss removal plot was placed in paper bags, dried at 80° C for 48 hours, and weighed. The total standing crop of clubmoss removed averaged 257 g m^{-2} (SE = 34) at Dundurn and 152 g m^{-2} (SE = 18) at Rudy. No disturbance was applied to control plots.

Basal cover of clubmoss and the amount of bare soil were determined in each 3- by 3-m plot in May 1997 at Dundurn and in May 1998 at Rudy using a point-frame (Coupland 1950). One hundred points were recorded in each plot for a total of 400 points per treatment at each site. In mid-July 1997 and 1998, canopy cover of forbs and graminoids in one 20- by 50-cm quadrat was estimated in each plot and converted to midpoints of cover (Daubenmire 1959). Clubmoss in the control plots covered about 79% of the soil surface at Dundurn and 68% at Rudy (Table 3). Basal cover was greater for dead than live clubmoss, and bare soil was negligible at both sites. Clubmoss was reduced 90%, and bare soil increased 14- to 33-fold with clubmoss removal. Forb cover at Dundurn was twice that at Rudy, but cover of graminoids was similar. Junegrass (*Koeleria cristata* Pers.), blue grama (*Bouteloua gracilis* [HBK.] Lag.), and needle-and-thread (*Stipa comata* Trin. & Rupr.) dominated the study sites; common dicots included fringed sagebrush (*Artemisia frigida* Willd.), late yellow locoweed (*Oxytropis campestris* L.), hairy golden aster (*Chrysopsis villosa* (Pursh) Nutt.), low goldenrod (*Solidago missouriensis* Nutt.), and moss phlox (*Phlox hoodii* Richardson).

Clubmoss treatments were factorially combined with natural precipitation, precipitation increased by irrigation, and reduced precipitation. Plots receiving natural precipitation were considered controls for the precipitation treatments. Irrigated plots simulated above-average precipitation, whereas reduced precipitation was

Table 3. Average basal cover of live and dead clubmoss, percentage of bare soil, and canopy cover of forbs and graminoids within clubmoss treatments at Dundurn and Rudy study sites.

Clubmoss treatment	Dundurn					Rudy				
	Basal cover					Basal cover				
	Clubmoss		Bare soil	Canopy cover		Clubmoss		Bare soil	Canopy cover	
	Live	Dead		Forbs	Graminoids	Live	Dead		Forbs	Graminoids
	(%)									
Control	36	43	4	14	27	30	34	1	7	24
Removed	3	7	55	10	17	6	3	33	8	19

intended to intensify seasonal drought. On irrigated plots, natural precipitation was supplemented with water applications of 40 mm in mid-May, mid-June, mid-July, and mid-August at Dundurn in 1997 and both sites in 1998 for a total increase of 160 mm over natural precipitation (Table 2). This additional water is about 75% greater than the long-term mean precipitation received from April through August in this area (Environment Canada 1982). The probability of daily precipitation events of 40 mm or more is about 1.1 to 2.3% in the Northern Mixed Prairie of Saskatchewan and Alberta. Plots were irrigated with well water applied to the 3- by 3-m plots at a rate of about 45 liter min^{-1}. The amount and rate of irrigation was controlled using a gas-powered pump and a hose with an adjustable nozzle. Irrigation was stopped periodically throughout the application if necessary to prevent runoff.

For the reduced precipitation treatment, rainout shelters were designed to permit plant growth, but limit the amount of precipitation reaching the plots, thus accentuating summer water deficits. Rainout shelters were constructed by building a 3- x 3-m frame using boards that were 3-m long, 5-cm wide and 10-cm high. Two additional boards of the same size were placed through the center of each shelter for support. Heavy-duty greenhouse plastic was stretched over the frame and secured. Details of the rainout shelter design are provided by Colberg (2000). Rainout shelters were positioned about 1.0-1.2 m above the plots by fastening them to posts in each corner of the 3- by 3-m plots. Water from rain was allowed to run off the shelters into the buffer areas between plots. Rainout shelters were established on 22 April 1997 at Dundurn and taken down in mid-October 1997. In 1998, the rainout shelters were established on 3 April at Dundurn and on 10 April at Rudy.

Rain gauges (Scientific Sales Inc., Model 6300) were placed in the center of plots under the rainout shelters and control treatments. Rain received was recorded every 1 to 5 days. Across the 3 site-years of study, 2 mm of precipitation were recorded in rain gauges under rainout shelters (Table 2). In addition some rain was blown under the rainout shelters during intense storms, but was not captured by rain gauges.

In 1997 Leaf$_{xwp}$ were measured on 9 and 20 May, 9 and 26 June, 8 and 26 July, and 5 and 21 August at Dundurn, and in 1998 Leaf$_{xwp}$ were determined on 7 and 21 May, 11 and 25 June, 9 and 28 July, and 7 and 18 August at both study sites. Leaf$_{xwp}$ were measured between 1100 and 1400 hours using a pressure chamber (Ritchie and Hinckley 1975). In May and June, the uppermost fully expanded leaf on a Junegrass tiller in each plot was selected whereas 1 blue grama tiller from each plot was chosen for measurement in July and August. Leaves of Junegrass were excised 3 to 4 mm above the collar; blue grama tillers with 2- to 4-fully emerged leaves were cut 3 to 4 mm above ground level. Leaf$_{xwp}$ were determined immediately after excision, and measurements were completed on a block-by-block basis to minimize temporal differences among treatments. Junegrass and blue grama were chosen for measurements of Leaf$_{xwp}$ to allow determinations through the growing season. Junegrass, a C$_3$ species, grows in May and June while blue grama, a C$_4$ grass, grows in July and August.

Peak standing crop was determined at Dundurn in early August 1997 and in late July 1998 at both sites. One quadrat (50 by 50 cm) was randomly located within the 2- by 2-m sample area of each plot, and current growing season phytomass was clipped at ground level, sorted by species, and placed in paper bags. Standing dead material from previous growing seasons was considered litter and excluded from estimates. Samples were dried at 80° C for 48 hours and weighed.

Experiment 2—Simulated Precipitation Events and Clubmoss Effects on Leaf$_{xwp}$

This study was designed to determine the effects of clubmoss and varying amounts of simulated rainfall events on Leaf$_{xwp}$. The treatment design was a 2- by 7-factorial in a randomized-complete-block with 4 replications. The experiment was repeated 7 times including 4-11 May, 8-15 June, and 13-20 July 1997 at Dundurn, and 4-11 May, 8-15 June, 13-20 July, and 10-17 August 1998 at Rudy. New plots were established each time the experiment was repeated.

Clubmoss treatments included control and clubmoss removal as described above. Five to 10 days before conducting the experiment, clubmoss was removed from randomly assigned plots measuring 85- by 85-cm in size. An undisturbed, 50-cm buffer zone was left between plots. After clubmoss was removed, a 5- by 5-m rainout shelter was placed over each treatment replication and left in place through the duration of the study. Design of the rainout shelters was the same as described earlier.

Precipitation events of various magnitudes were simulated by irrigation with a single water application of 0, 2.5, 5, 10, 15, 20, or 25 mm. These water amounts were selected because of the range of size and frequency of naturally occurring precipitation events in southern Saskatchewan and Alberta (Table 1). Leaf$_{xwp}$ were determined for Junegrass in May and June and for blue grama in July and August. Leaf$_{xwp}$ of Junegrass or blue grama were measured before irrigation (Day 0) using methods described earlier. The appropriate water amount for each treatment was then measured and applied to plots using garden watering cans between 1100 and 1700 hours. Leaf$_{xwp}$ of Junegrass or blue grama near the center of the plots were measured 1, 2, 4, and 7 days after irrigation.

Data analysis

In Experiment 1, data from the 3 site-years of study on clubmoss and precipitation effects on Leaf$_{xwp}$ were averaged for each replication of each treatment and date combination, and analyzed with repeated measures analysis of variance for a randomized-complete-block-design (Steel and Torrie 1980). Linear contrasts of mean Leaf$_{xwp}$ were then used to compare precipitation effects through time (Petersen 1985). Data for total standing crop and that of forbs and graminoids were analyzed with a factorial analysis of variance for a randomized-complete-block-design (Petersen 1985).

Data from all 7 repetitions of Experiment 2 were averaged for analyses. Leaf$_{xwp}$ before irrigation (Day 0) were analyzed with a factorial analysis of variance (amount of water and clubmoss treatment) for a randomized-complete-block-design (Petersen 1985). Data of Leaf$_{xwp}$ after irrigation were analyzed with repeated measures analysis of variance (Steel and Torrie 1980). Linear contrasts of mean Leaf$_{xwp}$ were used to compare responses through time between control and each irrigation amount (Petersen 1985). In both experiments statistical significance was assumed at $P \leq 0.05$.

Results

Experiment 1

During the course of the growing season, Leaf$_{xwp}$ were influenced by the interacting effects of precipitation treatment and date ($P < 0.01$), but not by clubmoss ($P = 0.33$). Clear differences in Leaf$_{xwp}$ were not apparent among precipitation treatments until July and August when Leaf$_{xwp}$ were lowest in the reduced precipitation treatment (Table 4). Contrasts of

Table 4. Average Leaf$_{xwp}$ for Junegrass and blue grama from May through August in control, plots in which precipitation was reduced, and irrigated plots. Leaf$_{xwp}$ were determined for Junegrass in May and June and for blue grama in July and August.

Date of determination	Precipitation treatment Control	 Reduced	 Irrigated
	-------------(MPa)-----------		
Early May	–1.7	–1.9	–1.8
Late May	–1.8	–1.7	–1.6
Early Jun.	–3.0	–2.8	–3.0
Late Jun	–1.5	–1.8	–1.4
Early Jul.	–1.3	–1.8	–1.1
Late Jul.	–1.7	–2.4	–1.4
Early Aug.	–4.6	–5.2	–4.6
Late Aug.	–1.3	–3.7	–1.4
Standard error (precipitation x Date)		0.35	

means through time indicated that Leaf$_{xwp}$ were lower when precipitation was reduced than in control ($P < 0.01$) and the irrigation treatment ($P < 0.01$); however, Leaf$_{xwp}$ were similar ($P = 0.46$) through time in the control and when irrigated.

Total standing crop (83 g m^{-2}, SE = 5.6, $P = 0.70$) and standing crop of forbs (28 g m^{-2}, SE = 2.2, $P = 0.22$) and graminoids (55 g m^{-2}, SE = 5.7, $P = 0.35$) were similar in control and the clubmoss removal treatment. Precipitation had no effect on standing crop of forbs (28 g m^{-2}, SE = 2.2, $P = 0.13$), but graminoid ($P = 0.02$) and total standing crop ($P = 0.05$) increased with precipitation. Graminoid standing crop was greatest when irrigated (74 g m^{-2}), intermediate in control (53 g m^{-2}), and least (36 g m^{-2}) in reduced precipitation (SE = 8.7). Likewise, total standing crop ranged from 102 g m^{-2} when irrigated to 76 g m^{-2} in the control and 69 g m^{-2} (SE = 9.0) in reduced precipitation. Interacting effects of clubmoss and precipitation had no influence on standing crop of forbs ($P = 0.55$), graminoids ($P = 0.61$), and total standing crop ($P = 0.42$).

Experiment 2

Before irrigation on Day 0, Leaf$_{xwp}$ were similar among irrigation amounts ($P = 0.295$), between clubmoss treatments ($P = 0.81$), and their interacting effects ($P = 0.92$), averaging –2.7 MPa (SE = 0.03). Leaf$_{xwp}$ increased after irrigation, and declined over the 7-day drying period (Table 5). The decline in Leaf$_{xwp}$ from days 1 to 7 was due to the interacting effects of the amount of irrigation water and days after irrigation ($P \leq 0.01$), but not by clubmoss ($P = 0.06$). Although there was a trend for higher Leaf$_{xwp}$ when irrigated with at least 5 mm of water (Table 5), more than 10 mm of irrigation were required to impart a significant increase ($P \leq 0.05$) in Leaf$_{xwp}$ over control through time (Table 6).

Discussion

The fact that clubmoss grows in many plant communities of the Northern Mixed Prairie logically leads to the conclusion that clubmoss uses water and competes for it with other species. Whether the magnitude of the effects of clubmoss on associated species is greater than those imposed by environmental conditions, particularly the amount of precipitation, formed the basis for our studies. Van Dyne and Vogel (1967) speculated that clubmoss competes for water with most associated plants. Competition for water is possible between clubmoss and some species, but it was not significant for Junegrass and blue grama on our study in which clubmoss cover was high. In our studies, clubmoss had no significant ($P \leq 0.05$) influence on Leaf$_{xwp}$ or standing crop of plants. Therefore, the hypothesis that clubmoss reduces Leaf$_{xwp}$ and productivity of associated plant species in the Northern Mixed Prairie is rejected. Similarly the alternative hypothesis that Leaf$_{xwp}$ and plant production are increased in the presence of clubmoss is not accepted. Clarke et al. (1943) also concluded that the clubmoss has minimal influence on plant communities in the Northern Mixed Prairie because of its low water requirements. Significant effects of precipitation or irrigation, and similar Leaf$_{xwp}$ and plant standing crop between clubmoss treatments, indicated that the amount of precipitation received overshadowed any effects of clubmoss on Leaf$_{xwp}$ and plant production. Gold and Bliss (1995) also reported that cryptogamic crusts did not affect plant water relations in arctic ecosystems.

Water availability is arguably one of the most important factors governing structure and function of the Northern Mixed Prairie (Redmann 1976, Sims and Singh 1978, Smoliak 1986, Willms and Jefferson 1993). Increased precipitation in the Northern Mixed Prairie enhances plant production (Branson 1956, Cosper and Thomas 1961, Klages and Ryerson 1965). Each species or group of species responds to precipitation in unique ways (Klages and Ryerson 1965, Olson et al. 1985). Response of vegetation to precipitation may also be tempered by nutrient cycling, timing and amount of precipitation, range condition, vigor of plants, range site characteristics, stage of growth, genetic limitations of the vegetation, past management, and landscape position (Weaver and Albertson 1944, Smoliak 1956, 1986, Perry 1976, Bork et al. 2001).

Most precipitation events in the Northern Mixed Prairie of Canada are small (Table 1). We predicted that clubmoss would have it greatest effects on Leaf$_{xwp}$ when irrigated with small amounts of water because losses to interception by clubmoss were expected to be greatest for small precipitation events (Couturier and Ripley 1973). However, clubmoss had no effect on Leaf$_{xwp}$ over the range of 0 to 25 mm of irrigation. We therefore conclude that clubmoss has negligible impacts on the water balance of a site across a range of precipitation events.

More than 10 mm of precipitation were required before Leaf$_{xwp}$ increased in Junegrass and blue grama. This response contrasts with the results of Sala and Lauenroth's (1982) study in which Leaf$_{xwp}$ and stomatal conductance of blue grama increased after a 5 mm precipitation event. However, Coupland (1950) concluded that precipitation amounts of about 7 mm or less have minimal influence on soil water and production in the Mixed Prairie of Canada. Physical and chemical properties of soil, canopy and litter characteristics (Naeth et al. 1991a), and antecedent precipitation events alter the effectiveness of different sized precipitation events. Differences in rooting patterns of plants among sites may also influence

Table 5. Average Leaf$_{xwp}$ for Junegrass and bluegrama from 1 to 7 days after irrigation with 0 to 25 mm of water.

Days after irrigation	Amount of water added through irrigation (mm) 0	 2.5	 5	 10	 15	 20	 25
				(MPa)			
1	–2.6	–2.1	–1.9	–1.6	–1.5	–1.6	–1.5
2	–2.4	–2.2	–1.9	–1.7	–1.6	–1.4	–1.5
4	–2.5	–2.5	–2.3	–2.0	–1.8	–1.7	–1.8
7	–2.4	–2.3	–2.3	–1.9	–2.0	–1.8	–1.9
Standard error (Irrigation x Days)							0.08

Table 6. Probabilities that Leaf_{xwp} are different through time between control and 6 amounts of irrigation on plots. Leaf_{xwp} were determined for Junegrass and blue grama.

Irrigation treatment comparison					
0 vs. 2.5 mm	0 vs. 5 mm	0 vs. 10 mm	0 vs. 15 mm	0 vs. 20 mm	0 vs. 25 mm
	---------- (P) ----------				
0.21	0.07	0.16	0.03	0.04	0.02

plant responses to precipitation. Although Junegrass and blue grama did not respond ($P \leq 0.05$) to precipitation events <10 mm, small precipitation events may be important to ecosystem functions. In fact, photosynthesis and other physiological activities in clubmoss increase quickly after precipitation (Webster and Steeves 1964, Eickmeier 1979, 1983, Harten and Eickmeier 1987). Similarly rainfall events <4 mm can benefit cryptogams (Noy-Meir 1973), and microbial respiration and nutrient cycling may be stimulated by small rainfall events (De Jong et al. 1974).

Despite the absence of research on the ecological roles of clubmoss, improved plant water relations and increased plant production by eliminating or reducing clubmoss have been the primary reasons for mechanically disturbing rangeland on which this species is abundant (Dolan 1966, Wagner 1966, Taylor 1967, Ryerson et al. 1970). Many of the beliefs about the influence of clubmoss on soil and plant water relations were derived from assumptions about its effects on various aspects of the hydrologic cycle. Improved soil water and production after mechanical disturbances of rangelands that support high populations of clubmoss are likely due to changes in the chemical and physical properties of soils, micro-relief of the soil surface (Ryerson et al. 1970), and increased amounts of litter (Dolan 1966, Dolan and Taylor 1972) rather than clubmoss per se. Furthermore, precipitation is more important in determining plant productivity than mechanical disturbance in rangelands on the Northern Great Plains (Haferkamp et al. 1993). Mechanical disturbances to decrease the cover of clubmoss may be unnecessary and counterproductive to conservation of rangeland resources, and may not be economically feasible (Kulshrehtha et al. 2002).

Modifying grazing practices to improve water relations may be an alternative to mechanical disturbance on rangeland. Grazing intensity significantly affects water relations in prairie ecosystems (Johnston 1962, Naeth et al. 1991b). Other grazing management practices that maintain or increase natural litter and mulch cover may also improve water relations on a site. Litter and mulch play important roles in the dynamics of soil water on the Northern Mixed Prairie (Rauzi 1960, Willms et al. 1986,1993) by reducing incident solar radiation on the soil surface (Willms et al. 1986), which reduces soil temperatures and evaporation (Weaver and Rowland 1952, Hopkins 1954) and increases herbage yields (Willms et al. 1986, 1993, 2002). Most precipitation events in the Northern Mixed Prairie are small, and any improvement in water-use efficiency should improve the water balance of a site. In summary, range managers in the water-limited Northern Mixed Prairie may want to identify and implement grazing management practices that improve water relations before considering mechanical modification of rangeland to reduce clubmoss.

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Seed germination of willow species from a desert riparian ecosystem

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Abstract

The restoration of riverine riparian areas following mechanical, herbicidal, or biological control of the invasive species tamarisk (*Tamarix ramosissima* Ledeb.) is a major issue in the western United States. Recruitment of seedlings of native woody species is necessary in these restoration efforts. Species of willow (*Salix*) are often considered essential in these efforts. We studied the germination of seeds of tree willow (*Salix lutea* Nutt.) and coyote willow (*S. exigua* Nutt.) at a wide range of constant or alternating incubation temperatures. Seeds were collected from native stands in the delta of the Walker River in western Nevada over a 3 year period. Seed germination was very similar for both species. On 2 of the 3 years of testing the seeds had 100% germination at some incubation temperatures and some germination over almost all of the 55 temperature regimes used in the experiments. A late frost in May of 2000 markedly reduced total germination of both species, but did not greatly restrict the temperature regimes where some germination occurred. Optimum germination, defined as that not lower than the maximum observed minus one half the confidence interval at the 0.01 level of probability, occurred over a very wide range of temperatures, but for tree willow only the temperature regimes 15/25 (15° C for 12 hours and 25° C for 8 hours in each 24 hour period) and 15/30° C always supported optimum germination. No temperature regime always supported optimum germination of coyote willow seeds, but the most frequent optima tended to be at lower temperatures than for tree willow. Because of the similarity in germination responses and overlapping phenology, seeds of these 2 species probably compete for germination safesites.

Key Words: *Salix exigua, S. lutea,* coyote and tree willow, incubation temperatures, seedbed temperatures

Resumen

La restauración de áreas ribereñas después del control mecánico, químico o biológico de la especie invasora "Tamarisk" (*Tamarix ramosissima* Ledeb.) es un problema mayor en el oeste de Estados Unidos. El establecimiento de plántulas de especies leñosas nativas es necesario en estos esfuerzos de restauración. Especies de "Willow" (*Salix*) a menudo son consideradas esenciales en estas acciones de restauración. Estudiamos la germinación de semillas de "Tree willow" (*Salix lutea* Nutt.) y "Coyote willow" (*S. exigua* Nutt.) en un amplio rango de temperaturas de incubación constantes y alternantes. Las semillas se colectaron durante un periodo de 3 años en poblaciones nativas del delta del río Walker en el oeste de Nevada. La germinación de la semilla fue muy similar para ambas especies. En 2 de 3 años de prueba, las semillas tuvieron 100% de germinación en algunas de las temperaturas de incubación y algo de germinación en casi todos los 55 regímenes de temperatura evaluados en el experimento. Una helada tardía en Mayo de 2000 redujo marcadamente la germinación total de ambas especies, pero no restringió grandemente los regímenes de temperatura donde algo de germinación ocurrió. La germinación óptima, definida como no menos que el máximo observado menos una mitad del intervalo de confianza a un nivel de significancia de 0.01, ocurrió en un amplio rango de temperaturas, pero para "Tree willow"solo los regímenes de temperatura 15/25 (15° C por 12 horas y 25° C por 8 horas en cada periodo de 24 horas) y 15/30° C siempre produjeron la máxima germinación. No hubo un régimen de temperatura que mantuviera la germinación óptima para las semillas de "Coyote willow", pero la germinación optima tiende a ser a mas bajas temperaturas que para el "Tree willow". Debido a la similitud en la respuestas de germinación y la frenología que se traslapa, las semillas de en estas dos especies probablemente compitan por sitios seguros para germinación.

Willow species (*Salix* sp.) are important components of riparian communities throughout much of North America. They occur as both small to moderate sized trees and as shrubs. Many, but not all of the shrubby willows are browsed by wildlife or domestic livestock (Sampson 1924). Despite having flowers arranged in catkins, willow species are insect pollinated. When they flower, large numbers of insects are attracted to the catkins. Insectivorous birds follow their prey, making willow communities important habitats for birds. In the virtually treeless landscapes of the Great Basin, riverine willow communities often provide the only woody nesting cover for a variety of birds.

In the central Great Basin and extending throughout the Southwest, the exotic shrub or small tree tamarisk (T*amarix ramosissima* Ledeb.) has invaded vast reaches of riverine habitats. On any specific sites it is an open question if tamarisk replaced the native woody species or the woody species were destroyed and tamarisk invaded the ecological void. Currently, limited releases have been made in the Great Basin of a biological control agent for the suppression of tamarisk. A beetle (*Diorhabdo elongata*), imported from Asia, shows promise for suppressing tamarisk. Will this biological suppression lead to seedling recruitment of the native woody species?

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The western Great Basin riverine riparian areas most impacted by the invasion of tamarisk are the sink of the Humboldt River, the north sink of the Carson River in the Stillwater marsh area, and the delta of the Walker River. The Humboldt River sink is naturally treeless. The north discharge arm of the Carson River has well developed gallery forest of Fremont cottonwood (*Populus fremontii* S. Watson), almond willow (*Salix amygduloides* Anderson), tree willow (*S. lutea* Nutt.), coyote willow (*S. exigua* Nutt.), buffalo berry (*Shepherdia argentea* Nutt.) and the exotic Russian olive (*Elaeagnus angustifolius* L.). In the Stillwater marsh itself, there are vast linear stands of tamarisk on water control structures and along road banks. The few Fremont cottonwoods present are probably adventive since tail water was delivered to the area as drainage from the Newlands Irrigation District.

The delta of the Walker River is the site of one of the most extensive stands of tamarisk. In 1909 the shore of Walker Lake was located just south of Schurz, Nevada. Up-stream diversion of water for agricultural, municipal, and wildlife habitat uses in both California and Nevada have resulted in a dramatic drop in lake level. The river currently periodically enters the lake about 25 km to the south and about 100 m lower in elevation than the 1909 shore level based on unpublished maps on file with the Walker River Paiute tribe. The vast lake plain exposed by this drying has been incised by the meandering Walker River as it attempts to erode to a new base level. Tamarisk, Fremont cottonwood, tree, and coyote willow invasion has followed the dropping lake level. Tamarisk has been the much more successful of these woody species. Coyote willow is the second most abundant species, probably because it forms extensive clonal stands. Tree willow and Fremont cottonwood are both heavily preyed upon by beavers (*Castor canadensis*). Fremont cottonwood has also been utilized as a source of fuel wood.

Fremont cottonwood and the willow species belong to the family Salocaceae. Tamarisk is a member of the completely un-related family Tamaricaceae. Despite having no phylogenetic relationship, Fremont cottonwood, tree, and coyote willow all produce relatively small seeds that are wind dispersed with the aide of seed borne hairs, and have very short periods of seed of viability. The seeds of all of these species require quite specific moist seedbeds for germination and seedling establishment. As a first step in understanding the seed and seedbed ecology of these species, our purpose in this study was to investigate the germination of seeds of tree and coyote willow at a wide range of constant and alternating temperature regimes.

Methods

Seeds of tree and coyote willow were harvested from native stands located in the Walker River delta (38° 53.539'N 118° 46.733°) Win 1999, 2000, and 2001. The seeds were collected at maturity in late May or early June each year. Seeds were collected from many different trees over an extensive area of the delta. The seeds were transported to the laboratory and the experiments established immediately, with as little time as possible between collection and the seeds being wet in the germination plates.

In all experiments 4 replications of 25 seeds each were used in a randomized block design. Seeds were placed on top of non-toxic commercial germination paper in closed Petri dishes and kept wet with tap water. Germination trials were conducted in the dark. Seeds were considered germinated when the radical emerged 5 mm. Germination counts were made after 1, 2, and 4 weeks incubation. Constant incubation temperatures were 0, 2, and 5° C and at 5 degree increments through 40° C. In addition, alternating regimes included 16 hours at each constant temperature, plus 8 hours at each possible higher temperature per 24 hours. For example, 35° C alternated with 40° C only, while 0° C alternated with 2, 5, 10, 15, 20, 25, 30, 35, and 40° C. This made a total of 55 constant and alternating temperature regimes (Young et al. 1991).

The germination response of seeds of the 2 species of willow was compared using the seedbed temperature definitions (Young and Evans 1982):

a. Very cold: 0/0 (constant 0° C), 0/2 (0° C for 16 hours and 2° C for 8 hours in each 24 hours), 0/5 and 2/2° C.
b. Cold: 0/10, 0/15, 2/5, 2/10, 2/15, 5/5, and 5/10° C.
c. Cold fluctuating: 0/20, through 0/40° C and 2/20 through 2/40° C.
d. Fluctuating: 5/30 through 5/40° C, 10/35, 10/40, 15/40° C.
e. Moderate: 5/15 through 5/25, 10/10 through 10/30° C, 15/15 through 15/35° C, 20/20 through 30/35° C, and 25/35° C.
f. Warm: 20/40, 25/35, and 25/40° C, 30/30 through 30/40° C, 35/35, 35/40, and 40/40° C.

The categories of seedbed temperatures reflect germination environments of field seedbeds based on several years of monitoring in the Great Basin (Evans et al. 1970, Evans and Young 1970, 1972).

Data from each base temperature and its alternating temperature regimes were used to generate a quadratic response surface with estimated means and confidence intervals at the 1% level of probability (Young et al. 1980, Evans et al. 1982). A number of germination parameters were calculated from the quadratic response surfaces (Table 1) (Young and Evans 1982). Profiles were compared using the multiple response surface comparison method described by Palmquist et al. 1987.

Results and Discussion

The seeds of willow species are small, fragile, light, and sufficiently aerodynamic to be dispersed by the wind. The aerodynamics is enhanced by relative dense covering of silky hairs. These hairs are many times longer than the diameter of the seed. The seeds of most species of willow only remain viable for short periods of time (Young and Young 1992).

It is immediately apparent when you examine the temperature-germination profiles for tree (Table 2) and coyote willow (Table 3) that the seeds of these species germinate over a wide range of constant or alternating incubation temperatures. Coyote willow seeds germinated at all 55 temperatures tested and tree willow seeds had some germination at all temperature regimes except a constant 40° C.

The second factor that is apparent when examining the profiles is the seeds of both species are highly viable with 100% germination occurring at least at 1 temperature regime (Tables 2 and 3). At least 90% germination occurred over a wide range of temperatures.

Germination responses were very similar for the seeds of both species for the 1999 and 2001 seed production years (Table 4). In 2000 a severe frost occurred on May 10th. This dropped average germination from an average of 67 to 74% for both species to 27 to 29%. Maximum germination dropped from 100% to 67 to 79%. Despite the severe late frost, some germination occurred at 93 and 96% of the temperature tested for tree and coyote willow respectively.

Table 1. Germination parameters calculated from quadratic response surfaces (Young and Evans 1982).

Calculated parameter	Derived parameter	Purpose
Calculated within profile		
Mean germination	Sum divided by 55	Gross comparison of profiles
Percentage of regimes with germination response	Number with germination divided by 55	Indication of breath of germination
Percentage of regimes with optimum	Number of regimes with germination no less than Maximum observed minus confidence interval divided 55	Indication of breath of temperatures that suppot optimum germination
Mean of optima	Sum of optima divided by number of optima	Provides measure of potential germination
mum germination	Highest observed germination	Indication of potential viability
Calculated among germination profiles		
Frequency of optima	Times temperature regime supports optima divided byotal number of profiles	Provides an estimate of optimum temper or germination with statistical precision

Table 2. Quadratic response surface with estimated percentage germination and confidence interval (P ≥ 0.01) for seeds of tree willow incubated at 55 constant or alternating temperatures. Seed produced in the Walker River Delta in 1999.[1]

Cold period temperature C	Percentage germination Warm period temperature C									
	0	2	5	10	15	20	25	30	35	40
	(%)									
(C°)										
0	15 ± 11	24 ± 10	40 ± 9	76 ± 11	80 ± 13	92 ± 13	92 ± 13	90 ± 13	74 ± 14	20 ± 11
2		35 ± 14	42 ± 15	70 ± 10	92 ± 14*	94 ± 7*	91 ± 10	90 ± 11	86 ± 13	50 ± 12
5			585 ± 17	98 ± 8*	80 ± 8	88 ± 11	96 ± 6*	88 ± 11	86 ± 12	58 ± 9
10				70 ± 16	76 ± 6	86 ± 10	[100 ± 4*	100 ± 8]*	94 ± 10	80 ± 12
15					70 ± 8	88 ± 8	[100 ± 10]	*98 ± 8*	90 ± 8	90 ± 11
20						90 ± 13	80 ± 19	88 ± 14	94 ± 14*	96 ± 9*
25							78 ± 12	80 ± 9	98 ± 1	84 ± 14
30								90 ± 9	84 ± 10	80 ± 16
35									76 ± 16	60 ± 18
40										0 ± 20

[1] Number following mean is one half the confidence interval as determined from regression equations used to develop response surface (Palmquist et al. 1987). The maximum calculated germination is enclosed by brackets [ ]. Means not lower than the maximum and one half of its confidence interval, our definition of optimum germination, are marked with and asterisk *.

We define optimum germination by relating optima to the maximum germination minus one half of its confidence interval at the 0.01 level of probability. Note that in the 3 years of testing the mean of optima and percentage of regimes supporting optima did not significantly vary between tree and coyote willow (Table 4). Only in 2000 when the seed quality was lowered by frost damage was the mean of optima lower for both species. The percentage of temperature regimes supporting optimum germination differed significantly for both species for each year of seed production. Seed quality was exceptional for both species in 2001. To have 60 and 78% of the temperature regimes supporting optimum germination when the maxi-

Table 3. Quadratic response surface with estimated percentage germination and confidence interval (P ≥ 0.01) for seeds of coyote willow incubated at 55 constant or alternating temperatures. Seed produced in the Walker River Delta in 1999.[1]

Cold period temperature C	Percentage germination Warm period temperature C									
	0	2	5	10	15	20	25	30	35	40
	(%)									
(C°)										
1	0 ± 9	15 ± 7	70 ± 8	80 ± 8	[100+10]*	90 ± 8*	90 ± 8	85 ± 11	80 ± 9	80 ± 11
2		15 ± 7	72 ± 6	90 ± 11*	95 ± 11*	90 ± 10*	90 ± 9*	90 ± 9*	89 ± 11	80 ± 9
5			80 ± 11	85 ± 9	90 ± 8*	92 ± 9*	90 ± 10*	84 ± 10	85 ± 10	80 ± 7
10				90 ± 11*	92 ± 9*	86 ± 9	84 ± 7	82 ± 6	80 ± 8	78 ± 11
15					70 ± 11	89 ± 9	90 ± 8*	85 ± 10	90 ± 11*	85 ± 8
20						85 ± 7	90 ± 9*	95 ± 4*	90 ± 10	80 ± 9
25							80 ± 11	96 ± 7*	95 ± 8*	90 ± 9*
30								98 ± 10*	86 ± 5	80 ± 12
35									95 ± 10*	70 ± 14
40										10 ± 14

[1] Number following mean is one half the confidence interval as determined from regression equations used to develop response surface (Palmquist et al. 1987). The maximum calculated germination is enclosed by brackets [ ]. Means not lower than the maximum and one half of its confidence interval, our definition of optimum germination, are marked with and asterisk *

Table 4. Comparison of temperature germination profiles for seeds of tree and coyote willow collected in the Walker River delta in 1999, 2000, and 2001.

Germination parameter	Year of seed production and species					
	1999		2000		2001	
	Tree willow	Coyote willow	Tree willow	Coyote willow	Tree willow	Coyote willow
	(%)					
-						
Mean germination	71a	74a	27b	29b	67a	70a
Temperature regimes with some germination	98	100	93	96	93	89
Mean of optima	96a	92a	63b	79b	100a	100a
Regimes with optimum germination	20b	40b	9c	4c	60a	78a
Maximum	100a	100a	67b	79b	100a	100a
Seedbed temperature categories						
Very cold	21a	19a	5b	17a	1b	8b
Cold	77b	86b	25c	37c	70b	100a
Cold fluctuating	78a	87a	35b	44b	82a	80a
Fluctuating	74a	83a	27c	22c	72b	60b
Warmer	87a	88a	27b	12c	77a	79a
Moderate	87a	81a	42b	39b	100a	99a

[1]Means within rows followed by the same letter are not significantly different at the 0.01 of probability based on overlap of the confidence intervals (Palmquist et al. 1987).

mum observed is 100% exceeds the species potential of any of the some 800 temperature-germination profiles that have been completed in our laboratory.

In terms of categories of seedbed temperatures, the seeds of both species of willow had exceptional germination at every category except very cold temperatures (Table 4). Very cold temperatures are characteristic of seedbeds that freeze at night and barely thaw during the day. Even in 2000 when the seed quality was damaged by frost, there was some germination at very cold seedbed temperatures. Surprisingly, in 2001 when overall germination responses were the highest, the germination of both species was the lowest at very cold temperatures, but the highest at the cold category of seedbed temperatures (Table 4).

The frequency that a given temperature supports optimum germination provides an excellent indication of the true optimum temperature for germination of seeds of a given species. For tree willow seeds, only 15/25° C (16 hours at 15° C and 8 hours at 25° C in each 24 hours period) and 15/30° C always supported optimum germination (Table 5). For coyote willow seeds, no single temperature regime always supported optimum germination (Table 6). Optima were spread over a vast range of temperatures from a constant 2° C to 30° C and included 10/40, 15/40, and 20/40° C. Two thirds of the time 29% of the temperature regimes supported optimum germination. These temperatures were generally colder than the 100% constancy regimes for tree willow. Some of the 66% frequency temperature regimes for optimum germination extended into regimes with 0° C cold period temperatures.

Despite their world-wide distribution and ecological importance, very little research has been conducted on the seed and seedbed ecology of the willow species. The seeds have a very transitory period of viability making them available for research purposes for only a very short period annually. The hair covered seeds are difficult to collect, process, and count. In forestry and horticulture most species of willow can readily be propagated by cuttings. Junttila (1976) determined that for 4 species of willows from Norway, optimum temperatures for germination ranged from 26 to 32° C. The optima for tree and coyote willow seed extend broader than this range, but certainly cover these incubation temperatures. In one of the few other germination studies for willow seeds and incubation temperatures, Gorobets (1978) found that seeds of 2 species of Russian willows could germinate at a wide range of temperatures.

Tree willow and coyote willow grow in the Walker River Delta sympatricly. There growth forms are radically different. As the name implies, tree willow tends to form a single dominant trunk and becomes a small tree. Coyote willow occurs in dense clumps with multiple stems more or less the same size. Coyote willow clumps are much more abundant than the tree willows, but beavers prefer tree willows and generally shun coyote willow stems. In the Walker River delta, cattle prefer the tree willow browse and there seldom is evidence of browsing on coyote willow.

Comparing the germination of these 2 species of willow, it is obvious that in terms of germination requirements for incubation temperature they are very similar. They both produce super abundant, highly viable, widely distributed seeds. Conventional observations and nursery

Table 5. Frequency that a given temperature regime supported optimum germination of seeds of tree willow collected in the Walker River delta from 1999 through 2001.

Cold period temperature C	Frequency of optima Warm period temperature C									
	0	2	5	10	15	20	25	30	35	40
	(%)									
(C°)										
0							33	33		
2					66	66	33	33		
5				33	33	33	66	33	33	
10				3	33	33	66	66	33	
15					33	66	100	100	33	
20						33	66	33	66	3
25							33	33	33	33
30								33	33	
35									33	
4										

Table 6. Frequency that a given temperature regime supported optimum germination of seeds of coyote willow collected in the Walker River delta from 1999 through 2001.

Cold period temperature C	Frequency of optima Warm period temperature C									
	0	2	5	10	15	20	25	30	35	40
(C°)					(%)					
0				33	66	66	66	33	66	
2			33	66	66	66	66	66	66	
5				33	66	66	66	33	33	
10				66	66	33	33	33	33	
15					33	66	33	33	33	33
20						33	33	33	33	33
25							33	33	33	33
30								33		
35									33	
40										

practices (Young and Young 1992), suggest that willow seeds must disperse to damp sandy to silt seedbeds soon after maturity to have a chance for seedling establishment. In the Walker River delta, tree and coyote willow seeds probably compete for the same safe sites for germination and establishment. Their phenology of flowering and seed dispersal is quite close, but tree willow usually disperses seeds before coyote willow.

The management of riverine willow populations to enhance seedling recruitment is obviously a very complex under taking. This study provides a first step toward understanding the seed and seedbed ecology of these species.

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Defoliation effects on reproductive biomass: Importance of scale and timing

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Abstract

Community-level (per unit area) and individual tiller reproductive biomass inside and outside of long-term exclosures on the northern winter range of Yellowstone National Park, USA were compared. Grazed areas had twice the number of reproductive tillers m^{-2} (186 compared to 88 tillers m^{-2}), and greater total reproductive biomass m^{-2} than ungrazed plots (13 compared to 7 g m^{-2}). In contrast, seed number tiller^{-1} was greater for grasses in exclosures. Because of these offsetting responses, seed production (no. m^{-2}) was unaffected by herbivores. On an area basis, grazed grasses allocated proportionally more biomass to reproduction (reproductive biomass/aboveground biomass) than ungrazed grasses. We propose that altered plant demography and morphology following defoliation explain how grazers might increase the allocation of biomass to reproduction in Yellowstone grasslands.

To understand these results in light of ecological and agronomic studies, we reviewed literature from 118 sources that reported the effects of defoliation on the production of reproductive biomass. The review suggested that the results of herbivory or defoliation on plant reproductive biomass depended on the scale of measurement (community vs. plant). In addition, timing of grazing or defoliation emerged as a key factor that determined whether sexual reproduction was inhibited. Like the early season grazing that is typical of Yellowstone's northern winter range, studies often showed that early season defoliation stimulated production of community-level reproductive biomass. Our results rectify disagreements in the literature that ultimately derive from differences in either timing of defoliation or measurement scale.

Resumen

Se comparó la biomasa de tallos reproductivos a nivel individual y de comunidad (por unidad de área)dentro y fuera de exclusiones de largo plazo localizadas en un pastizal de invierno del norte del Parque Nacional Yellowstone, E.U.A. Las áreas apacentadas tuvieron el doble de hijuelos reproductivos m^{-2} (186 contra 88 hijuelos m^{-2}) y una mayor biomasa reproductiva m^{-2} que las parcelas sin apacentar (13 versus 7 g^{-2}). En contraste, el número de semillas por hijuelo^{-1} fue mayor en los zacates dentro de la exclusión. Debido a estas respuestas compensatorias, la producción de semilla (número m^{-2}) no fue afectada por los herbívoros. En términos de área, los zacates apacentados destinaron proporcionalmente más biomasa a la reproducción (biomasa reproductiva/biomasa aérea) que los zacates sin apacentar. Proponemos que la demografía y morfología vegetal alterada después del apacentamiento explica como los apacentadores pueden incrementar la asignación de biomasa a la reproducción en los pastizales del Yellowstone. Para entender estos resultados a la luz de estudios ecológicos y agronómicos revisamos literatura de 118 fuentes que reportaron los efectos de la defoliación en la producción de biomasas reproductiva. La revisión sugiere que los resultados de la herviboría o defoliación en la biomasa reproductiva de la planta depende de la escala de medición (comunidad vs. planta). Además, la época de apacentamiento o defoliación surgió como un factor clave que determinó si la reproducción sexual fue inhibida. Como el apacentamiento a inicios de la estación es típico en los pastizales invernales del norte de Yellowstone, los estudios a menudo mostraron que la defoliación temprana estimulo la producción de biomasa reproductiva a nivel de comunidad. Nuestros resultados rectifican desacuerdos de la literatura que finalmente se derivan de diferencias tanto en el tiempo de defoliación o en la escala de medida.

Key Words: grassland, ungulate, grazing, clipping, seed production and yield, Yellowstone National Park, literature review

Seed production can influence the structure, composition, and function of grassland ecosystems. Recruitment from seed facilitates colonization after disturbance, offsets mortality of individual plants in a community, and maintains genetic variability of populations, allowing them to adapt to environmental change. There are 2 disparate views of how large herbivores influence grassland seed production. To plant ecologists studying the effect of herbivory on fitness at the individual plant level, grazing should reduce carbon allocation to seed production. This generality seems to be well supported; defoliation reduces biomass of flowers, fruits, seeds, and reproductive tillers of individuals (for examples see Jameson 1963, Crawley 1983, Belsky 1986a, Maschinski and Whitham 1989, Whitham et al. 1991), with a few exceptions (Paige and Whitham 1987, Lennartsson et al. 1998). This viewpoint is reinforced by observations that grazing ecotypes of several grass species allocate less biomass to seed pro-

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duction than conspecific nongrazing ecotypes (Stapledon 1928, Kemp 1937, Hickey 1961, Detling and Painter 1983, Jaramillo and Detling 1988, Painter et al. 1993, Smith 1998).

In contrast, agricultural managers of seed crops, interested in seed yield per unit area, find that the response of grassland seed production to herbivory depends on the timing and intensity of defoliation. Several studies suggest that grazing does not decrease seed yield (Roberts 1958, 1965, Bean et al. 1979, Watson and Watson 1982, Hebblewaite and Clemence 1983, Winter and Thompson 1987, Conlan et al. 1994) and in many cases increases it (Sprague 1954, Day et al. 1968, Steiner and Grabe 1986, Sharrow and Motazedian 1987, Miller et al. 1993, Conlan et al. 1994, Young et al. 1996). In some studies, grazing or clipping increased the number of reproductive tillers per unit area (Herron 1976, Brown 1980), however this was not always followed by a corresponding increase in seed yield. Thus, the effect of defoliation on production of reproductive biomass is viewed differently by plant ecologists and agricultural managers. Plant ecologists tend to expect inhibition and agricultural researchers report neutral or even positive effects.

Approximately 2,000 elk (*Cervus elaphus* L.), 300–700 bison (*Bison bison* L.), and 600 pronghorn (*Antilocarpa americana* Ord.) graze the northern winter range of Yellowstone National Park from November–April each year (Singer and Mack 1993). Ungulates increase rates of plant production and nutrient cycling in Yellowstone grasslands (Frank et al. 1998, Frank and Groffman 1998). Moreover, comparisons of grasslands inside and outside long-term exclosures indicate that grazers have not significantly influenced grassland species composition (Houston 1982, Coughenour 1991, Singer 1995). Our objective was to determine how migratory native grazers influence seed production on the northern winter range of Yellowstone National Park.

Materials and Methods

Site Description

We sampled the effects of grazing on aboveground reproductive tiller numbers per plot, seed numbers per tiller and per plot, and allocation to reproductive versus vegetative biomass at the plot level. Field data were collected on the northern winter range of Yellowstone National Park, USA (44°55' to 45°10' N and 110°10' to 110°50' W), from July 1999–Sep. 1999. Long-term effects of excluding ungulates on community level patterns of reproductive biomass allocation in grasses was studied by sampling grassland plots inside and outside of 5 exclosures erected between 1958 and 1962. Soils of the northern winter range are largely derived from andesitic and sedimentary glacial till that was deposited during the Pleistocene (Keefer 1987). The climate in the northern winter range is cool and dry; 15 year 95% confidence intervals for mean annual precipitation and temperature from 2 weather stations range from 33.7–38.6 cm (mean = 36.1 cm) and 4.6–5.3° C (mean = 4.9° C) at Mammoth (44°59'N/110°42'W) to 39.2–45.5 cm (mean = 42.3 cm) and 1.7 – 2.4° C (mean = 2.1° C) at Tower (44°55'N/110°25'W) (NOAA 2001). Neither mean annual precipitation nor annual temperature in the year of our study was significantly different from the 15-year average at either weather station; 1999 annual precipitation and temperature was 34.8 and 43.2 cm, and 5.2 and 1.8° C, at Mammoth and Tower, respectively (Table 1).

Two treatments, fenced for ~40 years and unfenced, were replicated across the 5 sites. At each site, 2 paired grassland plots, 1 inside and 1 outside exclosures, approximately 100 m^2 (usually 10 x 10 m) each, were chosen to minimize variation in slope, aspect, and water drainage. Dominant native grass species at the sites were *Festuca idahoensis* Elmer, *Koeleria macrantha* (Ledeb.) Schult., *Poa secunda* Presl., *Pseudoroegneria spicata* (Pursh) A. Love, and *Hesperostipa comata* (Trin. & Rupr.) Barkworth. The non-native species *Agropyron cristatum* (L.) Gaertn. was dominant at 1 of the sites, but was equally abundant inside and outside of the exclosure. Less common grasses were *Eremopyrum triticeum* (Gaertn.) Nevski, *Bromus* sp., *Danthonia* sp., *Achnatherum hymenoides* (Roemer & Schult.) Barkworth, *Elymus elymoides* (Raf.) Swezey, and *Nassella viridula* (Trin.) Barkworth. Common genera of forbs and shrubs were *Artemisia, Achillea, Antennaria, Chrysothamnus, Cirsium, Crepis, Erigeron, Lupinus, Potentilla, Taraxacum,* and *Trifolium.* The 3 most common grazers at the sites were elk, bison, and pronghorn. Descriptions of the 5 grassland sites, 2 at Stephen's Creek, 2 at Blacktail Plateau, and 1 at Junction Butte, are described in detail elsewhere (Houston 1982).

Sampling Methods

Within a plot, aboveground biomass, species richness, and the number of reproductive tillers on grasses were sub-sampled at 4 random locations. Aboveground grass biomass was estimated by clipping all live grass within one, 50 x 50 cm quadrat at each of the 4 sub-sampling locations to ground level. Samples were then dried at 70° C for at least 2 days and weighed. Total aboveground live biomass and species composition were estimated by counting the number of vegetation contacts from 50 randomly located pins passed through a 50 cm high frame at a 53° angle within each of the 4 sub-sampling locations. The number of pin contacts was used to estimate total aboveground biomass inside and outside exclosures using previously established regression equations for the herbaceous vegetation of Yellowstone (Frank and McNaughton 1990).

Grass reproductive tiller density was estimated by counting reproductive tillers within three, 50 x 50 cm quadrats placed randomly within each of the 4 sub-sampling locations. From 1 of the 3 quadrats, all reproductive tillers were collected and dried for at least 2 days at 70° C. Tillers were sorted by species, and then separated into stem and inflorescence. After drying,

Table 1. Mean annual precipitation and temperature from 2 weather stations on the northern winter range of Yellowstone National Park, Wyo., USA. Data are from 1999 (the year of our study) and the mean for the previous 15 years.

			Precipitation			Temperature	
Weather Station	Location	1999	15 yr. mean	95% confidence interval for mean	15 yr. 1999	95% confidence mean	interval for mean
			(cm)			(°C)	
Mammoth	44°59'N/110°42'W	34.8	36.1	33.7 – 38.6	5.2	4.9	4.6 – 5.3
Tower	44°55'N/110°25'W	43.2	42.3	39.2 – 45.5	1.8	2.1	1.7 – 2.4

stem and inflorescence mass was weighed and lengths were measured. As an index of seed number, we estimated the number of reproductive florets per tiller for grass each species. When the number of tillers in a sub-sample for a given species was > 10, a random sample of 10 seed heads was selected and the florets were counted. The mean number of florets per tiller for the 10 seed heads was then multiplied by the number of tillers of each species to derive species-specific estimates of floret number per sub-sample. When sub-samples contained $\leq$ 10 seed heads of a species, all florets were counted.

Grass Demography

As part of a separate study on spatial heterogeneity of Yellowstone grasslands, baseline data on grass density and size were collected at 1 exclosure from Steven's Creek and Blacktail. Data were also collected at Lamar, at which grass reproductive biomass was not measured, but is similar in grazing, precipitation, and species composition to Junction Butte. A grid of 80 evenly spaced points (8 x 10) was established inside and outside of each of the 3 exclosures. At each point, the distance to the center of the nearest grass and the basal lengths of 2 perpendicular axes of the nearest individual were measured. Plant density (D, plants m^{-2}) was estimated by the nearest individual method, $D = 1/(k*L)^2$, where the method correction factor k = 2 and L is the average distance (in m) to the nearest plant for each grid (Cottam and Curtis 1956). Plant size was estimated by calculating elliptical basal area (cm^2) from the lengths of the 2 axes for each individual.

Data analysis

Tiller density is reported per unit area (no. m^{-2}), while floret number and tiller biomass components (inflorescence, stem, and total) are reported per unit area (no. m^{-2} and grams m^{-2}) and per tiller (no. $tiller^{-1}$ and grams $tiller^{-1}$). Data presented per plot represent the mean community response to a treatment. Data per tiller were averaged by tiller within a sub-sample and then averaged within a plot to calculate a tiller-based mean. Data per plot are summed within a sub-sample and then averaged within a plot to calculate a plot mean. Finally, to determine the effects of excluding grazers on community level patterns of biomass allocation, we compared reproductive biomass per unit of aboveground biomass (the ratio inflorescence biomass:plot aboveground biomass) between treatments with a Wilcoxon matched pair test.

Grazer effects were determined with paired t-tests, with sites as replicates, when differences between paired treatment means were normally distributed (determined with a Shapiro – Wilks' W test; $P > 0.05$). When differences were not normally distributed, data were analyzed with a Wilcoxon matched pair test. Because of small sample sizes, all P-values < 0.10 were considered significant. All statistical analyses were performed in Statistica release 5 (1998).

Literature Review

We summarized published literature that reported effects of grazing, clipping, or seed removal on seed yields or plant reproductive biomass. The primary literature was searched with online databases such as Agricola and Cambridge Scientific Abstracts, using keywords such as "defoliation", "grazing", "clipping", "reproduction", "seeds", etc. Our main objective was to compile data sets that allowed quantitative assessment of how plant tissue removal influenced plant reproductive biomass at 2 scales, whole plots and individual plants, from as ecologically diverse sources as possible. Therefore, studies of all natural defoliators or seed predators (insects, birds, etc.) were included. Moreover, we included studies that reported grazer effects on soil seed banks and studies where populations of plants with different grazing histories were compared. Studies were hierarchically grouped by the spatial scale of measurement (individual plant or whole plot), by broad functional group (graminoids or non-graminoids), by the method of defoliation (clipping or grazing), and by identity of defoliator (insect or ungulate). Within each category, we listed all plant species for which data were presented and assessed the effects of defoliation on reproductive biomass as reported by the authors. Results were reported as positive (+), negative (–), or no difference (0) among defoliation and control treatments. Studies in which the timing of defoliation relative to anthesis was manipulated commonly had early, intermediate, or late defoliation treatments. Biomass removal well before the initiation of flowering (i.e. before internode elongation for grasses) was classified as early, several weeks prior to flowering was classified as intermediate (i.e. boot stage for grasses), and at or later than the initiation of flowering was classified as late. Defoliation was categorized as intermediate when information on the timing of defoliation relative to flowering was not provided. Results from studies that include the effects of the severity of defoliation are also reported.

Results

Yellowstone National Park Study

Grazing did not affect species richness ($t_4 = 0.848$; $P = 0.44$). The mean ($\pm$ SE) percentage similarity of species composition inside and outside of exclosures was 70.5% ($\pm$ 1.3) and ranged from 67.0 to 74.4% across the 5 sites. Total aboveground biomass was unaffected by grazers ($t_4 = 1.185$, $P = 0.30$; Table 2), as was aboveground grass biomass ($t_4 = 1.269$, $P = 0.273$; Table 2). However, grazing resulted in a nearly doubling of the number of reproductive grass tillers per plot ($t_4 = 3.542$, $P = 0.024$; Table 2). Likewise, grazed plots had greater total reproductive tiller biomass per area ($Z_4 = 2.023$; $P = 0.043$), which was caused by both greater total inflorescence ($Z_4 = 2.023$; $P = 0.043$) and total stem weights ($t_4 = 2.210$; $P = 0.091$). However, on a per tiller basis, neither reproductive tiller mass ($t_4 = 1.624$; $P = 0.180$) nor the inflorescence mass ($t_4 = 1.190$; $P = 0.300$) differed between grazed and ungrazed plots (Table 2). Thus, increased reproductive tiller mass per plot in grazed areas was caused by an increase in reproductive tiller number, rather than by greater individual tiller mass.

On a per tiller basis, florets were more numerous on tillers that were excluded from grazers ($Z_4 = 1.753$; $P = 0.078$). However, the total number of florets per plot was unaffected by grazing ($t_4 = 1.392$, $P = 0.236$), as a result of the greater number of reproductive tillers per area in grazed plots. Reproductive tiller length was greater in ungrazed areas ($Z_4 = 2.023$; $P = 0.043$); this was attributed to differences in both stem length ($Z_4 = 2.023$; $P = 0.043$) and inflorescence length ($t_4 = 2.949$; $P = 0.042$).

Defoliated plants allocated significantly more biomass to reproduction per unit of standing biomass than did plants in ungrazed plots ($Z_4 = 2.03$, $P = 0.043$, Table 2). Whether or not grazers also increased the ratio of reproductive to aboveground biomass after accounting for foliage removed by herbivores early in the growing season cannot be determined from this study, nor has it been addressed in any study of which we are aware.

Few significant differences exist between grazed and ungrazed dominant native plants when data are analyzed on a species-specific basis (Table 3). Only *P. spicata* had significantly more reproduc-

Table 2. Mean ± 1 S.E. values for vegetation characteristics on a per area and per tiller basis for grazed and ungrazed plots in Yellowstone National Park. Associated P-values from statistical analyses (either paired t-test or Wilcoxon matched pair test) tested for effects of grazing. Total reproductive biomass = stem + inflorescence.

Variable	Ungrazed mean ± SE	Grazed mean ± SE	P-value
	Plot means		
Total aboveground live biomass (g m^{-2})	71.2 ± 8.6	64.6 ± 7	0.30
Aboveground live grass biomass (g m^{-2})	34.8 ± 5.5	28.8 ± 4	0.27
Reproductive tiller density (no. m^{-2})	87.8 ± 16.2	186.4 ± 31.3	**0.02***
Inflorescence biomass per plot (g m^{-2})	1.5 ± 0.5	3.4 ± 1.4	**0.04***
Reproductive stem biomass per plot (g m^{-2})	5.4 ± 1.3	9.2 ± 2.7	**0.09**
Total reproductive biomass per plot (g m^{-2})	6.8 ± 1.8	12.6 ± 4.1	**0.04***
Number florets per plot (no. m^{-2})	2,944 ± 485	4,348 ± 954	0.24
Reproductive : aboveground biomass ratio	0.26 ± 0.12	0.53 ± 0.25	**0.04***
	Tiller means		
Inflorescence biomass per tiller (g $tiller^{-1}$)	0.02 ± 0.01	0.02 ± 0.01	0.30
Reproductive stem biomass per tiller (g $tiller^{-1}$)	0.07 ± 0.02	0.05 ± 0.01	0.17
Total reproductive biomass per tiller (g $tiller^{-1}$)	0.10 ± 0.03	0.07 ± 0.02	0.18
Number florets per tiller (no. $tiller^{-1}$)	41.9 ± 7.7	24.1 ± 4.8	**0.08**
Reproductive tiller stem length (mm)	257.1 ± 8.8	207.7 ± 13.5	**0.04***
Reproductive tiller inflorescence length (mm)	54.1 ± 4.5	42.5 ± 3.7	**0.04***

*Treatment means significantly different at $P < 0.05$
Bold type indicates treatment means significantly at $P < 0.10$

tive tillers per plot (t_4= 3.553, P = 0.038) and greater ratio of tillers to aboveground biomass (t_4= 2.740, P = 0.071) in grazed compared to ungrazed plots. Likewise, estimates for reproductive tiller mass and length are statistically greater only for *K. macrantha* (t_4= 5.772, P = 0.010). Thus, even though mean estimates of reproduction are not different for grazed and ungrazed dominant grasses, the effect of defoliation on reproductive biomass clearly emerges when plant responses are analyzed at the community level (Table 2).

Basal areas of grasses were smaller in grazed compared with ungrazed plots, suggesting that previous grazing reduced plant size (inside mean = 7.1 cm^2, outside mean = 3.7 cm^2, t_2 = 7.07; P = .02, from a paired t-test for a difference in $\log_e$ transformed mean basal area, Table 4). Grass tiller densities were greater in grazed than ungrazed plots at all 3 sites measured (inside mean = 56.6 tillers m^{-2}, outside mean = 110.3 tillers m^{-2}, Table 4).

Literature Review

We identified 118 articles that reported the effects of defoliation on reproductive biomass of 115 plant species from 88 genera (Appendix 1). Taxonomic references and authorities in Appendix 1 follow directly from the original studies; authori-

Table 3. Mean aboveground biomass and tiller characteristics of 4 dominant grass species inside (UG) and outside (G) herbivore exclosures at 5 sites in Yellowstone National Park. P = P-value from a paired t-test. Sample sizes are reported in parentheses next to species names.

	Species											
	Festuca Idahoensis (3)			*Koeleria macrantha* (4)			*Poa secunda* (5)			*Psudoregnaria spicata* (4)		
	UG	G	P	UG	G	P	UG	G	P	UG	G	P
Aboveground live biomass (g m^{-2})	31.2	20.5	0.29	9.1	14.3	0.36	1.7	2	0.51	14.3	20.2	0.14
Reproductive tiller density (no. m^{-2})	57.4	72.8	0.37	22.7	53.3	0.14	6.8	9.2	0.55	15.4	45.8	**0.04***
Tillers per gram biomass (no. m^{-2} g^{-1})	1.8	3.8	0.15	3.4	3.9	0.82	3.9	4.3	0.83	0.9	2.3	**0.07**
Total reproductive biomass per tiller (g $tiller^{-1}$)	0.04	0.02	0.24	0.06	0.04	**0.09**	0.03	0.04	0.21	0.13	0.09	0.31
Total reproductive tiller length (mm)	340.5	267.4	0.15	250.4	209	**0.01***	219.1	240.9	0.53	386.9	302.4	0.20
Number florets per tiller (no. $tiller^{-1}$)	8.7	9.1	0.77	79.1	74.4	0.45	25.7	24.1	0.76	4.9	5.2	0.37

*Treatment means significantly different at $P < 0.05$
Bold type indicates treatment means significantly at $P < 0.10$

Table 4. Grass sizes and densities for grasses measured inside and outside of 3 Yellowstone National Park exclosures. Values represent means from data collected from the nearest individuals to each point in an 8 x 10 grid.

Site	Ungrazed mean ± SE	Grazed mean ± SE
------ Plant basal area (cm^2) ------		
Lamar	3.1	1.9
Blacktail	6.8	3.1
Steven's Creek	11.2	6.2
------ Plant density (no. m^{-2}) -----		
Lamar	59.6	184.7
Blacktail	83.2	113
Steven's Creek	26.9	33.3

ties are not presented if not provided in the original paper. Investigations examined individual plant traits (n = 73), whole plot effects (n = 50), or both (n = 3). Whole plot studies included data for 39 plant species, 30 of which were grasses or sedges. Graminoids were disproportionately represented in whole plot studies because of their agronomic importance and the tendency for crop biomass to be measured per unit area. Likewise, 5 of the remaining 10 forbs were crop or forage species. The 84 species included in studies of individual plants were more evenly distributed between graminoids (n = 36) and forbs (n = 48).

Where data were collected at the plot level, the previous studies showed that early defoliation stimulated reproductive biomass in 33%, had no effect in 56%, and reduced it in 11% of the cases. For plot-level studies, intermediately timed defoliation stimulated reproductive biomass in 11% of the cases, had no effect in 36%, and decreased reproductive biomass in 52% of the 85 cases. For late defoliation treatments measured at the whole plot, reproductive biomass was stimulated in only 8% of the cases, was unaffected in 21%, and reduced in 71% of the 71 cases. In all, over half the studies that measured the effects of defoliation on reproductive biomass per unit area reported either no effect (37%) or a stimulatory effect (16%) of defoliation (Table 5). This was the case for both graminoids and non-graminoid species, but a lower percentage of non-graminoids increased reproductive biomass after defoliation (11 compared to 18%; Table 5). For whole-plot studies, similar percentages of negative effects from defoliation were reported for graminoids (47%) and non-graminoids (45%).

For individual plants, of the 19 studies that included an early defoliation treatment, 16% reported an increase in reproductive biomass, 42% reported no effect, and 42% reported a negative effect. For both studies in which the timing of seed removal was controlled, early removal increased seed production. For the 122 individual plant studies with a single defoliation of intermediate timing, reproductive biomass increased in 10%, was unaffected in 39%, and decreased in 51% cases. In the 29 individual plant studies that included a late defoliation treatment, reproductive biomass was not stimulated in any case, but was unaffected in 17%, and negatively affected in 83%. Compared to whole-plot studies, a greater percentage of individual plant studies reported negative effects of defoliation (55 compared to 47%). Graminoids and non-graminoids from individual plant studies contributed roughly equally to this result; 55 and 56% of the graminoid and non-graminoid studies, respectively, reported a decrease subsequent to defoliation.

To compare the effects of defoliation on reproductive biomass of cool-season with warm-season grasses, graminoid studies that reported the effects of clipping or grazing were grouped according to photosynthetic pathway (C_3 or C_4). The percentage of studies reporting positive, negative, and no effects were determined for whole-plot studies, individual plant studies, and the 2 combined (Table 6). When timing treatments and study scales were combined, defoliation reduced reproductive biomass of C_4 grasses in more cases than for C_3 grasses (67% compared to 47%). Reproductive biomass of C_4 grasses was rarely stimulated by defoliation (2%

Table 5. Results from 118 studies that measured the effect of defoliation on vegetation reproductive biomass or number of reproductive structures. Table values represent the percentage of n studies that report positive (+), no (0), or negative (–) effects of defoliation on the production of reproductive biomass or number or reproductive structures. Studies are separated by early, intermediate, and late defoliation treatments and grouped hierarchically by study scale (whole-plot or individual plant), vegetation type (graminoids or non-graminoids), and type of defoliation (see text). Totals in the last column are the combined results of early, intermediate, and late treatments. See Appendix 1 for the studies used to generate table values.

	Timing															
	Early				Intermediate				Late				Total			
	n	–	0	+	n	–	0	+	n	–	0	+	n	–	0	+
	(%)															
Whole-plot	64	11	56	33	88	52	36	11	73	71	21	8	225	47	37	16
Graminoids	47	11	49	40	69	51	38	12	54	74	19	7	170	47	35	18
Grazing	12	17	50	33	15	67	20	13	14	57	29	14	41	49	32	20
Cutting	35	9	49	43	54	46	43	11	40	80	15	5	129	47	36	18
Non-graminoids	17	12	76	12	19	58	32	11	19	63	26	11	55	45	44	11
Grazing	5	40	60	0	7	43	29	29	7	29	43	29	19	37	42	21
Cutting	12	0	83	17	12	67	33	0	12	83	17	0	36	50	44	6
Individual plant	19	42	42	16	122	51	39	10	29	83	17	0	170	55	36	9
Graminoids	13	46	31	23	62	45	50	5	22	86	14	0	97	55	39	6
Grazing					6	0	83	17					6	0	83	17
Clipping	11	55	36	9	41	56	41	2	20	90	10	0	72	65	32	3
Transplants					13	38	62	0					13	38	62	0
Seed removal	2	0	0	100	2	50	0	50	2	50	50	0	6	33	17	50
Non-graminoids	6	33	67	0	60	57	28	15	7	71	29	0	73	56	32	12
Insects	1	0	100	0	16	69	19	13	1	100	0	0	18	67	22	11
Grazers					12	25	50	25					12	25	50	25
Clipping	5	40	60	0	32	63	25	13	6	67	33	0	43	60	30	9

Table 6. Results from 38 whole-plot and 27 individual plant studies that measured the effect of grazing or clipping (transplants and seed removals are not included) on reproductive biomass for C_3 and C_4 graminiods. Table values represent the percentage of n studies that report positive (+), no (0), or negative (–) effects of defoliation on the production of reproductive biomass or number or reproductive structures. Studies are separated by early, intermediate, and late defoliation treatments. All studies represent the result of whole-plot and individual plant studies combined. Totals in the last column are percentages for the sum of early, intermediate, and late treatments. See Appendix 1 for the studies used to generate table values.

	Timing															
	Early				Intermediate				Late				Total			
	n	–	0	+	n	–	0	+	n	–	0	+	n	–	0	+
	(%)															
C_3 grasses																
All studies	50	14	48	38	77	49	40	10	54	74	19	7	181	47	36	17
Whole-plot	46	11	50	39	56	54	34	13	48	71	21	8	150	46	35	19
Individual plant	4	50	25	2	21	38	57	5	6	100	0	0	31	52	42	6
C_4 grasses																
All studies	8	50	38	13	35	60	40	0	15	93	7	0	58	67	31	2
Whole-plot	1	0	0	100	11	45	55	0	4	100	0	0	16	56	38	6
Individual plant	7	57	43	0	24	67	33	0	11	91	9	0	42	71	29	0

of the cases), while a moderate percentage of studies reported some stimulatory effect for C_3 grasses (17% of the cases). For both study scales, the results of summing early, intermediate, and late defoliation treatments produced similar trends; C_4 grasses respond more negatively to defoliation than do C_3 grasses. Individual plant studies of C_4 grasses reported more negative responses (71%) compared to C_3 grasses (52%), and out of 42 cases no stimulatory effects were reported for the C_4 species. Likewise, at the whole-plot scale, 19% of C_3 studies reported an increase in reproductive biomass subsequent to defoliation, while stimulatory effects were reported in only 6% of the C_4 studies. This was a result of the strong negative response of C_4 grasses to intermediate and late defoliation treatments, which was reported in 60% and 93% of the studies respectively (Table 6).

In general, stimulation of reproductive biomass in individual plant studies was usually associated with morphological changes such as increased number of branches or basal rosettes leading to greater flower and fruit production without an associated decrease in seed number, weight, or viability. Stimulatory effects of defoliation were not reported in any of the studies that compared the response of grasses with variable grazing history. Historically grazed grass populations had equal or lower reproductive to vegetative biomass ratios than conspecifics from historically ungrazed sites.

Discussion

Early season grazing on the northern winter range of Yellowstone Park more than doubled the number of reproductive tillers per unit area across sites, despite similar aboveground biomass and vegetation cover inside and outside of exclosures at peak biomass. Correspondingly, the inflorescence mass per unit area was over twice as great in grazed compared with ungrazed plots. Stimulation of community level reproductive biomass by grazing is consistent with reports from agricultural systems. However, our results from Yellowstone are inconsistent with findings from other natural grassland systems (McNaughton 1979, O'Connor and Pickett 1992), where grazers directly consumed seed heads and reduce seed production. In the northern winter range of Yellowstone, migratory herds of elk and bison graze newly emerging vegetation early in the growing season, usually in April and May, then move off the sites. The seasonal pattern of grazing in Yellowstone's northern winter range matches management strategies developed to reduce removal of reproductive meristematic tissue and increase seed yield in agricultural systems (Young et al. 1996).

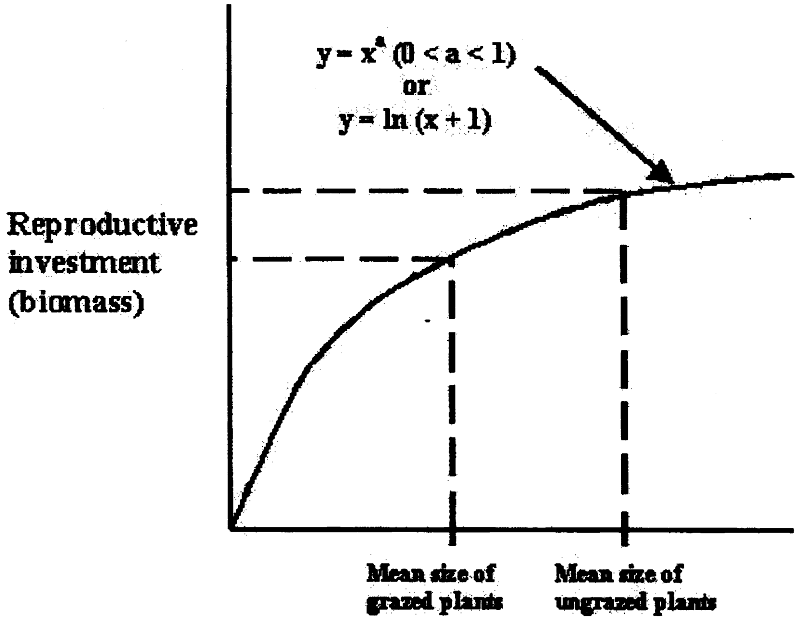

Fig. 1. The proposed function between mean plant size and investment in reproductive biomass for grasses in Yellowstone National Park. The saturating curve, along with evidence that mean plant size is smaller and density greater in grazed Yellowstone grassland, may explain the greater proportional reproductive biomass m^{-2} identified in our grazed plots.

Grazer mediated changes in plant species composition, implicated in other seed production or seed bank studies (Jones 1968, Kinucan and Smeins 1992, O'Connor and Pickett 1992, Willms and Quinton 1995), are not likely to explain the results from Yellowstone grasslands. First, species similarity measures between treatments were high. In addition, species found in different proportions inside and outside of exclosures at 1 site were often found at inverse proportions at another site; this lowered percentage similarity between treatments but also argues strongly against differences in reproductive biomass across exclosures resulting from an artifact of species compositional differences. Finally, prior studies have found no differences in species composition between communities inside and outside of the Yellowstone exclosures (Houston 1982, Coughenour 1991, Singer 1995, Stolgren et al. 1999, Augustine and Frank 2001).

The increase in reproductive tiller density by grazers is consistent with the phenomenon of herbivory increasing vegetative tillering in a number of grasses (Jewiss 1972, Detling and Painter 1983, Belsky 1986b). However, reductions in floret number per tiller in grazed plots suggests that defoliation may have an inhibitory effect per plant, but a stimulatory effect when plants are measured per unit area. A potential explanation might be the general relationship between reproductive output and plant size and the effects of grazers on reducing plant size and increasing plant density. In addition to this study, large herbivores reduced bunchgrass basal size in several grasslands (Hickey 1961, Butler and Briske 1988, Pfeiffer and Hartnett 1995). Thus, if a positive saturating function of reproductive investment on plant size exists for Yellowstone grasses (Fig. 1), such as has been described for plants elsewhere (Crawley 1983), smaller plants that result from grazing might invest relatively more in reproductive growth. In addition to influencing plant size, 2 lines of evidence suggest that plant density differed between grazed and ungrazed plots. First, grass tiller density was greater in grazed plots for the 3 sites measured. Second, that biomass was not statistically different inside and outside exclosures, but grazed plants were smaller, further suggests plant density was greater in grazed plots. Therefore, the stimulation of reproductive biomass observed in plots in our study may be the result of grazers promoting more dense populations of smaller individuals that allocated proportionally more to reproduction than ungrazed grasses.

Thus, the stimulation of reproductive biomass subsequent to defoliation may result from 2 different mechanisms, which may be identifiable at different scales. 1) Reproductive biomass per individual is increased because plants allocate more biomass to reproduction after defoliation; this mechanism could be identified in studies of individual plants. 2) Reproductive biomass per individual is reduced or unaffected, but since plants are smaller and more dense per unit area, community-level reproductive biomass is greater subsequent to defoliation; this mechanism could be identified in whole-plot studies. Both mechanisms will be influenced by the phenological stage of vegetation at the time of defoliation, but the latter less so because a community-level stimulatory effect can result even if reproduction per individual is decreased. In addition, precipitation, and more importantly soil water, will influence phenological stage and the capacity for regrowth after grazing.

The literature clearly demonstrates that the timing of grazing is of critical importance to the production of reproductive biomass in many of the studies that we reviewed. The grazing of leaf material before internode expansion does not result in the removal of apical meristems and thus regrowth can ensue if soil water is adequate, whereas grazing after internode elongation may remove terminal meristems of developing floral buds (Jewiss 1972). Thus, timing and intensity of grazing in natural systems determines the outcome of grazing on reproductive tiller number and seed yield (Young et al. 1996, O'Connor and Pickett 1992). Hebblethwaite and Clemence (1983) reported that if grazing of perennial ryegrass (*Lolium perenne* L.) ceased before spiklet initiation, seed yield was not affected; if grazing continued after the initiation of spiklets, seed yield was greatly depressed. Similar results have been reported for tall fescue (*Festuca arundinacea* Schreb.) (Watson and Watson 1982), spring oats (*Avena* sp.) (Morris and Gardner 1958, Gardner and Wiggins 1960) and wheat (*Triticum aestivum* L.) (Finnell 1929, Aldrich 1959, Winter and Thompson 1987).

In addition to the importance of phenological stage controlling the response of plants to grazing, environmental factors may interact with timing of herbivory. Microclimatic conditions conducive for regrowth often vary over the growing season. For example, in western U.S. rangelands, where soil water typically declines throughout the growing season, plants may not be able to recover if grazed late in the season when precipitation has little influence on regowth (Sneva 1977). Thus, phenology and growth conditions probably both play roles in the allocation to reproductive tissue by grazed plants.

Whether or not smaller, denser plants, that allocate relatively more to reproduction, explain increases in reproductive biomass in the previous studies is not known. Herbivory increases plant density in some natural communities (i.e. Crawley 1983), yet the generality of this response has not emerged from the literature. Alternatively, defoliation may increase reproductive biomass per plant, without an associated change in plant density. For example, Young et al. (1996) reported that grazing stimulated reproductive tiller production per unit area with no difference in plant density between grazed and control plots, suggesting that it was the phenological stage at the time of defoliation that was more important than density in their study. Additionally, results from agricultural studies usually reflect short-term grazing treatments rather than the longer time periods that may be necessary to produce differences in plant density. Thus, in studies that measure the influence of short-term defoliation, on the scale of seasons, the phenological stage of vegetation is likely more important than population level effects such as plant density. The results from studies that measured reproductive biomass at either of 2 scales, whole-plot and individual plant level, are complex but seem to suggest whole plot studies report stimulatory effects more often than individual studies. This suggests population level effects that lead to greater reproductive biomass per area, such as increased densities of smaller individuals with higher fecundity, might be implicated in at least some cases. Another possibility is that plant defoliation is less severe in whole-plot studies than in individual plant studies. Most of the individual plant studies reviewed were clipped as opposed to grazed, and previous research suggests that clipping to simulate grazing results in more severe defoliation than does actual grazing (Hart and Balla 1982).

Our review of the literature suggests that, in terms of sexually reproductive biomass, C_4 plants exhibit a more negative response to defoliation than do C_3 plants. This finding is intriguing because, in general, C_4 plants are more grazing tolerant than their C_3 counterparts (Heckathorn et al. 1999). It is not known why C_4 plants are more grazing tolerant than C_3 plants, or why defoliation suppresses sexually reproductive tissues during regrowth, however, physiological differences and different environmental conditions may be responsible. For example, C_4 plants have higher water and nutrient use efficiencies and maximum rates of photosynthesis, which may favor reallocation of biomass for vegetative versus sexual reproduction (Heckathorn et al. 1999). On the other hand, C_3 and C_4 plants vary in their distribution across rainfall and temperature gradients (e.g. Epstein et al. 1997 for the U.S. Great Plains). Growth conditions of C_4 may, on average, favor greater allocation to leaves and roots after defoliation and less to sexual reproduction. However, the relative importance of physiology and environment in producing different responses of C_3 and C_4 grasses to defoliation requires specific testing.

Our study was designed to address both community level and individual plant level effect of grazing on seed production of grasslands in Yellowstone National Park. We found that early season grazing leads to greater numbers of reproductive tillers per unit area and did not decrease seed yield per unit area. We suggest that grazing in Yellowstone's Northern winter range maintains populations of smaller, denser grasses that, if grazed early, produce (per unit area) more reproductive tillers, equal numbers of seed, and more reproductive biomass than where grazers are absent. These results, together with our literature review, suggest that the timing and organizational scale (individual versus community) of the plant trait measured may differentially influence interpretation of how herbivory influences seed production. Thus, grazing may reduce individual plant fitness, but need not reduce the reproductive capacity of plant communities. However, to answer this, one must assess whether or not grazing affects seed viability in addition to numerical production as was done in our study. There is evidence that defoliation history does not influence seed viability (Orodho et al. 1998), but whether seeds produced by grazed and ungrazed Yellowstone grasses exhibit similar viability is not known. We suggest that early spring defoliation in Yellowstone National Park's northern winter range has played a role in the persistence of grazed plant communities by maintaining community level seed production. Future studies that emphasize the individual versus per unit area effects of grazing on reproductive output may aid in understanding community organization and the sustainability of grazed ecosystems.

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Appendix 1. Defoliation impacts on the production of reproductive biomass, from 118 published sources, reported as positive (+), negative (–), or no effect (0). Results are separated by the timing of defoliation (early, intermediate, or late) when possible. Study species are grouped hierarchically by study scale (whole plot or individual plant), vegetation type (graminods, non-graminoids, or seed bank study), method of defoliation (cutting, grazing, transplant of previously grazed species, or removal of flowers or seeds), and identity of herbivore (ungulate or insect). References and notes are identified with superscripts. Study types are field (F), laboratory (L), and garden (G), which includes planted agricultural fields.

Species	Plant Functional Type	Study Type	Timing			Citation
			Early	Intermediate	Late	
Whole-plot studies						
Graminiods						
Grazing						
Agropyron spicatum (Prush) Scribn. & Smith	C_3 grass	F		–		Hanson and Stoddart 1941
Andropogon greenwayi Napp.	C_4 grass	F		–		Belsky 1986c
Avena sp^{1}	C_3 grass	G	0		0 (+)	Sprauge1954
Avena sp.^{2}	C_3 grass	G		–		Washko 1947
Festuca idahoensis Elmer	C_3 grass	F		0		Olson et al. 1997
Hordeum sp.^{2}	C_3 grass	G		–		Washko 1947
Lolium sp.^{3}	C_3 grass	G		– (+)		Brown 1980
Lolium multiflorum Lam.^{4}	C_3 grass	G	+ (0)	+ (0)	+ (0)	Young et al. 1996
Lolium multiflorum Lam.	C_3 grass	G	–			Herron 1976
Lolium perenne L.	C_3 grass	G	0	0		Hebblethwaite and Clemence 1983
Lolium perenne L.^{5}	C_3 grass	G	0		0 (–)	Roberts 1958
Phleum sp.^{5}	C_3 grass	G	0		– (0)	Roberts 1958
Secale sp.^{1}	C_3 grass	G	+		– (–)	Sprauge 1954
Secale sp.^{2}	C_3 grass	G		–		Washko 1947
Triticum aestivum L.^{6}	C_3 grass	G	–	–	–	Pumphrey 1970
Triticum aestivum L.	C_3 grass	G	+			Sharrow and Motazedian 1987
Triticum aestivum L.^{1}	C_3 grass	G	+		– (–)	Sprauge 1954
Triticum aestivum L.^{2}	C_3 grass	G	–			Washko 1947
Triticum aestivum L.^{7}	C_3 grass	G	0	–	–	Winter and Thompson 1987
Triticum dicoccoides	C_3 grass	G		0 (+)	– (–)	Noy-Meir and Briske 2002
Unspecified grasses	C4 grass	F		–		McNaughton 1979
Cutting						
Agropyron spicatum (Prush) Scribn. & Smith	C_3 grass	F	–	–	–	Blaisdell and Pechanec 1949

Species	Plant Functional Type	Study Type	Timing			Citation
			Early	Intermediate	Late	
Agropyron trachycaulum	C_3 grass	F	0	+	0	Mueggler 1967
Andropogon gayanus Kunth.	C_4 grass	F	+			Andrade and Thomas 1981
Andropogon gerardi Vit.	C_4 grass	G		0		Neiland and Curtis 1956
Andropogon scoparius Michx.	C_4 grass	G		0		Neiland and Curtis 1956
Avena sp.[10]	C_3 grass	G	0 (0)	– (0)	– (–)	Morris and Gardner 1958
Avena sp.[11]	C_3 grass	G		– (–)		Thakur and Shands 1954
Avena sp.	C_3 grass	G			–	Gardner and Wiggans 1960
Bouteloua curtipendula Michx.	C_4 grass	G		0		Neiland and Curtis 1956
Bromus marginatus	C_3 grass	F	+	+	+	Mueggler 1967
Bromus mollis[12]	C_3 grass	G	+	0	–	Laude et al. 1957
Bromus ruben[12]	C_3 grass	G	+	0	–	Laude et al. 1957
Dactylis glomerata	C_3 grass	G	0	–	–	Roberts 1965
Elymus canadensis L.	C_3 grass	G		0		Neiland and Curtis 1956
Festuca arundinacea Schreb.[13]	C_3 grass	F	+ (0)			Kroth et al. 1977
Festuca arundinacea Schreb.[14]	C_3 grass	G	0	0 (–)	–	Watson and Watson 1982
Festuca elatior	C_3 grass	G	0	–	–	Roberts 1965
Festuca idahoensis Elmer	C_3 grass	F	–	–	–	Mueggler 1967
Hordeum sp.[15]	C_3 grass	G	+	–	–	Hubbard and Harper 1949
Hordeum sp.[11]	C_3 grass	G		– (–)		Thakur and Shands 1954
Hordeum murinum L.	C_3 grass	F	0	–	–	El-Shatnawi et al. 1999
Hordeum vulgare L. emend Lam.	C_3 gras	G	+	0		Day et al. 1968
Lolium multiflorum Lam.[16]	C_3 grass	G	0	– (0)	–	Bean et al. 1979
Lolium perenne L.	C_3 gras	G	0	–	–	Hebblethwaite and Clemence 1983
Lolium perenne L.	C_3 grass	G	0	–	–	Roberts 1965
Panicum virgatum L.	C_4 grass	G		0		Neiland and Curtis 1956
Panicum virgatum L.[17]	C_4 grass	G		–	–	George et al. 1990
Panicum virgatum L.[18]	C_4 grass	G		0 (–)	– (–)	Brejda et al. 1994
Pennisetum hybrid[19]	C_4 grass	G		0	–	Diz et al. 1995
Phleum sp.	C_3 grass	G	0	–	–	Roberts 1965
Poa pratensis L.[20]	C_3 grass	G		0 (0)	0 (0)	Ahlgren 1938
Poa pratensis L.	C_3 grass	G	+ (+)	0 (+)	0 (0)	Evans 1975
Secale sp.[15]	C_3 grass	G	+	–	–	Hubbard and Harper 1949
Secale sp.[10]	C_3 grass	G	+ (+)	0 (+)	– (0)	Morris and Gardner 1958
Sorghastrum nutans (L.) Nash	C_4 grass	G		–		Neiland and Curtis 1956
Triticum aestivum L.[21]	C_3 grass	G	+	0	–	Cutler et al. 1949
Triticum aestivum L.[15]	C_3 grass	G	+	–	–	Hubbard and Harper 1949
Triticum aestivum L.[10]	C_3 grass	G	0 (0)	– (0)	– (–)	Morris and Gardner 1958
Triticum aestivum L.[10]	C_3 grass	G		0 (0)		Thakur and Shands 1954
Triticum aestivum L.[7]	C_3 grass	G	–	–	–	Pumphrey 1970
Triticum aestivum L.[22]	C_3 grass	G	+ (0)	0 (+)	– (+)	Miller et al. 1993
Triticosecale hybrid[22]	C_3 grass	G	0 (0)	– (–)	– (–)	Miller et al. 1993
Non-graminiods						
Grazing						
Medicago murex Zodiac	leguminous forb	G	0	–	0	Conlan et al. 1994
Ornitopus compressus L.	leguminous forb	G	–	–	–	Conlan et al. 1994
Trifolium subterraneum L.[23]	leguminous forb	G		+	0 (+)	Steiner and Grabe 1986
Trifolium subterraneum L.[24]	leguminous forb	G	0	+	+	Conlan et al. 1994
Trifolium subterraneum L.[24]	leguminous forb	G	0	0	0	Conlan et al. 1994
Trifolium subterraneum L.[24]	leguminous forb	G	–	–	–	Conlan et al. 1994
Trillium sp.	perennial forb	F		–		Augustine and Frelich 1998
Cutting						
Aster integrifolius	perennial forb	F	0	–	–	Mueggler 1967
Balsamorhiza sagitta[9] (Prush) Nutt.	perennial forb	F	0	–	–	Blaisdell and Pechanec 1949
Glycine max (L.) Merr.[25]	leguminous forb	G		0 (–)	– (–)	Begum and Eden 1965
Glycine max (L.) Merr.[26]	leguminous forb	G	+ (+)		0 (–)	Pickle and Caviness 1984
Glycine max (L.) Merr.[26]	leguminous forb	G	0 (0)	0 (–)		Teigen and Vorst 1975
Glycine max (L.) Merr.	leguminous forb	G	0	–	–	Thomas et al. 1974
Potentilla gracilis	perennial forb	F	0	–	–	Mueggler 1967
Ricinus communis L.[27]	ann. or per. forb	G	0 (0)	0 (0)	0 (–)	Kittock and Williams 1967
Trifolium subterraneum L.	leguminous forb	G	0	–	–	Collins et al. 1983
Trifolium incarnatum L.	leguminous forb	G	0	–	–	Knight and Hollowell 1962

Species	Plant Functional Type	Study Type	Timing Early	 Intermediate	 Late	Citation
Seed banks						
Grazing						
Grasses and forbs[28]		F		0		Kinucan and Smeins 1992
Grasses and forbs[28]		F		+		Willms and Quinton 1995
Individual Plant Studies						
Graminiods						
Grazing						
Andropogon gerardii Vit.	C_4 grass	F		0		Vinton and Hartnett 1992
Festuca idahoensis Elmer	C_3 grass	F		0		Olson et al. 1997
Lolium multiflorum Lam.	C_3 grass	G		+		Herron 1976
Oryzopsis hymenoides (Roem. & Schult.) Ricker	C_3 grass	F		0		Trlica and Orodho 1989
Oryzopsis hymenoides (Roem. & Schult.) Ricker	C_3 grass	F		0		Orodho et al. 1998
Panicum virgatum L.	C_4 grass	F		0		Vinton and Hartnett 1992
Clipping or Defoliation						
Agropyron desertorum (Fisch. Ex Link) Schult.	C_3 grass	F		–		Caldwell et al. 1981
Agropyron spicatum (Prush) Scribn. & Smith	C_3 grass	F		–		Caldwell et al. 1981
Agropyron spicatum (Prush) Scribn. & Smith	C_3 grass	F	–		–	Mueggler 1972
Agropyron spicatum (Prush) Scribn. & Smith	C_3 grass	F	0		–	Mueggler 1975
Agropyron spicatum (Prush) Scribn. & Smith	C_3 grass	F	–	–		McLean and Wikeem 1985
Andropogon gerardii Vit.	C_4 grass	L		–		Hartnett 1989
Andropogon gerardii Vit.	C_4 grass	L		–		Heckathorn and Delucia 1996
Andropogon semiberbis (Nees) Kunth.	C_4 gras	G		–		Silva and Raventos 1999
Aristida armata[29]	C_4 grass	L			–	Brown 1985
Asrebla lappacea[29]	C_4 grass	L			–	Brown 1985
Bouteloua curtipendula Michx.	C_4 grass	F	0	–	–	Sims et al. 1971
Bromis inermis Leyss	C_3 grass	F	0	0	–	Harrison and Romo 1994
Cenchrus ciliaris[29]	C_4 grass	L			–	Brown 1985
Cynodon dactylon	C4 grass	L	0			Van Auken 1994
Digitaria ammophila[29]	C_4 grass	L			–	Brown 1985
Elymus lanceolatus[30]	C_3 grass	F		–		Jones and Nielson 1993
Elymus lanceolatus[30]	C_3 grass	F		– (0)		Jones and Nielson 1993
Elymus lanceolatus[30]	C_3 grass	F		– (0)		Jones and Nielson 1993
Elymus lanceolatus[30]	C_3 grass			0		Jones and Nielson 1993
Elymus lanceolatus[30]	C_3 grass			0		Jones and Nielson 1993
Eriophorum vaginatum L.[31]	C_3 sedge	F	+	0	–	Archer and Tieszen 1983
Eulalia trispicata[32]	C_4 grass	L	– (–)	– (0)	– (–)	Pemadasa and Amarasinghe 1982
Festuca idahoensis Elmer	C_3 grass	F		0	–	Mueggler 1975
Heteropogon contortus[33] (L.) P. Beauv. ex Roem. & Schult.	C_4 grass	L		0 (0)		Goergen and Daehler 2001
Kyllinga nervosa Steud.	C_4 sedge	L		–		McNaughton et al. 1983
Kyllinga nervosa Stued.	C_4 sedge	L		–		Ruess et al. 1983
Luzula arcuata[34] Swartz ssp. *confusa* (Lindeb.) Blytt	C_3 sedge	L		0 (–)		Brathen et al. 2000
Panicum virgatum (L.) var. Caddo	C_4 grass	F	0	–	–	Sims et al. 1971
Panicum virgatum L.	C_4 grass	L		–		Hartnett 1989
Panicum virgatum L.[35]	C_4 grass	L		+		Hartnett 1989
Pennisetum polystachyon[32]	C_4 grass	L	– (0)	– (0)	– (0)	Pemadasa and Amarasinghe 1982
Pennisetum setaceum[33] (Forssk.) Chiov	C_4 grass	L		0 (–)		Goergen and Daehler 2001
Schizachyrium scoparium[36] (Michx.) Nash	C_4 grass	G		–		Wallace 1987
Schizachyrium scoparium (Michx.) Nash	C_4 grass	L		–		Heckathorn and Delucia 1996
Spartina pectina Link	C_4 grass	L		–		Heckathorn and Delucia 1996
Themeda triandra	C_4 grass	F	–		–	Tainton and Booysen 1965

Species	Plant Functional Type	Study Type	Timing Early	 Intermediate	 Late	Citation
Thyridolepis mitchelliana[29]	C_4 grass	L			–	Brown 1985
Triticum aestivum L	C_3 grass	G	–		–	Simmons et al. 1982
Triticum dicoccoides[37]	C_3 grass	G		0 (0)	– (0)	Noy-Meir and Briske 2002
Trachypogon plumosus (Humb. & Bonpl.) Nees	C_4 grass	G		–		Silva and Raventos 1999
Transplants with Different Grazing Histories						
Agropyron smithii Rydb.	C_3 gras	L		–		Painter et al. 1989
Andropogon gerardii Vit.	C_4 grass	L		0		Painter et al. 1993
Bouteloua curtipendula var. *caespitosa* Gould & Kapadia	C_4 grass	L		–		Smith et al. 2000
Bouteloua gracilis (H. B. K.) Griffiths	C_4 grass	L		–		Jaramillo and Detling 1988
Bouteloua gracilis (H. B. K.) Griffiths	C_4 grass	L		–		Painter et al. 1989
Bouteloua gracilis (H. B. K.) Griffiths	C_4 grass	L		0		Painter et al. 1993
Danthonia linkii Kunth.	C_3 grass	L		0		Scott and Whaley 1984
Danthonia racemosa R. Br.	C_3 grass	L		0		Scott and Whaley 1984
Danthonia richardsonii Cashmore	C_3 grass	L		0		Scott and Whaley 1984
Oryzopsis hymenoides (Roem. & Schult.) Ricker	C_3 grass	F		0		Trlica and Orodho 1989
Oryzopsis hymenoides[38] (Roem. & Schult.) Ricker	C_3 grass	F		0 (–)		Orodho et al. 1998
Schizachyrium scoparium Michx.	C_4 grass	L		0		Painter et al. 1993
Seed Removal						
Triticum aestivum L.	C_3 grass	G	+		0	Simmons et al. 1982
Zea mays L.	C_4 grass	G		+		Dyer 1975
Zea mays L.[39]	C_4 grass	G	+	–	–	Woronecki et al. 1980
Non-graminiods						
Natural Defoliation						
Insects						
Allium porrum L.[39]	biennial forb	G	0	+	–	Boscher 1979
Aristolochia reticulata	perennial forb	F		–		Rausher and Feeny 1980
Cardamine cordifolia	perennial forb	F		–		Louda 1984
Chelone sp.	perennial forb	F		–		Stamp 1984
Jurinea mollis Ascherson[40]	perennial forb	F		+		Inouye 1982
Mirabilis hirsuta (Prush) MacM.	perennial forb	F		–		Kinsman and Platt 1984
Pastinaca sativa L.[41]	biennial forb	F		0 (–)		Hendrix 1979
Quercus robar L.	tree	F		–		Crawley 1985
Rhus glabra L.	perennial shrub	F		–		Strauss 1991
Rosa nutkana Presl.	perennial shrub	F		–		Myers 1981
Rumex crispus L.	perennial forb	F		0		Bentley et al. 1980
Rumex obtusifolius L.	perennial forb	F		–		Bentley et al. 1980
Salix lasiolepis	perennial shrub	G		–		Sacchi et al. 1988
Solidago altissima L[42]	perennial forb	L		– (0)		Meyer and Root 1993
Grazers or Browsers						
Baptista braceata[43] Muhl. ex Ell. var. glabrescens (Larisey) Isley	leguminous forb	F		0 (0)		Damhoureyeh and Hartnett 1997
Echium plantagineum L.	annual forb	F		–		Smyth et al. 1997
Jurinea mollis Ascherson	perennial forb	F		–		Inouye 1982
Pteronia empetrifolia D. C.	perennial shrub	F		–		Milton 1995
Rhus glabra L.[44]	perennial shrub	F		+		Strauss 1991
Salvia azurea Lam.[43]	perennial forb	F		0 (0)		Damhoureyeh and Hartnett 1997
Solidago missouriensis Nutt.[43]	perennial forb	F		+ (0)		Damhoureyeh and Hartnett 1997
Veronia baldwinii Torr.[43]	perennial forb	F		0 (+)		Damhoureyeh and Hartnett 1997
Clipping or Defoliation						
Acacia farnesiana L.	tree	F		–		Rockwood 1973
Albutilon theophrasti Medic.[45]	annual forb	L		0 (–)		Lee and Bazzaz 1980
Anthyllis vulneraria L.[46]	leguminous forb	L		0 (–)		Bastrenta and Belhassen 1992
Aralia nudicaulis L.	perennial forb	F		–		Edwards 1985

Species	Plant Functional Type	Study Type	Timing			Citation
			Early	Intermediate	Late	
Aristolochia reticulata Nutt.	perennial forb	L		0		Fowler and Rausher 1985
Astrocaryum mexicanum[47] Liebm.	understory palm	F		– (+)		Mendoza et al. 1987
Bauhinia ungulata L.	tree	F		–		Rockwood 1973
Brassica napus L.[48]	annual forb	L			0 (–)	Pechan and Morgan 1985
Catalpa speciosa (Warder ex Barney) Engelm.	tree	F		–		Stephenson 1980
Cochlospermum vitifolium (Willd.) Spreng.	tree	F		–		Rockwood 1973
Crescentia alata H. B. K.	tree	F		–		Rockwood 1973
Desmanthus virgatus[49]	leguminous shrub	L	–			Muir and Pitman 1991
Desmodium heterocarpon[49]	leguminous shrub	L	–			Muir and Pitman 1991
Epilobium angustifolium L.[50]	perennial forb	L	0		– (–)	Michaud 1991
Erythroxylum havanense[55]	proleptic shrub	F		0 (–)		Dominguez and Dirzo 1994
Gentianella campestris (L.) Borner	biennial forb	F	0	+	0	Lennartsson et al. 1998
Gliricidia sepium (Jacq.) Steud.	tree	F		–		Rockwood 1973
Indigofera spinosa Forsk.[51]	leguminous shrub	F		– (–)		Keya 1997
Ipomopsis aggregata (Prush) V. Grant	perennial forb	F		+		Paige and Whitham 1987
Ipomopsis arizonica (Greene) Wherry	perennial forb	F	0		–	Maschinski and Whitham 1989
Melampyrum pratense L.[52]	annual forb	F		– (–)		Lehtila and Syrjanen 1995
Melampyrum sylvaticum L.[52]	annual forb	F		+ (–)		Lehtila and Syrjanen 1995
Piper arieianum C. DC.	perennial shrub	F		–		Marquis 1984
Rubus chamaemorus L.[53]	annual forb	F		0 (–)		Agren 1989
Saponaria officinalis L.[54]	perennial forb	F		0 (–)		Lokker and Cavers 1995
Spondias purpurea L.	tree	F		–		Rockwood 1973
Triglochin palustris L.	perennial forb	F		0		Mulder and Ruess 1998
Trillium grandiflorum Michx.	perennial forb	F		0		Lubbers and Lechowicz 1989
Vicia sativa L.	leguminous forb	G		–		Koptur et al. 1996
Flower and Seed Removal						
Melampyrum pratense L.	annual forb	F		0		Lehtila and Syrjanen 1995
Melampyrum sylvaticum L.	annual forb	F		–		Lehtila and Syrjanen 1995

1 – Autumn (early) and spring (late) grazing; spring after fall in parentheses
2 – Spring grazing to March 15 + fall grazing into November
3 – Results for number of fertile tillers in parentheses
4 – Results are for number of fertile tillers with second year in parentheses; no effect of grazing on seed production in either year
5 – Winter (early) and spring (late) grazing; spring after winter in parentheses
6 – Early treatment similar in timing to intermediate treatment in other studies
7 – Severe grazing in all treatments
8 – Results are for plot level biomass, effect on plot level ratio of reproductive:total biomass shown in parentheses; see reference for taxonomic reference.
9 – Severe clipping; fall clipping had no effect
10 – 2x fertilization results shown in parentheses
11 – Early (May) and intermediate (June) clippings are late in comparison to other studies; 2x fertilization in parentheses
12 – Weight of spiklet decreased with clipping date
13 – Increased at 1 site, no effect at another; results are for no N addition
14 – No effect on panicle m^{-2}; spikes $panicle^{-1}$ shown in parentheses
15 – Results shown for moderate intensity; severe cutting decreased seed production in all treatments
16 – Effect on tiller number in parentheses
17 – Their first defoliation treatment (May 30) was intermediate in relation to other defoliation treatments
18 – No effect of intermediate treatment (late may) on reproductive tiller density in year 1, negative effects in year 2 because tiller elongation had begun; seed yields shown in parentheses
19 – Intermediate treatment cut in June and August, late treatment cut in June, August and September
20 – No significant differences, but the author interpreted the continuous increase in total seed biomass of clipped plants as trend towards increased production. Results of fertilization shown in parentheses
21 – Results shown for normal year; all results were negative for drought year
22 – Year 2 in parentheses
23 – Extended grazing in parentheses, includes intermediate and late grazing
24 – Different varieties: T.s. subterraneum cv. Karridale, var. brachycalycinum cv. Clare, var. yanninicum cv. Trikkala
25 – No early treatment applied; parentheses show results of severe defoliation
26 – Results are for 1/4 defoliation; results for 1/2 defoliation are shown in parentheses
27 – Results are for 1/2 defoliation; 3/4 defoliation shown in parentheses; complete defoliation reduced reproductive biomass in all treatments
28 – Associated with species compositional changes
29 – All species had begun to flower when defoliation was initiated
30 – Different hybrids of *Elymus lanceolatus* ssp. *wawawaaiensis* (Scribner & Gould) J.R. Carlson & D. R. Dewey and E. l. ssp. *lanceolatus* (Scribner & J. G. Smith) Gould
31 – Results for different frequency treatments; only fall recovery defoliation increased flowering
32 – Experiment conducted on seedlings; data are for intermediate densities, low density reported in parentheses
33 – Results are for seed production, effect on time to flower reported in parentheses
34 – Data are for flowers $plant^{-1}$ in second season when cut to 6 cm, data for plants cut to 3 cm in parentheses
35 – Grown from ramets rather than seeds

36 – Result is for entire reproductive tiller (stem + flowers); clipped plants did not flower
37 – Effects for survival of reproductive plants after clipping, results for spikelet number per reproductive plant shown in parentheses; see paper for nomenclature
38 – Results of clipping shown in parentheses
39 – Results are for low, moderate, and high intensity treatments
40 – Increased the number of basal rosettes
41 – Results depended on size; results for small plants shown in parentheses
42 – Beetles reduced seed production but aphids (in parentheses) had no effect
43 – Results are for grazing by cattle; results for bison grazing shown in parentheses
44 – Increase in the number of stems capable of reproducing
45 – Results were density dependent; high density treatment shown in parentheses
46 – Results of proportion of plants flowering shown in parentheses
47 – Results of the removal of old portions of leaves shown in parentheses
48 – Defoliation at anthesis; no effect on seed number, negative result on seed pod weight shown in parentheses
49 – Autumn defoliation; controls produced very little reproductive biomass so results are difficult to interpret
50 – Continuous defoliation decreased reproductive biomass
51 – 3 intensities and 2 frequencies all reduced pod output; effects of irrigating shown in parentheses
52 – Results are for clipping branches; results of defoliation given in parentheses
53 – No effects on seed number; effects on seed mass and complete defoliation shown in parentheses
54 – Effects on flower removal shown in parentheses
55 – Result is for 25% defoliation; effects of 100% defoliation shown in parentheses.

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Bowen ratio versus canopy chamber CO_2 fluxes on sagebrush rangeland

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Abstract

Because of their expansiveness, sagebrush (*Artemisia* spp.)-steppe rangelands could contribute significantly to the global carbon budget. However, it is important to determine if there are differences between methods for determining CO_2 fluxes on these rangelands. The objective of this study was to compare the Bowen ratio-energy balance and canopy chamber techniques for measuring CO_2 fluxes in a sagebrush-steppe ecosystem. A Bowen ratio-energy balance system was installed at a sagebrush-steppe site near Dubois, Ida., U.S.A to continuously measure the vertical gradients of air temperature, water vapor, and CO_2 concentration in conjunction with associated micrometeorological characteristics. The canopy chamber technique, which employed a 1-m^2 (1,020 liter) clear plexiglass/plastic film chamber in combination with a portable gas exchange system, was used periodically during May through August across 4 years (1996–1999) to obtain instantaneous measurements of CO_2 fluxes across 3 replicate blocks during a 2-min. measurement period. For the same measurement dates and times across the 4 years of study, CO_2 fluxes ranged from –0.22 to 0.55 mg m^{-2} sec^{-1} for the Bowen ratio-energy balance technique and from –0.18 to 0.48 mg m^{-2} sec^{-1} for the canopy chamber technique. Estimates of CO_2 fluxes by the 2 techniques were not statistically different ($P > 0.05$) for the early (May) and mid-season (June to mid-July) portions of the growing season; however, fluxes measured by the 2 techniques were significantly different ($P < 0.05$) for the late-season period (late-July to late-August). Despite this difference during the hot-dry, late-season period, flux estimates from the 2 techniques were significantly and positively correlated during the early ($r^2 = 0.71$), mid- ($r^2 = 0.88$), and late- ($r^2 = 0.72$) season periods. Thus, both techniques showed similar patterns of CO_2 fluxes at our sagebrush-steppe study site across 4 years of study, although caution should be used when the canopy chamber technique is used during hot, dry conditions.

Key Words: *Artemisia* spp., carbon dioxide fluxes, CO_2 exchange, Bowen ratio, canopy chambers, closed chambers, micrometeorology, rangeland

Resumen

Debido a su expansión, las pastizales de estepa de "Sagebrush" (*Artemisia* spp.) Pudieran contribuir significativamente al balance global del carbón. Sin embargo, es importante determinar si hay diferencias entre métodos para determinar los flujos de CO_2 en estos pastizales. El objetivo de este estudio fue comparar el balance de energía de la relación Bowen y la técnica de cámara de copa para medir los flujos de CO_2 en un ecosistema de estepa de "Sagebrush". Un sistema de balance de energía de la relación Bowen se instaló en un sito de estepa de "Sagebrush" cerca de Dubois, Ida. E.U.A. para medir continuamente los gradientes verticales de temperatura del aire, vapor de agua y concentración de CO_2, en conjunto con las característica micrometerológicas asociadas. La técnica de la cámara de copa, la cual empleó una película plástica transparente de plexiglás de 1m^2 (1,020 litros) en combinación con un sistema portátil de intercambio de gases, se utilizó periódicamente de Mayo a Agosto durante 4 años (1996–1999) para obtener mediciones instantáneas de los flujos de CO_2 a través de 3 bloques de repetición durante un periodo de medición de 2 minutos. Para las mismas fechas y tiempos de medición a través de los 4 años del estudio, los flujos de CO_2 variaron de –0.22 to 0.55 mg m^{-2} sec^{-1} para la técnica de balance de energía de la relación Bowen y de –0.18 to 0.48 mg m^{-2} sec^{-1} para la técnica de la cámara de copa. Las estimaciones del flujo de CO_2 de las 2 técnicas no fueron estadísticamente diferentes ($P > 0.05$) para las porciones de inicios (Mayo) y mediados (Junio a Julio) de la estación de crecimiento; sin embargo, los flujos medidos por las 2 técnicas fueron significativamente diferentes ($P < 0.05$) a fines de la estación de crecimiento (fines de Julio a fines de Agosto). A pesar de la diferencia del flujo durante el período caliente y seco (que es a fines de la estación de crecimiento), las estimaciones obtenidas por las dos técnica estuvieron significativa y positivamente correlacionados durante los periodos de inicio ($r^2 = 0.71$), mediados ($r^2 = 0.88$) y fines ($r^2 = 0.72$) de la estación. A lo largo de los 4 años de estudio, ambas técnicas mostraron patrones similares de flujo de CO2 en nuestro sitio de estudio de la estepa de "Sagebrush", aunque se debe poner cuidado cuando se use la técnica de cámara de copa durante condiciones clientes y secas.

Estimates of C fluxes in ecosystems can be obtained by various methods. Measurement of C stocks can provide estimates of C fluxes across decades or longer (Bliss et al. 1995, Gilmanov and Oechel 1995, Fallon et al. 1998). For shorter time frames, such as within a day or across a growing season, C fluxes must be esti-

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mated with micrometerological techniques such as the eddy covariance and Bowen ratio-energy balance techniques (Rosenberg et al. 1983, Frank and Dugas 2001, Sims and Bradford 2001), or canopy chamber methods (Vourlitis et al. 1993, Angell and Svejcar 1999). A detailed description of micrometeorological techniques and the theories behind them can be found in Moncrieff et al. (1997) and for canopy chamber methods are reported in Reicosky (1990).

The eddy covariance technique is a direct method of determining CO_2 fluxes that measures vertical wind speed, wind direction, and CO_2 concentration of air moving past a sampling point. The eddy covariance method, however, requires expensive and electronically sophisticated equipment, complex data processing and quality assurance procedures, and until recently was not available commercially. In addition, net radiation, sensible heat flux, latent heat flux, and soil heat flux should be determined concurrently with the eddy covariance measurements to correct for lack of energy balance closure (Twine et al. 2000).

The Bowen ratio-energy balance technique is an indirect method of measuring CO_2 fluxes that quantifies the rate of diffusion down a concentration gradient. The Bowen ratio-energy balance method uses relatively simple instrumentation, but the technique has limitations in canopies with small gradients (Raupach 1988). The Bowen ratio-energy balance method also is difficult to apply during periods when net radiation is small, such as at sunrise and sunset. Although eddy covariance and Bowen ratio-energy balance techniques have shown acceptable agreement in semiarid environments (Unland et al. 1996), reliable surface energy fluxes were easier to determine with the Bowen ratio-energy balance method, but the eddy covariance method provided greater accuracy for short time periods. Both eddy covariance and Bowen ratio-energy balance techniques require relatively large areas and considerable labor for calibration and maintenance.

Techniques using canopy chambers are easy to use, equipment for the technique is relatively inexpensive (if a portable infrared gas analyzer is available), and they are adaptable to a wide range of field conditions (e.g., Reicosky 1990); however, canopy chamber methods are labor intensive, particularly for large-sized chambers. Costs associated with labor for the canopy chamber method can be particularly high if frequent measurements are required to provide detailed characterizations of CO_2 fluxes. In addition, high solar radiation can markedly increase air temperature inside chambers compared to ambient conditions unless air conditioning equipment is added to the chambers. As a result, without cumbersome air conditioning, the canopy chamber technique can only be used for brief exposure periods of several minutes so that canopy chamber determinations represent instantaneous flux values. Because canopy chambers are relatively easy to transport, experiments can be more easily replicated compared to experiments that use eddy covariance and Bowen ratio-energy balance techniques. A more detailed discussion of the particular advantages and disadvantages of the various techniques for measuring CO_2 fluxes is presented in Reicosky (1990) and Moncrieff et al. (1997).

Although rangelands occupy about 50% of the total world land surface area (Holechek et al. 1998), only limited data are available concerning CO_2 fluxes in rangeland ecosystems. The USDA-ARS Rangeland CO_2 Flux Network (Svejcar et al. 1997) was established to quantify CO_2 fluxes on rangelands of the western U.S.A. As part of this effort, Angell et al. (2001) found generally good agreement between Bowen ratio-energy balance and canopy chamber measurement techniques at 2 sites dominated by sagebrush (*Artemisia* spp.); however, these measurements were conducted during only 1 growing season. In an effort to evaluate the 2 measurement techniques across a broader range of environmental conditions and to test their agreement across multiple growing seasons, we designed this current study to compare CO_2 fluxes measured with canopy chamber and Bowen ratio-energy balance techniques across 4 growing seasons in a sagebrush-steppe ecosystem in Idaho.

Materials and Methods

Study Site

The field site is at the U.S. Sheep Experiment Station (44° 16' N, 112° 08' W), which is located 10 km north of Dubois on the Upper Snake River Plain of northeastern Idaho. The site is situated in the northeastern portion of the sagebrush-steppe ecosystem (West 1983) at an elevation of about 1,700 m. The dominant shrub, grass, and forb on the study site are 3-tipped sagebrush (*Artemisia tripartita* Rydb.), bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A Löve), and arrowleaf balsamroot (*Balsamorhiza saggitata* (Pursh) Nutt.). Other important shrubs include big sagebrush (*Artemisia tridentata* Nutt.), green rabbitbrush (*Chrysothamnus viscidiflorus* (Hook.) Nutt.), and grey horsebrush (*Tetradymia canescens* DC.). Other important grasses at the study site include needle-and-thread grass (*Stipa comata* Trin. & Rupr.), Sandberg's bluegrass (*Poa secunda* J. Presl), and junegrass (*Koeleria pyramidata* (Lam.) P. Beauv.). Other common forbs include yarrow (*Achillea millefolium* L.), tapertip hawksbeard (*Crepis acuminata* Nutt.), milkvetches (*Astragalus* spp.), and longleaf phlox (*Phlox longifolia* L.).

The climate at the site is semiarid with cold winters and warm summers. Mean annual precipitation for the area during a 64-year period was 325 mm, which included 70 cm of snow with a mean annual temperature of 6° C (Anonymous 1993). Temperatures range from 38° C in summer to –34° C in winter with the normal frost-free period of 70 to 90 days (Blaisdell 1958). Soils at the study site are loamy and derived from wind-blown loess, residuum, or alluvium (National Resource Conservation Service [NRCS] 1995). Soils at the experiment station are composed of 3 mollisols on slopes ranging from 0–12%. With increasing depth and degree of development, soils are classified as Typic Calcixerols (Anatolian series), Pachic Haploxerolls (Maremma series), and Pachic Argixerols (Akbash series).

The sagebrush-steppe ecosystem at the U.S. Sheep Experiment Station has been a primary source of forage for sheep in both spring and fall, and the Station has been the site for long-term grazing studies initiated in 1924 (Laycock 1967). In 1995, a relatively undisturbed area (400 x 400 m) was fenced to exclude grazing, and CO_2 flux measurements were initiated. The Bowen ratio-energy balance instrumentation was installed near the center of this enclosure, and 1-m^2 plots for canopy chamber measurements were located about 150 m north of the Bowen ratio-energy balance system. Thus, the site had uniform vegetation and allowed at least 150 m of fetch (upwind distance) from a relatively flat surface from all directions for the Bowen ratio-energy balance method.

Bowen Ratio-Energy Balance Technique

A Bowen ratio-energy balance system was used to obtain continuous measurements of CO_2 fluxes at the study site during the growing seasons of 1996, 1997, 1998, and 1999. The theory and operation of the Bowen ratio-energy balance system (Model 023/CO_2 Bowen Ratio, Campbell Scientific Inc., Logan, Utah) were described in detail by Dugas (1993) and Dugas et al. (1999). Briefly, CO_2 and water vapor concentrations were measured with an infrared gas analyzer (Model LI-6262, Li-Cor Inc., Lincoln, Nebr.) in the differential mode. Air samples from 2 heights (0.8 and 1.8 m above the soil surface) were drawn and routed to the infrared gas analyzer, which measured the concentration gradients between the 2 heights. Height of the vegetation, including grasses, forbs, and sagebrush canopies, ranged from 0.1 to 0.5 m. Thus, the 2 air sampling heights were at least 0.3 and 1.3 m above the vegetation surface, which is required to ensure adequate distance above the plant canopy for determining CO_2 and water vapor gradients.

A low-power pump (Model TD-3LSC, Brailsford and Co., Inc., Rye, N.Y.) aspirated the air through 1-µm teflon filters (Model Acro 50, Gelman Sciences, Ann Arbor, Michigan), which prevented dust and liquid water contamination in the air tubes and infrared gas analyzer. A solenoid valve (Model 236-102B, Numatics Inc., Highland, Mich.) was programmed to reverse the air drawn through the infrared gas analyzer every 2 min. Another solenoid valve was programmed to control the air stream at the beginning of each hour; thus, the infrared gas analyzer sample cell was scrubbed to determine absolute concentrations of CO_2 and water vapor. The air temperature gradients at the 2 heights were simultaneously measured with fine-wire, chromel-constantan thermocouples. The CO_2, water vapor, and temperature gradients were measured every second, and the average gradients were calculated and stored every 20 min. with a datalogger and storage module (Models 21X and SM192, Campbell Scientific Inc.).

Fluxes of CO_2, water vapor, and energy were calculated using these 20-min. averages. Bowen ratios were calculated from temperature and water vapor gradients. Sensible heat flux was calculated from the Bowen ratio, net radiation (Model Q*7.1 net radiometer, REBS, Seattle, Wash.), soil heat flux (Model HFT3, REBS), and soil temperature (Model TCAV, Campbell Scientific Inc.) measured above the soil heat flux plates. The eddy diffusivity, which was assumed equal for heat, water vapor, and CO_2, was calculated from sensible heat flux and temperature gradients. The eddy diffusivity may not be valid when the direction of sensible/latent heat flux is opposite the sign of temperature/water vapor gradient, or when the Bowen ratio approaches –1.0 (Ohmura 1982). Under such conditions, the eddy diffusivity was calculated using wind speed, atmospheric stability, and canopy height (Dugas et al. 1999). This alternate method for calculating eddy diffusivity was applied at sunset, sunrise, and sometimes at night when fluxes and gradients were small; these instances occurred for about 14% of the 20-min. averages. The CO_2 flux was calculated as the product of the eddy diffusivity and CO_2 gradient, and corrected for vapor density gradients at the 2 heights (e.g., Webb et al. 1980). Fine-wire thermocouple measurements indicated that temperatures were the same for the air entering the sample and reference chambers of the infrared gas analyzer so corrections for temperature differences were not applied (Angell et al. 2001). Means for CO_2 fluxes for the Bowen ratio-energy balance method were averaged from 3 to 6, 20-min. measurements that coincided with the time periods when the canopy chamber measurements were obtained.

Canopy Chamber Technique

A chamber, which had a volume of 1,020 liters and covered a 1-m^2 area, was used to obtain instantaneous measurements of CO_2 fluxes at select times during the growing seasons of 1996, 1998, and 1999. We used an identical chamber design and measurement protocols as described by Angell and Svejcar (1999). Three, 1-m^2 plots were permanently identified by pressing 1-m^2 angle-iron frame into the soil surface at the beginning of the 1995 growing season. Each plot included a 3-tipped sagebrush plant canopy, plus associated grasses and forbs within the 1-m^2 frame. A canopy chamber measurement was initiated by placing the chamber on top of the frame. A layer of 0.6-mm thick, closed-cell foam mounted under the canopy chamber provided an air-tight seal between the canopy chamber and the plot frame. Circulation and mixing of air in this closed gas exchange system was achieved by a generator-powered fan (rated at 11 m^3 min^{-1}), which routed the trapped air from duct openings near the ground surface to duct openings near the top of the chamber. The canopy chamber measurements were conducted at least 150 m away from the Bowen ratio-energy balance system. A portable generator was used to operate the mixing fan within the canopy chamber, and depending on the wind direction for the particular measurement day, the generator in conjunction with a long extension cord was positioned in a downwind direction from the Bowen ratio system. This minimized the effects that periodic CO_2 emissions from the generator had on the Bowen ratio-energy balance measurements. Air mixing and circulation were allowed for at least 15 seconds before actual canopy chamber measurements were initiated. The canopy chamber was interfaced with a portable photosynthesis system (Model LI-6200; Li-Cor Inc., Lincoln, Nebr.), which was programmed to obtain measurements every second. A total of about 2 min. was required to complete a canopy chamber measurement. Means of CO_2 fluxes (± 1 SE) for the canopy chamber method were obtained from 3, 1-m^2 plots.

Statistical Procedures

Net ecosystem CO_2 fluxes measured with the canopy chamber and Bowen ratio-energy balance techniques were calculated on various dates during the 4 growing seasons (1996–1999). Following the tradition used in ecophysiology, positive CO_2 flux values indicated a net positive flux from the atmosphere to the earth's surface (photosynthesis exceeds ecosystem respiration), while negative values indicated release of CO_2 from the earth to the atmosphere (ecosystem respiration exceeds photosynthesis). Data for 1997 were published in Angell et al. (2001) to compare CO_2 fluxes across locations, but are also included here to provide a complete analysis of all available data from Dubois for comparing the 2 measurement methods. As a result, a total of 16 measurement periods were available for direct comparisons between the 2 techniques; the canopy chamber measurements were not obtained on 20–21 July and 23–24 August in 1996, 23–24 August in 1997, and 24–25 May in 1998. Data were grouped into 3 time periods: early (14 to 25 May), mid- (15 June to 21 July), and late- (26 July to 25 August) seasons. Mean CO_2 fluxes (± 1 SE) for the canopy chamber technique were calculated from 3, 1-m^2 plots, while the CO_2 fluxes for the Bowen ratio-energy balance technique were calculated from CO_2 gradients and eddy diffusivities averaged across 3 to 6, 20-min. values for the time period required to conduct the canopy chamber measurements. Paired mean comparisons between the 2 techniques were conducted with PROC TTEST (SAS System). The paired comparisons also were analyzed for normal distribution with PROC UNIVARIATE (SAS System) using the Shapiro-Wilk test. The REG procedure (SAS System) was used to test whether the combined slopes and intercepts of the regression lines were statistically different from the 1:1 relationship for the early, mid-, and late-season periods.

Results and Discussion

Values of CO_2 fluxes were obtained by the canopy chamber and Bowen ratio-energy balance techniques during late-May to late-August across 4 growing seasons (Fig. 1). The 24-hour patterns for both canopy chamber and Bowen ratio-energy balance measurements of CO_2 fluxes were characterized by uptake of CO_2 (positive values) during sunrise to sunset and efflux of CO_2 (negative values) during the nighttime period. Variations in CO_2 fluxes within a day largely depend on photosynthetic photon flux density (Frank and Dugas 2001, Sims and Bradford 2001), whereas the dynamics of nighttime CO_2 efflux are usually dominated by belowground respiration (Kim et al. 1992), which generally depends on soil temperature and water content (Dugas 1993, Wagai et al. 1998, Mielnick and Dugas 2000). Across 4 growing seasons of measurement, values of CO_2 fluxes determined with the canopy chamber ranged from a maximum CO_2 efflux of –0.18 mg m^{-2} sec^{-1} on 15 June 1999 to a maximum CO_2 uptake of 0.48 mg m^{-2} sec^{-1} on 16 June 1999, which was near the seasonal peak of vegetation activity. Values of CO_2 fluxes measured with the Bowen ratio-energy balance technique for the same measurement dates and times across the 4 years of study ranged from a nighttime maximum CO_2 efflux of –0.22 mg m^{-2} sec^{-1} to a daytime maximum CO_2 uptake of 0.55 mg m^{-2} sec^{-1}.

Differences between CO_2 fluxes measured with the Bowen ratio-energy balance and canopy chamber techniques were normally distributed ($P > 0.05$), as indicated by the Shapiro-Wilk test ($P > 0.05$, Table 1), with the paired comparisons for the late-season period nearly significant ($P = 0.06$). As indicated by paired t-test comparisons, values of CO_2 fluxes obtained by the 2 techniques were not statistically different ($P > 0.05$) for the early and mid-season portions of the growing season. However, CO_2 fluxes measured by the 2 methods differed statistically ($P = 0.01$) for the late-season period, with the canopy chamber method showing lower CO_2 fluxes than the Bowen ratio-energy balance method. A statistical test for evaluating whether combined slopes and intercepts for the regression line were different from

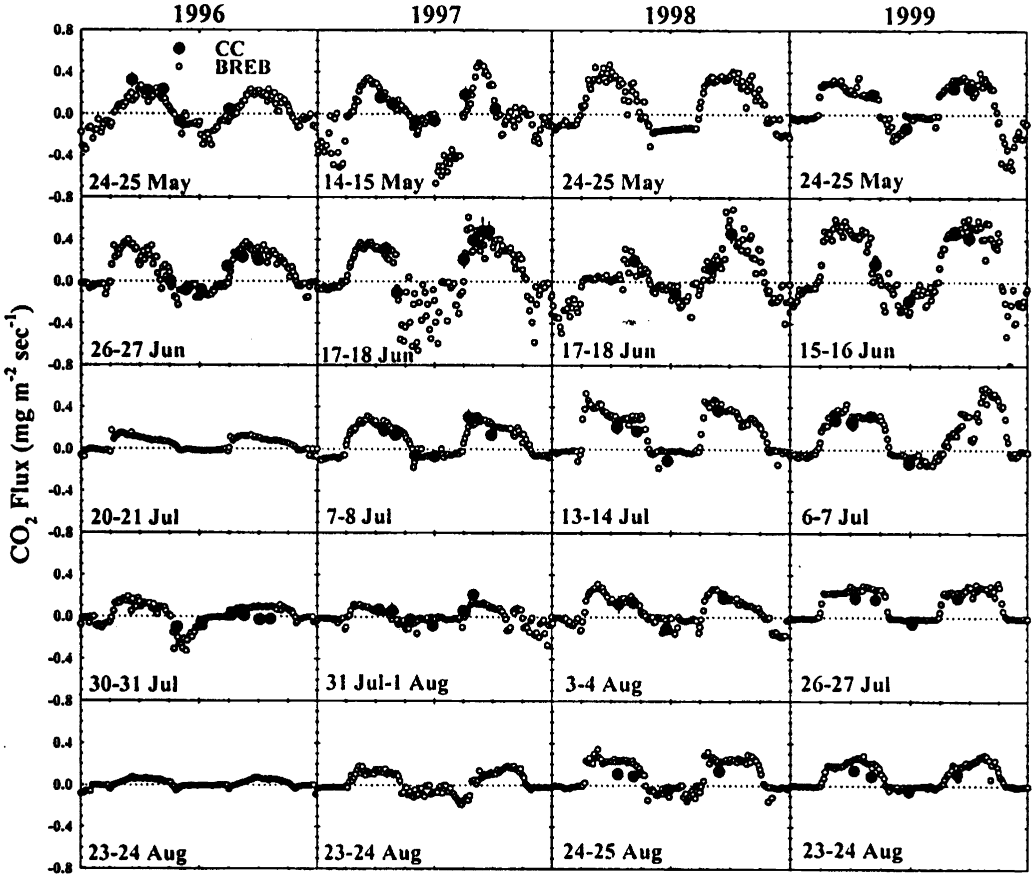

Fig. 1. Net ecosystem CO_2 fluxes in a sagebrush-steppe ecosystem measured with the canopy chamber (CC) and Bowen ratio-energy balance (BREB) techniques on various dates during 4 growing seasons. The average CO_2 fluxes (± 1 SE) for the canopy chamber technique were obtained from 3, 1-m^2 plots, while the CO_2 fluxes for the Bowen ratio-energy balance technique were calculated from CO_2 gradients and eddy diffusivities averaged every 20 min. The canopy chamber measurements were not obtained on 20–21 July and 23–24 August in 1996, 23–24 August in 1997, and 24–25 May in 1998. Positive CO_2 flux values indicate a net positive flux from the atmosphere to the earth's surface (photosynthesis exceeds ecosystem respiration), while negative values indicate release of CO_2 from the earth to the atmosphere (ecosystem respiration exceeds photosynthesis).

Table 1. Statistical analyses with the PROC TTEST (SAS System) that utilized the paired comparisons of means (using data shown in Fig. 2) of net ecosystem CO_2 flux measured with the Bowen ratio-energy balance (BREB) and canopy chamber (CC) techniques (n-number of observations; df-degrees of freedom). The paired comparisons (Difference = BR CO_2 Flux–CC CO_2 Flux) were analyzed for normal distribution using PROC UNIVARIATE (SAS System). Data across the 4 growing seasons of measurements (1996–1999) were grouped into 3 time periods: early (14 to 25 May), mid (15 June to 21 July), and late (26 July to 25 August). Positive CO_2 flux values indicate a net positive flux from the atmosphere to the earth's surface (photosynthesis exceeds ecosystem respiration), while negative values indicate release of CO_2 from the earth to the atmosphere (ecosystem respiration exceeds photosynthesis).

		Statistics				
Season	n	Variable	Mean	Std Err	Minimum	Maximum
		(mg CO_2 m^{-2} sec^{-1})				
Early	15	BREB CO_2 Flux	0.073	0.042	-0.248	0.312
		CC CO_2 Flux	0.108	0.037	-0.133	0.320
		Difference	-0.035	0.022	-0.181	0.065
Mid	35	BREB CO_2 Flux	0.182	0.035	-0.218	0.551
		CC CO_2 Flux	0.172	0.034	-0.176	0.478
		Difference	0.010	0.012	-0.161	0.131
Late	28	BREB CO_2 Flux	0.090	0.024	-0.184	0.267
		CC CO_2 Flux	0.054	0.018	-0.112	0.209
		Difference	0.036	0.013	-0.086	0.127

Paired Comparisons (t-tests for Difference)

Season	df	t Value	P > |t|
Early	14	-1.53	0.15
Mid	34	0.80	0.43
Late	27	2.84	0.01

Test (Shapiro-Wilk) for Normal Distribution

Season	n	W Value	P < W
Early	15	0.90	0.10
Mid	35	0.96	0.25
Late	28	0.93	0.06

the 1:1 relationship indicated that the regression lines for the early and late-season periods were not statistically different ($P < 0.05$) from the 1:1 line. The slopes and intercepts for the regression line for the late-season period, however, were statistically different ($P > 0.05$) from the 1:1 relationship.

A similar difference during late summer was observed by Angell et al. (2001) at their Oregon study site where they found lower CO_2 fluxes with the canopy chamber technique compared to the Bowen ratio-energy balance method, which they attributed to possible chamber effects. Because of the mixing required within canopy chambers, air turbulence inside canopy chambers is typically greater than ambient conditions outside the chamber, which may alter the gradients of temperature, CO_2, and water vapor within enclosed chamber canopies compared to ambient canopy conditions (Held et al. 1990). In our study, we initially thought that air temperatures in the canopy chamber may have been higher than those in the ambient environment so that resulting vapor pressure deficits might have been greater inside the canopy chamber, resulting in greater stomatal closure and subsequently lower CO_2 fluxes for plants inside than outside the canopy chamber. However, examination of our data showed that calculated vapor pressure deficits were the same inside and outside the canopy chamber. Other factors that could contribute to these late-season differences include differences in spatial scales of the 2 techniques with the Bowen ratio-energy balance technique integrating measurements across a much larger area (and possibly areas subjected to less water stress) than the 1-m^2 canopy chambers. Despite these differences during the hot, dry late-season period, CO_2 fluxes measured by the 2 techniques in our study were significantly ($P < 0.05$) and positively correlated for the early ($r^2 = 0.71$, n = 15), mid- ($r^2 = 0.88$, n = 35), and late-season ($r^2 = 0.72$, n = 28) periods (Fig. 2).

Given the wide range of environmental conditions across our measurement dates and 4 growing seasons, the spatial heterogeneity present in sagebrush-steppe ecosystems, and the inherent differences in the 2 CO_2 techniques, r^2 values ranging from 0.71 to 0.88 between the 2 methods are probably quite reasonable and acceptable. Although differences between the canopy chamber and Bowen ratio-energy balance methods were observed during the late-season period, our results showed that CO_2 fluxes obtained with the 2 techniques similarly characterized the patterns of daily and seasonal CO_2 fluxes in the sagebrush-steppe ecosystem at Dubois. The canopy chamber and Bowen ratio-energy balance techniques have been compared in field crops and more mesic systems (e.g., Held et al. 1990), but comparisons between these 2 techniques are limited in arid and semiarid environments (e.g., Angell et al. 2001). As a result, generalizations cannot be made concerning extrapolations to other rangeland ecosystems. The results of our study support the findings of Angell et al. (2001), and provide comprehensive data across multiple growing seasons and a greater range of environmental conditions.

Similar to the eddy covariance technique, the Bowen ratio-energy balance method is advantageous because it can be used to provide continuous measurements of CO_2 fluxes. In addition, these techniques can detect rapid, short-term changes in CO_2 fluxes, which are difficult to observe with the canopy chamber method because frequency of measurements is limited by available human resources. The initial cost of a Bowen ratio-energy balance system and an eddy covariance system, however, exceeds $25,000, whereas the canopy chamber method is relatively inexpensive to set up (less than $1,500), if a portable photosynthesis system (about $14,000) is available to the project. Bowen ratio-energy balance systems and eddy covariance systems require large, relatively uniform areas which can make locating treatments difficult. In addition, the canopy chamber technique can be used in conjunction with soil respiration chambers (Norman et al. 1992) to partition CO_2 fluxes into above and belowground components, and to obtain estimates of spatial variability across the landscape. The canopy chamber method, however, is labor-intensive and does not provide continuous measurements of CO_2 fluxes. Frequent sampling with the canopy chamber to assess CO_2 fluxes requires considerable labor to transport the canopy chamber from plot to plot and obtain the required measurements.

Results from our study indicated that the canopy chamber and Bowen ratio-energy balance technique gave similar results; however, differences were observed during the hot, dry summer period. Despite differences during this period, data values for the 2 techniques were still positively correlated ($r^2 = 0.72$) at this period and the other 2 periods ($r^2 = 0.71$ and 0.88). As a result, depending on the specific experimental objectives and resources available for the particular project, data from our study indicate that both the canopy chamber and Bowen ratio-energy balance methods would likely give similar patterns of CO_2 fluxes in sagebrush-steppe ecosystems; however, caution should be used with the canopy chamber during hot, dry conditions.

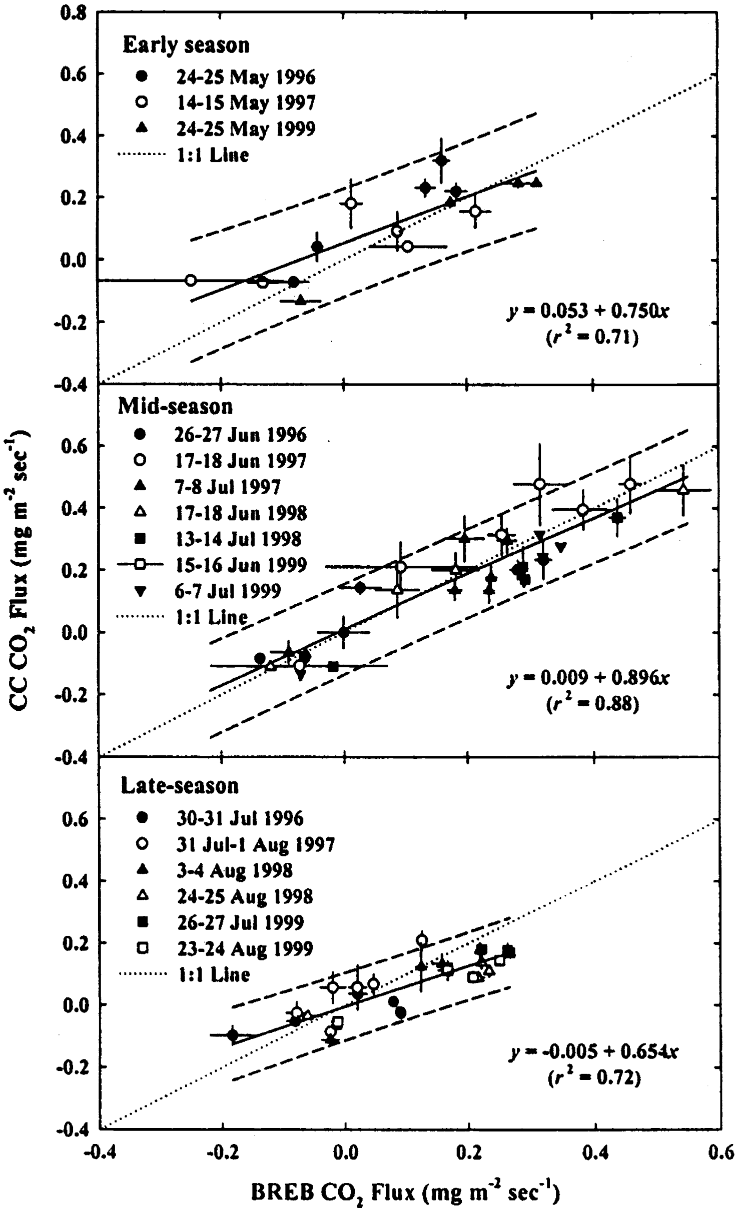

Fig. 2. Net ecosystem CO_2 fluxes measured with a canopy chamber (CC) technique compared to those measured with a Bowen ratio-energy balance (BREB) technique for early season (14 to 25 May), mid-season (15 June to 21 July), and late-season (26 July to 25 August) periods during 4 growing seasons (1996-1999). Data from different dates are represented by different symbols. Means of CO_2 fluxes (± 1 SE) for the canopy chamber method were obtained from 3, 1-m^2 plots, while means for CO_2 fluxes (± 1 SE) for the Bowen ratio-energy balance method were averaged from 3 to 6, 20-min. measurements that coincided with the time periods when the canopy chamber measurements were obtained. Positive CO_2 flux values indicate a net positive flux from the atmosphere to the earth's surface (photosynthesis exceeds ecosystem respiration), while negative values indicate release of CO_2 from the earth to the atmosphere (ecosystem respiration exceeds photosynthesis). The dashed lines represent the prediction interval for the regression line at 95% confidence, whereas the fine-dotted lines represent the 1:1 relationship. The REG procedure (SAS System) indicated that the combined slopes and intercepts of the regression lines were not statistically different ($P < 0.05$) from the 1:1 relationship for the early and mid-season period, but they were different for the late-season period.

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Mechanism by which ammonium fertilizers kill tall larkspur

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Abstract

Environmental concerns of using pesticides on public lands have greatly reduced the use of herbicides to control tall larkspur (*Delphinium barbeyi* Huth). An alternative method of control used ammonium sulfate placed at the base of individual plants. The objective of this study was to determine the mechanism by which fertilizers kill tall larkspur. We hypothesize the salt from the fertilizers kill the plant. We applied ammonium sulfate, ammonium nitrate and sodium chloride at equivalent salt concentrations and evaluated their effect on tall larkspur plants. There was no difference among treatments in larkspur mortality ($P > 0.10$). The high rate of all treatments (ammonium sulfate 400 g plant^{-1}, ammonium nitrate 264 g, and sodium chloride 180 g, at equivalent salt concentrations) killed greater than 70% of larkspur plants. We conclude the salt in fertilizers kills tall larkspur, not the nitrogen. It is necessary to place the fertilizer or salt at the base of the plant to concentrate it in the root zone, rather than broadcast it. At the end of the study, bare areas left around the dead tall larkspur plants were only 13% of the original size of the tall larkspur plants at Yampa Colo. and Cedar Ut., and 46% at Emery Ut., indicating the surrounding vegetation was quickly filling in the vacated space. The relative cost of materials per plant for both ammonium sulfate and nitrate was 12.9¢, and 2.6¢ for salt.

Key Words: *Delphinium barbeyi*, weed control, herbicide, fertilizer, ammonium sulfate, ammonium nitrate, sodium chloride

Resúmen

La preocupación por los efectos ambientales del uso de pesticidas en tierras públicas ha reducido significativamente el uso de herbicidas para el control del larkspur alto (*Delphinium barbeyi* Huth). Un método alternativo de control es el uso de sulfato de amonio en la base de las plantas. El objetivo de este estudio fue determinar el mecanismo por el cual los fertilizantes matan al larkspur alto. Nuestra hipótesis es que la sal de los fertilizantes matan la planta. Aplicamos sulfato de amonio, nitrato de amonio y cloruro de sodio a concentraciones equivalents de sal y evaluamos sus efectos en las plantas de larkspur. No hubo diferencia entre tratamientos en relación a la mortalidad de larkspur ($P > 0.10$). Los tratamientos a altas concentraciones (sulfato de amonio 400 g plant^{-1}, nitrato de amonio 264 g, y cloruro de sodio 180 g, a concentraciones equivalents de sal) mataron mas del 70% de las plantas. Concluimos que las sales en los fertilizantes y no el nitrógeno matan al larkspur alto. Es necesario colocar el fertilizante o la sal en la base de la planta para concentrarlo en la zona de raiz, en lugar de dispersarlo. Al final del estudio, las areas descubiertas dejadas alrededor de las plantas muertas de larkspur fueron solamente el 13% del tamaño original de las plantas de larkspur alto en Yampa Colo. y Cedar, Ut., y 46% en Emery Ut., indicando que la vegetación de los alrededores ocupo rápidamente el lugar vacante dejado por el larkspur. El costo relativo de los materials por planta para sulfato y nitrato de amonio fue de 12.9 ¢, y 2.6 ¢ , respectivamente.

Tall larkspur (*Delphinium barbeyi* Huth) kills more cattle on mountain summer rangeland in the western U.S. than any other plant, disease or predator (Pfister et al. 1999). Herbicides have been used to control larkspur in areas of persistent losses. Cronin and Nielsen (1972) reported 2,4,5-T and Silvex were most effective in controlling tall larkspur, but these herbicides were subsequently banned. Mickelsen et al. (1990) and Ralphs et al. (1992) recommended picloram, metsulfuron, and glyphosate for specific times of the growing season and site conditions.

Environmental sensitivity and the reluctance of federal land management agencies have greatly curtailed the use of pesticides on public lands. Alternative control agents have been investigated. Binns et al. (1971) experimented with 2,4,5-T mixed with ammonium sulfate placed at the base of tall larkspur plants. Near complete control was achieved, but the experimental design precluded separating the effects of the herbicide and fertilizer. Cronin et al. (1977) broadcast ammonium sulfate at the rate of 140 kg N ha^{-1} in one experiment, and 84 to 1,344 kg N ha^{-1} in another experiment. They reported no mortality to tall larkspur, but the higher rates burned its leaves and those of associated grasses. Little (1979) claimed the difference in results between the 2 previous experiments was the method of application. He applied ammonium sulfate to the base of individual plants of duncecap larkspur (*D. occidentale* S. Watts) in southern Idaho at 84 g (3 oz), 168 g (6 oz), and 336 g (12 oz) and obtained 50%, 82% and 100% kill (respectively) the following year. He stated the 168 g rate killed most plants, but the 336 g rate was required to kill the larger robust plants. Clementson (1999) applied ammonium sulfate to individual plants of tall larkspur in western Colorado at rates of 100 g (1/2 cup), 150 g (3/4 cup), and 200 g (1 cup). She obtained 100% control from all 3 treatments the following year, and no larkspur remained in the treated plots 9 years later. This program was applied on several Forest Service allotments to control tall larkspur in patches where cattle losses occurred.

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The objective of this experiment was to evaluate the mechanism by which fertilizers kill larkspur. We hypothesize that the salt from fertilizers kill the plant. We applied ammonium sulfate, ammonium nitrate, and sodium chloride (common salt) to individual tall larkspur plants in amounts containing similar salt equivalents. We predicted that there would be no difference in mortality among treatments.

Methods

Site Description

The study was replicated at 3 locations. The Cedar Mountain site was located 40 km east of Cedar City, Ut. at 2,800 m elevation (N 37° 32.175', W 112° 58.705') The plant community consisted of tall forbs under an aspen (*Populus tremuloides* Michx.), with tall larkspur the dominant forb, and western coneflower (*Rudbeckia occidentalis* Nutt.), sweet cicely (*Osmorhiza chilensis* H&A) and meadow rue (*Thalictrum fendleri* Engelm. ex Gray) as subordinates. Mountain brome (*Bromus carinatus* Hooker & Arn.) and slender wheatgrass (*Elymus trachycaulus* (Link) Gould ex Shinners) were the dominant grasses. The soil was a Faim clay loam; fine, montmorillonitic Argic Pachic Cryoboroll. Detailed descriptions of soils at all 3 locations are in Table 1.

The Emery site was located 34 km west of Emery, Ut., on the Manti-LaSal National Forest at 3,200 m elevation (N 39° 2.454', W 111° 30.543'). The Forest Service habitat type was a tall larkspur / slender wheatgrass/mountain brome complex. Soils were clayey-skeletal, montmorillonitic Pachic Cryoboroll.

The Yampa site was located 16 km west of Yampa, Colo., on the Routt National Forest (N 40° 11.886', W 107° 2.801'). The habitat type was aspen/tall forb. Tall larkspur was the dominant forb, with cow parsnip (*Heracleum lanatum* Michx.), sweet cicely, and meadow rue as subdominants. Mountain brome was the dominant grass. Soils were of the Clayburn series and were fine-loamy, mixed Argic Pachic Cryoboroll.

Table 1. Soil characteristics of the study sites at the 3 locations.

Location Emery Ut	Depth cm	Texture	Sand	Silt	Clay	OM
				(%)		
1998 trt	0-13	Clay loam	28	40	32	4.5
	13-36	Clay loam	22	44	34	2.9
	36 +	Clay loam	26	40	34	2.1
1999 trt	0-23	Silty-clay loam	17	46	37	4.5
	23-46	Clay loam	23	46	31	3.9
	46 +	Silty-clay loam	15	47	38	3.6
Cedar Ut	0-10	Loam	40	39	21	10.5
	10-56	Loam	31	43	26	4.3
	56-107	Clay	8	36	56	1.6
	107+	Loam	25	50	25	0.8
Yampa Colo.	0-22	Loam	38	41	21	11.2
	28-76	Loam	28	45	27	4.3
	76-99	Silty-clay	1	44	55	1.4
	99-117	Clay	16	40	44	1.4

Treatments and Rates

Ammonium sulfate (sulfate), ammonium nitrate (nitrate), and sodium chloride (salt) were applied to the base of individual plants in amounts equalizing the salt equivalent. The salt index (Calif. Fertilizer Assoc. 2002) accounts for differences in the osmotic potential of each of the different ions. The salt index of each compound was: ammonium sulfate = 69.0, ammonium nitrate = 104.7, sodium chloride = 153.8. Since ammonium sulfate was used in past research and had the lowest salt index, it was selected as the standard and was given the relative value of 1.0. The salt index of sulfate (69.0) was divided by the index of nitrate (104.7) and salt (153.8) to obtain the ratio amount relative to sulfate (Table 2).

We selected the ammonium sulfate rates used by Clementson (1999): low rate 100 g and high rate 200 g. The nitrate ratio was 0.66 or 66 g for the low rate and 132 g high rate; and the salt ratio was 0.45 or 45 g for the low rate and 90 g for the high rate (Table 2).

Ten transects were established at each location (about 50 m long and 10 m apart) and represented blocks or replications of each treatment. Nine distinct plants of uniform size (each about 0.5 m^2 foliar cover or area occupied) were selected along each of the transects and marked with wood stakes. The 3 treatments and 2 rates were randomly applied to individual selected plants in a randomized complete block design. In addition to the fertilizers and salt treatments, the granular herbicide tebuthiuron was also applied to individual plants at 3 rates for a total of 9 plants on each transect. The tebuthiuron results are reported elsewhere (Ralphs et al. 2003).

Treatments were applied in 1998 and again to new plants in new transects in 1999. They were applied at Cedar, Ut. on 16 July 1998 and 15 July 1999; Yampa, Colo. 28 July 1998 and 28 July 1999; and Emery, Ut. 14 Aug. 1998 and 5 Aug. 1999. Larkspur plants were in the early flower stage, representing peak production, when treatments were applied and evaluated.

Following the first year evaluation of the 1998 treatments, it appeared that mortality was low for all treatments and did not represent a sufficient range to evaluate the hypothesis. Therefore, we doubled the rates for the 1999 treatments (Table 2). Winter and monthly growing season precipitation for each year are presented in Table 3.

Table 2. Fertilizer treatments, salt index, equivalent mass, and application rates in 1998 and 1999.

						Application Rates			
						1998		1999	
Treatment	Salt index	Ratio	Mass	Nitrogen		1	2	2	3
			(g)	(%)	(g)		($g\ plant^{-1}$)		
Ammonium sulfate	69.0	1.0	100	21	21	100	200	200	400
Ammonium nitrate	104.7	0.66	66	34	22	66	132	132	264
Sodium chloride	153.8	0.45	45	0	0	45	90	90	180

Table 3. Winter and monthly precipitation during the growing season.

Location	Month	1998	1999	2000	2001
		(cm)			
Emery	Winter	54.6	54.4	40.1	47.2
	June	7.1	2.5	5.0	2.3
	July	6.1	6.8	2.3	3.8
	Aug	4.3	13.0	6.4	4.6
	Sep	10.7	5.0	4.6	1.8
	Total	82.8	77.7	58.1	62.2
Cedar	Winter	65	41.3	58.8	56.3
	June	4.2	5.3	2.2	1.3
	July	8.1	6.4	0.6	4.7
	Aug	2.4	7.1	8.9	4.7
	Sep	9.7	4.7	1.3	0.1
	Total	89.9	64.8	71.8	67.1
Yampa	Winter	52.6	58.2	50.3	49.8
	June	2.0	4.6	1.8	1.5
	July	16.6	0.5	2.5	1.3
	Aug	6.1	6.6	5.0	3.0
	Sep	2.8	4.6	9.9	4.5
	Total	80.0	74.5	69.6	60.2

Data Analysis

Mortality was evaluated 2 years after the 1998 and 1999 treatments. Treatment years were analyzed separately because of differences in application rates. Categorical data (dead or alive) were analyzed using the logistic procedure of PROC GENMOD and the GLIMMIX macro in the SAS 8e package (SAS 1999). The model evaluated locations, fertilizers, and rate (low and high), and their 2- and 3-way interactions. Where differences occurred ($P < 0.05$), means were separated by linear contrasts. A separate analysis was conducted for only rate 2, which was the same in both treatment years, to evaluate the year effect. The model compared locations, fertilizers, years and their interactions.

The impact on the environment by the fertilizer and salt treatments was estimated by the size of the bare areas left after the tall larkspur plants died. The bare area surrounding the dead tall larkspur plant was estimated by the area of a circle, with the radius calculated by summing the diameter of the bare area at 90° angles and dividing by 4. These measurements were taken for 3 years following the 1998 treatment and 2 years following the 1999 treatment. Many tall larkspur plants took 2 years to die, therefore the size of the bare area at the end of the study was the best indicator of environmental impact of the treatments and was used as the response variable in the mixed model. Data were analyzed by a mixed ANOVA using unstructured covariance (SAS 1999) to compare locations, treatments, and treatment year. There were no differences between treatment rates ($P > 0.23$), allowing comparison between treatment years. Measurement of bare areas was not continued beyond 2001 because of the difficulty of locating the stakes and treated areas due to the encroachment of the adjacent vegetation.

Results

There were no differences in mortality among treatments ($P > 0.10$, Table 4, grand treatment mean). This supports our hypothesis that it was not the nitrogen in the fertilizer, but the salt in the fertilizers that kill the plants. The amount of nitrogen applied was similar between the ammonium fertilizers, but there was no nitrogen in the salt treatment (Table 2). Furthermore, the actual quantity of treatment material placed on the plants varied by more than 100%, yet mortality was similar.

There was only 1 significant interaction; location-by-treatment in the 1998 applications ($P < 0.0001$). The salt treatment

Table 4. Mortality of tall larkspur plants 2 years after treating with fertilizers and salt applied at equal salt concentrations in 1998 and 1999.

		1998 Treatment Year				1999 Treatment Year			
Location	Rate	Nitrate	Sulfate	Salt	Location mean	Nitrate	Sulfate	Salt	Location mean
		(% mortality)							
Emery	1	30	40	0					
	2	70	70	10		50	40	50	
	3					90	80	70	
	mean	50	55	5	43^{b}	70	60	60	64^{a}
Cedar	1	20	10	50					
	2	70	30	50		67	70	30	
	3					90	90	80	
	mean	45	20	50	45^{b}	79	80	55	72^{a}
Yampa	1	70	89	80					
	2	80	100	90		40	50	50	
	3					80	78	80	
	mean	75	94	85	85^{a}	60	64	65	63^{a}
Treatment mean		57^{a}	56^{a}	47^{a}			70^{a}	68^{a}	60^{a}
Rate mean		1998	1999						
	1	50^{c}							
	2	63^{dE}	50^{cF}						
	3		82^{d}						

^{ab}Difference between fertilizer treatments in rows, or locations in columns ($P < 0.05$).
^{cd}Difference in rates within treatment years ($P < 0.05$)
^{EF}Application rate 2 differed between treatment years ($P = 0.02$)

Table 5. Initial size (aerial cover) of larkspur plants (± SE) and bare area surrounding dead larkspur plants at end of study.

Location	Treatment year	Initial plant size	Bare area following treatments Nitrate	Sulfate	Salt	Location mean
		(cm^2)				
Emery	1998	3,204 ± 236	1,050 ± 89	1,174 ± 145	1,723 ± 74	
	1999	4,901 ± 267	2,502 ± 218	2,762 ± 230	2,003 ± 245	
	mean		1,776	1,968	1,863	1,869a
Cedar	1998	5,823 ± 346	629 ± 224	500 ± 201	476 ± 69	
	1999	4,765 ± 305	673 ± 70	772 ± 104	807 ± 128	
	mean		651	636	641	643b
Yampa	1998	5,549 ± 405	587 ± 164	703 ± 174	1,171 ± 300	
	1999	4,991 ± 280	481 ± 86	543 ± 72	942 ± 297	
	mean		534	623	1,056	738b
Grand	mean	4,872	987a	1,076a	1,187a	

^{ab}Difference among fertilizer treatments in rows, or locations in columns differ ($P < 0.05$).

gave very low mortality at Emery, and the sulfate treatment gave low mortality at Cedar City (Table 4). Both of these locations received less precipitation in August 1998 following application of treatments than in subsequent years (Table 3), but these treatments were equally effective in other locations and years.

There was a rate difference in both years ($P < 0.0016$, Table 4, grand rate mean); the higher dose killed more plants in both years. There was a difference between treatment years when compared at the same rate ($P = 0.02$). Rate No. 2 in the 1998 treatment year caused higher mortality than in the 1999 treatment year. This was due almost entirely to the very high mortality from all 3 treatments at Yampa in the 1998 applications ($P < 0.0001$, Table 4). Yampa had more rain during the growing season in 1998 than in 1999 (Table 3). The soil was saturated from 16.6 cm of rain received before the treatments were applied in July, thus the 6.1 cm of rain in August may have distributed the salt rapidly throughout the root zone. There was no difference among locations for the 1999 applications.

Where tall larkspur plants died, bare areas remained (Table 5). There was no difference in size of bare areas between fertilizer treatments or rates of application ($P > 0.10$). The Emery site had larger bare areas than the other locations ($P < 0.0001$), due perhaps to the clay soil retaining the salts from the treatments. There was a location-by-treatment year interaction ($P < 0.001$); bare ground was greater in the 1999 treatment compared to the 1998 treatment at Emery, but was similar between years at the other locations. At the end of the experiment, the bare areas were only 13% of the original size of the larkspur plants at Cedar and Yampa, and 46% of the size of the original plants at Emery. Adjacent vegetation (mountain brome, slender wheatgrass and meadow rue) was encroaching upon the areas previously occupied by tall larkspur and is expected to quickly cover the bare areas. The relatively flat surface prevented soil erosion from these bare spots while they revegetated.

Discussion and Conclusions

We conclude the salt in fertilizers killed tall larkspur, not the nitrogen. We also found that it is necessary to place the fertilizer or salt at the base of the plant to concentrate the salts as they are leached into the root zone. This confirms the results of Little (1979) and Clementson (1999). The lack of effect of fertilizer reported by Cronin et al. (1977) was apparently due to the broadcast application of the fertilizers.

Salinity adversely affects plants by the combined effects of reducing and stopping metabolic processes, ion toxicity, and chemically reducing soil water availability; cumulatively resulting in mortality (Miller and Doescher 1995, Marschner 1995). Excessive uptake of salts inhibits enzyme activity resulting in disruption of protein synthesis and inadequate energy from photophosphoralation. The resulting ionic imbalance increases membrane permeability and disrupts osmoregulation, resulting in direct ion toxicity. The total concentration of solute particles in the soil water solution surrounding the plant causes the osmotic potential to become more negative, lowering soil water potential and making it increasingly more difficult for the plant to take up water (Richards 1969). The signs of stress in the treated tall larkspur plants did not differ among the treatments: stunted growth, curling and crumpled leaves, and necrotic brown spots, especially along the leaf edges. Adjacent tall larkspur plants did not show signs of water stress or salt toxicity, and there was no mortality from other causes.

The high rate of all treatments killed greater than 70% of tall larkspur plants. These rates were sulfate, 400g (2 cups); nitrate, 264 g (1 1/3 cup); and salt, 180 g (2/3 cup). The relative cost of the chemical per plant for both ammonium sulfate and nitrate was 12.9¢, and 2.6¢ for salt. The amount of salt required to kill a plant is lower and the cost is cheaper, but fertilizers may give a short term boost of fertility to surrounding vegetation. In comparison, spot treatment to individual plants using the herbicide tebuthiuron was 5¢ per plant (Ralphs et al. 2003).

Another practice to manage larkspur has been to graze it with sheep. Sheep are 4 to 6 times more resistant to larkspur poisoning than cattle (Olsen 1978). Many larkspur-infested allotments were allocated to sheep during adjudication as a solution to the larkspur problem. With the decline in the sheep industry, many sheepmen are seeking to convert back to cattle if the risk of larkspur poisoning can be reduced. Using salt or fertilizers to control tall larkspur, though labor intensive, is relatively inexpensive for the material, and poses little environmental risk compared to broadcast herbicides used under aspen and on public lands.

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Effects of aeration on phenolic amine content of guajillo

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Abstract

Aeration is a common range management technique used in southern Texas and northern Mexico to reduce shrub cover and increase biomass of more palatable forages. Guajillo (*Acacia berlandieri* Benth.) is an important forage plant for deer and domestic livestock throughout its range in northeastern Mexico and southern Texas. It responds to top removal, such as by aeration, by producing large numbers of juvenile sprouts which can have higher total leaf nitrogen content up to 6 months after treatment. However, the concentration of phenolic amines, potentially toxic secondary plant chemicals, may also increase. We compared concentrations of tyramine and N-methyl-phenethylamine (NMP), 2 prominent phenolic amines that can negatively affect reproduction in herbivores, between juvenile (regrowth) and mature stems of guajillo in areas that had been aerated and also between mature stems in aerated and control sites. Aeration increased NMP but not tyramine concentrations in mature stems. Juvenile stems had higher total nitrogen concentration than mature stems but also had higher amine concentrations until about 1 year after aeration. A greater percent of total nitrogen was incorporated into amines in juvenile stems (2.5–6.0%) than mature stems (1.8–4.2%). Amine concentrations peaked in summer and early autumn, a period when herbivores may rely heavily on browse because forbs are scarce. Our results suggest that while aeration may result in higher nitrogen concentrations in guajillo, increases in amines may limit benefits to herbivores.

Key words: *Acacia berlandieri*, Chihuahuan Desert, forage quality, México, nitrogen, Tyramine

Resumen

La aereación es una técnica de manejo de pastizales comúnmente usada en el sur de Texas y norte de México para reducir la cobertura de arbustos e incrementar la biomasa de especies forrajeras deseables. El "Guajillo"(*Acacia berlandieri* Benth.) es una planta forrajera importante para el venado y el ganado doméstico a lo largo de su rango en el noreste de México y Sur de Texas. Esta especie responde a la remoción de su parte aérea, tal como ocurre con la aereación, produciendo un gran número de rebrotes juveniles los cuales pueden tener un alto contenido de nitrógeno total en las hojas hasta 6 meses después del tratamiento. Sin embargo, la concentración de aminas fenólicas, químicos secundarios de la planta potencialmente tóxicas, también incrementa. Comparamos la concentración de tiramina y N-metil-fenetilamina (NMP), 2 aminas fenólicas prominentes que pueden afectar negativamente la reproducción de los herbívoros, entre tallos maduros de guajillo y juveniles (rebrote) en áreas que habían sido aereadas y también entre tallos maduros en sitios aereados y sitios control. La aereación incrementó la concentración de NMP pero no la de tiramina de tallos maduros. Los tallos juveniles tuvieron una mayor concentración de N total que los tallos maduros, pero también tuvieron mayores concentraciones de amina hasta 1 año después de la aereación. Los tallos juveniles incorporaron un mayor porcentaje del nitrógeno total en aminas (2.5–6.0%) que los tallos maduros (1.8–4.2%). Las concentraciones de aminas alcanzaron sus máximos niveles en verano e inicios de otoño, un periodo en el que los herbívoros dependen grandemente del ramoneo porque las hierbas son escasas. Nuestros resultados sugieren que mientras la aereación puede resultar en mayores concentraciones de nitrógeno en el "Guajillo", el incremento en las aminas puede limitar los beneficios para los herbívoros.

Aeration is a common range management technique used in southern Texas and northern Mexico to reduce shrub cover and increase biomass of more palatable forages (Holechek et al. 1989). This technique consists of pulling large, toothed, steel drums by a tractor or bulldozer over tracts of brush, effectively chopping off most above-ground stems of low-growing shrubs. Stems that are not completely severed are typically broken or bent over and subsequently defoliated. Guajillo (*Acacia berlandieri* Benth.), an important forage plant for deer and domestic livestock throughout its range in northeastern Mexico and southern Texas, responds to roller-chopping (a similar technique) by producing large numbers of juvenile root sprouts which can have higher total leaf nitrogen content up to 6 months after treatment (3.7 for leaves from roller-chopped stems versus 2.4 mg N/g dry matter for leaves from untreated stems; Reynolds et al. 1992).

Phenolic amines are a class of nitrogen-containing, carbon-based secondary plant compounds that can occur in high concentrations in native shrubs of southern Texas and northern Mexico. When consumed at even low concentrations, phenolic amines can have severe physiological effects on domestic livestock, such as reduced reproductive performance (Forbes et al. 1993, 1994, Vera-Avila et al. 1996, 1997). Forbes et al. (1995) found that tyramine and N-methyl-phenethylamine (NMP) concentrations significantly increased in regrowth guajillo after simulated

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browsing. They warned that part of the increase in total nitrogen often observed in severely browsed or mechanically treated plants may be a result of increased non-protein nitrogen such as phenolic amines.

We tested the hypotheses that: 1) amine concentrations of leaves from mature guajillo stems should be higher after aeration, and 2) leaves from juvenile guajillo stems, resprouting after aeration, should have higher concentrations of tyramine and NMP than leaves from mature plants.

Methods and Materials

Study Area

The study was conducted on the 10,000 ha Campo Santa Maria Management Area (26° 55', 100° 40') located on the border of Nuevo Leon and Coahuila, Mexico, about 160 km southwest of Laredo, Tex.. The Pajaros Azules mountains (1,700 m above sea level) border the southern and western boundaries of the ranch and drop sharply to the plains (400 m above sea level) that compose the majority of the ranch holdings. Climate is characterized by hot, dry summers and cool, mild winters. Average annual rainfall in Progresso, Coahuila (40 km from study site) is 383 mm with peaks in May and September (Secretary of Agricultural Promotion of Coahuila 1997). Rainfall during the sampling period was 50% greater than the annual average.

The study was conducted in the La Mesa, La Mona, and Tinajas pastures which were dominated by guajillo and blackbrush (*A. rigidula* Benth.). Soils in La Mesa pasture were shallow sandy loams. Other common shrubs in this pasture included whitebrush (*Aloysia gratissima* Gill. & Hook.), cenizo (*Leucophyllum frutescens* Berl.), guayacan (*Guaiacum angustifolia* Engelm.), and mesquite (*Prosopis glandulosa* Torr.). Soils in La Mona pasture included shallow sandy loams and moderately deep clay loams. Other common shrubs were cenizo, panalero (*Schaefferia cuneifolia* Gray), guayacan, whitebrush, and coyotillo (*Karwinskia humboldtiana* R. & S.). Soils in Tinajas pasture were characterized by shallow sandy and gravelly loams. Other shrubs included cenizo, oreganillo (*Lippia graveolens* H.B.K.), Texas kidneywood (*Eysenhardtia texana* Scheele), and coyotillo. La Mona and La Mesa pastures were deferred from livestock grazing from October 1996 to September 1997, heavily grazed by cattle from mid-September 1997 to mid-November 1997, then not grazed for the rest of the study. Cattle were excluded from Tinajas pasture from October 1996 through the end of the study.

Methods

In late September-early October 1996, one, 30-ha site in each of the 3 pastures was aerated with 1 pass using a dual-drum Lawson aerator pulled by a crawler tractor. Sites were chopped in 100–120 m wide strips separated by 10–15 m of untreated vegetation. A control site (30 ha) of similar vegetation and soil types was demarcated in each pasture, adjacent to treated sites.

Beginning in December 1996 and continuing monthly through January 1998, 5 mature guajillo shrubs were randomly selected in each treatment by pasture combination and 30–50 g fresh weight of current annual growth leaves were clipped from each shrub. Treated areas contained a sufficient number of intact mature stems after treatment (600 stems/ha; Windels 1999) for sample collection after leaves grew back on these stems. Every month from December 1996 until October 1997, 5 clusters of juvenile stump sprouts, as defined by Bryant et al. (1991b), were randomly selected in each of the 3 aerated areas and 30–50 g were clipped from each cluster. Leaf material was only collected from ungrazed stems. Juvenile sprouts were rare in control areas throughout the study period and in treated areas after October 1997 and were not collected. Samples were not collected in January 1997 because frost damaged most leaves in the treated areas. Juvenile plant samples from April defrosted before lyophilizing. Sufficient juvenile stems were not available in La Mona pasture in October for an adequate sample, therefore n = 2 for juvenile stems in October. Leaves were stored in Whirl-paks and frozen within 2 hours of clipping. Subsamples of approximately equal weight were selected from each of the 5 samples in each age/treatment/pasture combination, pooled, lyophilized for 24 hours, and ground over a 1 mm screen in a cyclone mill.

Amine analyses were conducted at the Texas A&M Agricultural Experiment Station in Uvalde, Texas following extraction and analysis procedures of Pemberton et al. (1993). Briefly, 1 g of ground material was added to 20 ml 1% glacial acetic acid and extracted overnight on a rotary shaker followed by filtering through filter paper to remove solid plant tissue. The extract was passed through a single-use Polysorb MP-3 high sulfonated, C18 polystyrene solid phase extraction tube, which had been conditioned with 2 ml HPLC-grade methanol, 2 ml deionized water, and 2 ml 1% glacial acetic acid. Four milliliters of extract were passed through the tube and eluted with 2 ml 10% ammonium hydroxide in methanol, after washing most unwanted compounds from the tube with 2 ml deionized water followed by 2 ml 50% methanol. The eluent was then acidified by addition of 1 ml 10% glacial acetic acid, followed by 1 ml 4% phosphoric acid. Amine standards (125 µl/ml) were prepared in 0.1% phosphoric acid and refrigerated until use. Tyramine (4-hydroxy-phenethylamine) and NMP were obtained from Aldrich Chemical Co., Inc. (Milwaukee, Wisc.) and phenethylamine from Spectrum Chemical Mfg. Co. (Gardena, Calif.). Both standards and extracts were separated by HPLC at ambient temperature on Waters Radial-pak cartridge (Nova-pak, 4cm, C18). Chromatograms and spectra were recorded with a Waters 490E programmable multiwavelength detector coupled to Waters 820 Maxima software.

We calculated plant nitrogen incorporated in tyramine and NMP by multiplying the mass of each amine per gram of plant by the percent nitrogen in each amine, as determined from the amine's molecular formula (tyramine ($C_8H_{11}NO$) = 137.18 g/mol; NMP ($C_9H_{13}N$) = 135.21 g/mol). The percent of total plant nitrogen that was incorporated into tyramine+NMP was calculated by dividing nitrogen in amines by total nitrogen in the plant determined from macro kjeldahl analysis at Texas A&M University-Kingsville.

Statistical Analysis

Differences in amine concentration of leaves from mature stems due to aeration were analyzed with analysis of variance in a randomized complete block design with treatment, month, and treatment*month interaction as main effects (PROC ANOVA, SAS Inst. 1996). Differences in amine concentrations of leaves from mature and juvenile stems in aerated areas were also tested with analysis of variance in a randomized complete block design with age, month, and age*month interaction as model variables (PROC GLM, SAS Inst. 1996). These tests were repeated for differences in total leaf nitrogen content and for percent of total leaf nitrogen incorporated into amines (tyramine+NMP). Post-hoc means separation tests were done using least squares means (SAS Inst. 1996). Results were considered significant at $P < 0.05$.

Results

Aeration did not affect tyramine concentrations in leaves from mature stems (P = 0.790) but did affect NMP concentrations (P = 0.010; Table 1); NMP concentrations increased an average of 11% in mature stems from aerated areas compared to control, with the largest differences in June, July, and October 1997 (Fig. 1). Amine concentrations were different among months for tyramine and NMP in mature leaves from aerated and control areas (P < 0.001 for both amine types). The treatment*month interactions were not significant (P > 0.05). Tyramine concentrations were low during December 1996, increased to moderate levels during summer, peaked in October 1997, and declined to low or moderate concentrations during the final 2 months of sampling. Concentrations of NMP peaked during September.

N-methyl-phenethylamine concentrations averaged 55% higher in leaves from juvenile leaves compared to mature stems from aerated areas (P < 0.001; Table 1) and there was no significant age*month interaction. A significant age*month interaction was detected for tyramine (P < 0.001). Tyramine concentrations in juvenile stems were nearly double those in mature stems during December 1996, February 1997, and May–July 1997 (Fig. 1). Amine concentrations were different among months for tyramine and NMP in juvenile leaves (P < 0.001 for both amine types). Tyramine concentrations in juvenile leaves peaked in June and July while NMP concentrations were elevated June-August and peaked in September (Fig. 1).

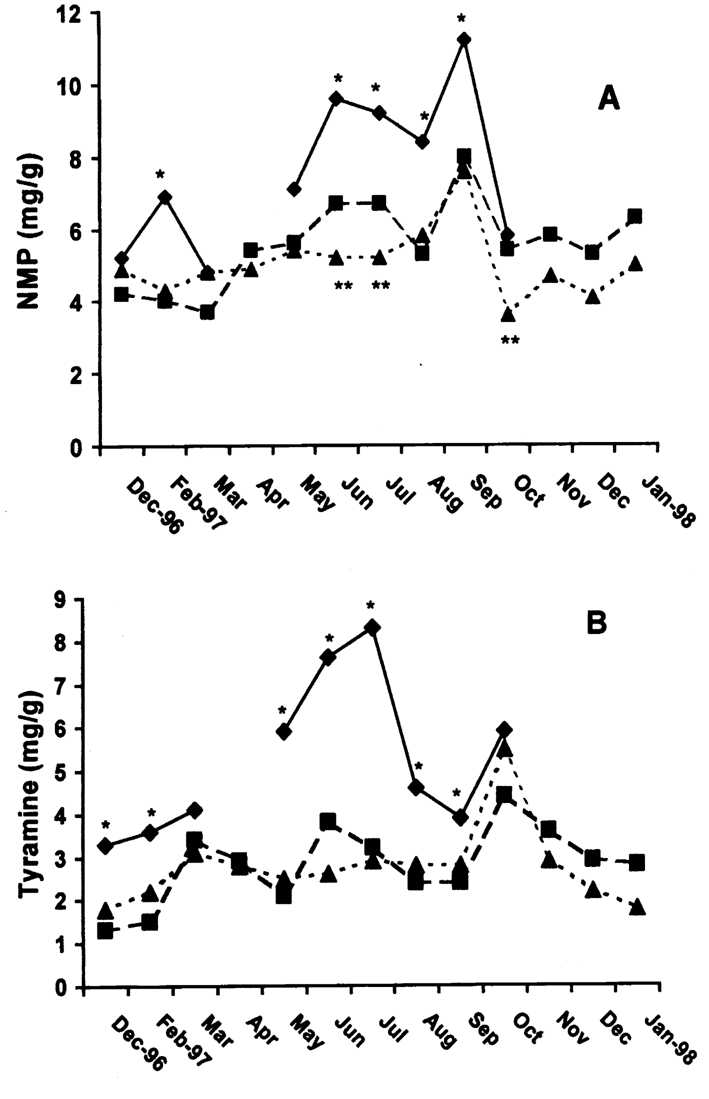

Fig. 1. Mean (N = 3) N-methyl-phenethylamine (NMP; panel A) and tyramine (panel B) concentrations (mg/g) in leaves from mature and juvenile-phase stems collected from areas aerated in October, 1996 and paired controls, Coahuila, Mexico. A "*" denotes months in which juvenile stems differed (P < 0.05) from mature stems in aerated plots and "" denotes months in which mature stems in aerated plots differed from mature stems in control plots. Juvenile stem data in October were excluded from analysis because of a missing sample (i.e. N = 2 instead of 3).**

Total leaf nitrogen in mature stems showed a treatment*month interaction (P = 0.03; Fig. 2). Nitrogen concentration differed between mature stems from control and treated plots only in March 1997. An age*month interaction (P < 0.001) was observed for differences in total leaf nitrogen between juvenile and mature stems from aerated areas; leaves from juvenile stems had higher total N in December 1996 and February, May, and July 1997 (Fig. 2).

Percent total leaf nitrogen incorporated into amine (tyramine+NMP) nitrogen was 0.3 percentage points greater (P = 0.04) in mature stems from aerated plots than from control plots (Table 1). No significant treatment*month interaction was observed. Amine nitrogen as a percent of total nitrogen peaked in summer for both juvenile and mature leaves in aerated plots (Fig. 2). The percent of nitrogen in amines was greater in juvenile stems than mature stems, although there was an age*month interaction (P = 0.04). Juvenile stems differed from mature stems in May-September (Fig. 2).

Table 1. Tyramine, N-methyl-phenethylamine (NMP), and nitrogen content of juvenile (N = 8 months) and mature (N = 13 months) guajillo stems, averaged across months, from plots aerated in October 1996 and paired controls, Coahuila, Mexico.

	Juvenile		Mature-Aerated		Mature-Control	
	Mean	SE	Mean	SE	Mean	SE
Tyramine (mg/g)	5.18[1]	0.67	2.82^{A}	0.25	52.76^{A}	0.26
NMP (mg/g)	7.80^{a}	80.7	5.58^{bA}	0.33	5.03^{B}	0.26
Nitrogen (mg/g)	33.2[1]	1.7	29.6[2]	1.2	30.5	1.5
Nitrogen in Amines (%)	4.21[1]	0.55	2.98^{A}	0.20	2.70^{B}	0.16

[1] An age*month interaction (P < 0.05) was detected in the comparison between juvenile and mature stems among months for this variable. Juvenile stems generally had greater means than mature stems, but differences varied by month. See text and figures for details.

[2] A treatment*month interaction (P < 0.05) was detected in the comparison between aerated and control stems among months for this variable. Control stems had greater nitrogen content only in March 1997.

^{ab}Juvenile and Mature-Aerated means followed by a different lower case letter were different (P < 0.05).

^{AB}Mature-Aerated and Mature-Control means followed by a different capital letter were different (P < 0.05).

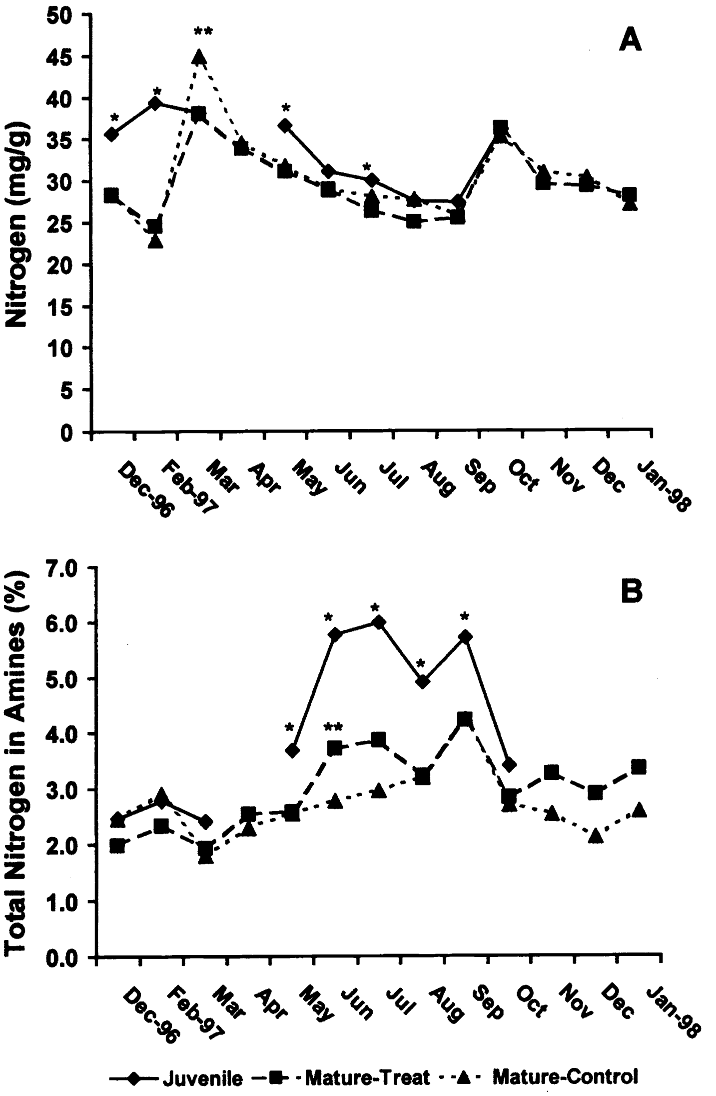

Fig. 2. Mean (N = 3) nitrogen concentration (panel A) and percent of total nitrogen composed of amine nitrogen (panel B) in leaves from mature and juvenile-phase stems collected from areas aerated in October, 1996 and paired controls, Coahuila, Mexico. A "*" denotes months in which juvenile stems differed ($P < 0.05$) from mature stems in aerated plots and "" denote months in which mature stems in aerated plots differed from mature stems in control plots. Juvenile stem data in October were excluded from analysis because of a missing sample (i.e. N = 2 instead of 3).**

Discussion

Reynolds et al. (1992) reported that total nitrogen in guajillo leaves could be temporarily increased during the nutritionally stressful times of late summer and early fall if roller-chopped in early July. Increased nitrogen concentration in guajillo leaves after aeration in our study was due primarily to growth of juvenile sprouts, which not only had higher nitrogen concentration but higher amine content compared to leaves on mature stems. The relative costs and benefits to an animal of mechanically treating guajillo will not be clear until nitrogen in mature and regrowth guajillo is fully characterized and more is known about the toxicity of guajillo's many secondary plant chemicals (Clement et al. 1997). However, range managers should be aware that mechanical treatment of guajillo is likely to increase concentration of amines, which in turn could negatively affect animal performance. Furthermore, it is unclear whether amine concentrations observed in juvenile stems in this study were affected more by plant age or seasonal climate and rainfall patterns, and therefore our results may not be applicable to guajillo treated in other seasons. If aeration can be timed such that early-stage juvenile sprouts with relatively lower amine:total nitrogen concentrations (i.e. juvenile sprouts in early spring of this study) are produced during the nutritionally stressful dry months, a valuable source of nitrogen can be provided while reducing intake of phenolic amines by wild and domestic herbivores. Further research is needed to investigate the effects of timing of aeration and rainfall on seasonal changes in amine and nitrogen concentrations in juvenile and mature-phase stems.

Forbes et al. (1995) demonstrated induction of chemical defense after simulated browsing by increased amine concentration in leaf regrowth from mature guajillo stems. Their study, however, did not investigate differences in amine concentrations between juvenile and adult-phase plants which is important in studying the effects of aeration because guajillo responds to top removal by producing multiple juvenile stems. Juvenility in plants is genetically controlled and phenotypically displayed in strong apical dominance (i.e. suppression of lateral branching and secondary growth) and low lignification (Kozlowski 1971, Bryant et al. 1991a). Juvenile plants of some species also display increased thorniness and variable leaf morphology (Kozlowski 1971). Severe browsing of juvenile plants can greatly reduce fitness by delaying reproduction. Therefore, juvenile stems of plants should be heavily defended (Bryant et al. 1983). Our observations of higher amine concentrations in leaves from juvenile stems than in leaves from mature stems support this hypothesis.

Nitrogen is often limiting for plants and therefore nitrogen-containing secondary compounds are expensive to produce, as they are ultimately derived from protein amino acids (Harbourne 1991). This is especially true in nitrogen-poor environments such as those found on our study site. During July–September, when total plant nitrogen was lowest and amines (tyramine + NMP) highest, nitrogen in tyramine and NMP was 4.9–6.0% of total leaf nitrogen in juvenile stems and 3.0–4.2% in mature stems (Table 2). More than 33 amines and alkaloids have been isolated from guajillo, with tyramine and NMP comprising 40-45% of total amine concentrations in spring and late fall (Clement et al. 1997). Therefore, though nitrogen incorporated into tyramine and NMP was only 2–6% of total nitrogen available, extrapolation to include nitrogen in other known nitrogen-containing plant secondary compounds suggests that 4-15% of total nitrogen is allocated to chemical defenses in the form of amines. Because guajillo does not have symbiotic associations allowing nitrogen-fixation (Forbes et al. 1995, Zitzer et al. 1996) and soil types in the study site are generally considered nutrient poor, the carbon/nutrient hypothesis predicts that guajillo's defenses should be carbon based instead of nitrogen based (Bryant et al. 1983). Dedication of large percentages of nitrogen in guajillo to chemical defenses seems to be an exception to the carbon/nutrient hypothesis, however, Jurena and Van Auken (1998) report nitrogen concentrations 5 times greater beneath guajillo canopies than in open areas, suggesting that nitrogen dynamics and the allocation of nutrients within woody plants in semiarid systems are not fully understood.

Tyramine and NMP concentrations in leaves from mature stems in treated areas did not differ from those in control areas 3 to 6 months post-treatment, suggesting any induction of defense in leaf regrowth from mature stems is not maintained. Forbes et al. (1995) showed significant increases in amine concentration up to 12 weeks after browsing but also concluded that induced defenses were not maintained. This short term induction may explain why we did not observe an increase in amine concentration in treated mature stems sampled 2 months after aeration. These observations and results from this study that amine concentrations varied between months support Forbes et al. (1995) conclusion that tyramine and NMP are 'dynamic' metabolites (Reichardt et al.1991).

Tyramine and NMP concentrations in mature leaves peaked in October and September, respectively, similar to a pattern described by Clement et al. (1997). Juvenile stems reached peak tyramine concentrations in July and peak NMP concentrations in September. Diet quality of ungulates during this period (July to September) is typically poor because low rainfall reduces biomass of forbs (Bozzo et al. 1992, Reynolds et al. 1992, Windels 1999). Wild and domestic ungulates rely heavily on browse from guajillo and blackbrush during dry summer and winter periods (Barnes et al. 1991, Martinez et al. 1997), and thus may be doubly stressed from low nutrient and high phenolic amine intake.

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Water, nitrogen and ploidy effects on Russian wildrye mineral concentrations

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Abstract

High quality forage for spring and autumn grazing can be obtained from Russian wildrye [*Psathyrostachys juncea* (Fisch.) Nevski], a cool-season bunchgrass. However, little is known about mineral concentrations critical to livestock production, especially in the relatively new tetraploid plants. A knowledge of plant mineral concentrations and how they can be manipulated to more nearly meet animal requirements is necessary to optimize animal production. A study was undertaken to determine the extent that concentrations of critical minerals in leaf and stem tissue of Russian wildrye were affected by ploidy level, growing-season water (50 and 150% of average), and N fertilizer (10 and 134 kg N ha^{-1}). Plants were sampled at vegetative, boot, anthesis, and anthesis plus 10-day stages of maturity in 1994, 1995, and 1996. Ploidy level resulted in small but significant differences in some mineral concentrations, with diploid plants usually having higher levels. An exception was P in stem tissue. This finding indicates that in breeding and selection for other traits, forage quality was not adversely affected. Growing-season water level also had minimal effects on mineral concentrations, except for P which was enhanced ($P < 0.05$) by greater amounts of soil water. Fertilizer N increased forage levels of Ca, K, Cu, and Zn, and decreased levels of P. Higher concentrations of K are not desirable, because they increase the possibility of a grass tetany problem. Advancing plant maturity caused a decrease in P and Zn concentrations, but Ca and Mg in leaf tissue increased as plants matured. These results suggest that concentrations of P, Ca, Mg, and Cu were marginal for high producing cattle at some stages of maturity, but we found the effects of nitrogen and growing-season water did not result in leaf and stem mineral concentration changes that would adversely affect the safety and nutritive quality of Russian wildrye.

Key Words: diploid, tetraploid, stage of maturity, rain shelter

Resumen

Forraje de alta calidad para el apacentamiento en primavera y otoño puede ser obtenido del "Russian wildrye" [*Psathyrostachys juncea* (Fisch.) Nevski], un zacate amacollado de crecimiento invernal. Sin embargo, poco se conoce acerca de las concentraciones minerales criticas para la producción del ganado, especialmente en las plantas tetraploides, las cuales son relativamente nuevas. Es necesario un conocimiento de las concentraciones de minerales en las plantas y como ellas pueden ser manipuladas para casi satisfacer los requerimientos del animal necesarios para optimizar su producción. Se condujo un estudio para determinar en que cantidad el nivel de poliploidia, el agua en la estación de crecimiento (50 y 150% del promedio) y la fertilización N (10 and 134 kg N ha^{-1}) afectaron las concentraciones de minerales críticos en el tejido de hoja y tallo del "Russian wildrye", Las plantas fueron muestreadas en 1994, 1995 y 1996 en los estados de madurez de: crecimiento vegetativo, embuche, antesis, y 10 días después de antesis. El nivel de poliploidia resulto diferencias pequeñas, pero significativas, de la concentración de minerales, las plantas diploides usualmente tuvieron los mayores niveles. Una excepción fue el P en el tejido del tallo. Estos hallazgos indican que en el mejoramiento y selección de otras características la calidad del forraje no fue afectada adversamente. El nivel de agua en la estación de crecimiento también tuvo efectos mínimos en las concentraciones de minerales, excepto el P el cual fue incrementado ($P < 0.05$) por las grandes cantidades de agua del suelo. La fertilización N incremento los niveles de Ca, K, Cu y Z y disminuyo los niveles de P. Altas concentraciones de K no son deseables porque ellas incrementan la posibilidad de tener problemas de tetania de los pastos. El avance de la madurez de las plantas causo una disminución en la concentración de P y Zn, pero el Ca y el Mg del tejido de la hoja incremento conforme la planta maduro. Estos resultados sugieren que en algunas etapas de madurez las concentraciones de P, Ca, Mg y Cu fueron marginales para ganado de alta productividad, pero encontramos que la fertilización N y el nivel de agua en al estación de carecimiento no resultaron en cambios de la concentración de minerales del tejido el hojas y tallos que pudieran afectar adversamente la seguridad y calidad nutritiva del "Russian wildrye".

Russian wildrye, a cool-season bunchgrass, was introduced into the United States from the U.S.S.R. in 1927 (Johnson and Nichols 1970). It has potential as a valuable forage for spring and autumn grazing in the Northern Great Plains, but little is known about the concentration of minerals critical to livestock production (NRC 1996), potential mineral concentration differences

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among cultivars, or the effect of environmental conditions on plant mineral levels. Some scientists (Asay and Mayland 1990, Jefferson et al. 2001) have indicated that Russian wildrye may cause grass tetany in spring, when its nutritive quality is high (Karn et al. 1983). Grass tetany (hypomagnesemia), is an often fatal metabolic disorder primarily affecting lactating cows. It is thought to be caused by low forage Mg and Ca levels, and is exacerbated by high levels of K and crude protein (Committee on Mineral Nutrition 1973). Research with tall fescue [(*Festuca arundinacea* Schreb.), Reeder et al. 1986, Sleper et al. 1989], annual ryegrass [*Lolium* L. (Poaceae), Hides and Thomas 1981] and Russian wildrye (Jefferson et al. 2001) suggests that the incidence of grass tetany could be reduced by modifying forage mineral concentrations, especially Mg, through plant breeding and selection. Little is known, however, about levels of other minerals in Russian wildrye, such as Cu, Fe, P, Mn, S, and Zn that are also known to be essential for optimal animal performance (NRC 1996).

Diploid Russian wildrye genotypes have been used in most grazing and nutritive quality research, but stands of this forage are often difficult to establish. Induced autotetraploid Russian wildrye developed by Berdahl and Barker (1991) has been reported to have superior seedling vigor, and natural tetraploids recently obtained from Kazakhstan were reported to have heavier seeds, greater seedling vigor, were slightly taller and had longer and wider leaves than diploid genotypes (Asay et al. 1996). Generally, water stressed forages have higher nutritive quality (Crasta and Cox 1996, Deetz et al. 1996), primarily because of increased leaf-to-stem ratios (Halim et al. 1990), but less is known about the effect of water stress on plant mineral concentrations. Nitrogen fertilizer usually increases plant crude protein concentrations (Perry and Baltensperger 1979), but its affect on other elements is less well known.

Numerous studies have shown that both sheep (*Ovis aries*) and cattle (*Bos taurus*) voluntarily consume more leaves than stems (Minson 1990), indicating the need to determine how essential mineral levels differ between leaf and stem tissues, and whether differences are affected by stage of maturity. The potential value of Russian wildrye for early and late grazing, coupled with its reputation as a tetany prone forage suggested a need to determine how some common natural and management situations would affect the concentration of minerals critical to animal production. In the northern plains, drought is a common natural occurrence and N fertilization is a common management practice, thus the effect of water or lack of water, and N fertilizer on forage mineral concentrations were logical treatments needing further study. The effect of ploidy level on forage mineral concentrations is important because of the recent introduction of tetraploid Russian wildrye, which has some desirable agronomic characteristics, but virtually nothing is known about its chemical composition. Thus, research was undertaken to determine the effect of ploidy, water, and fertilizer N levels on Russian wildrye tissue mineral concentrations at 4 stages of maturity, when plants were grown in a field environment using a rain shelter where water levels could be controlled. A secondary objective was to determine the effect of these variables on mineral levels essential for optimal beef cattle production.

Materials and Methods

Diploid and tetraploid populations of Russian wildrye were seeded in 1993 in plots containing 8 rows (3.6-m length, 0.33 m between rows) of plants, grown in a field environment under a movable rain shelter (Ries and Zachmeier 1985), that automatically covered the plots when activated by precipitation. Plots were located near Mandan, N.D. (46° 46' N, 100° 55' W). The seeding rate was 90 seeds m^{-1} of row length (Frank and Berdahl 2001). The movable rain shelter allowed precise application of water treatments to the plots by an overhead sprinkler system. The 2 populations included the diploid cultivar Vinall, which has been used as a standard in many Russian wildrye studies, and a tetraploid population which was a balanced composite of 6 populations, representative of tetraploid germplasm in the Mandan breeding program (Frank and Berdahl 2001). Soil was a Parshall fine sandy loam (coarse-loamy, mixed superactive, frigid, pachic Haplustolls).

There were 4 replicates of each population arranged in a split-split plot design. Main plots were water treatments, with N levels and populations as subplots. Water treatments provided 50 and 150% of the long-term average monthly precipitation for April through October at Mandan. Long-term averages (30 yr) were based on precipitation levels of 38, 55, 85, 61, 43, 38, and 24 mm for April, May, June, July, August, September, and October, respectively (Frank and Berdahl 1999). Treatment levels were achieved by 1 watering event per week. From November through March each year, plots were exposed to actual winter precipitation. Nitrogen treatments were randomly applied within water treatment and population in April of each year, using ammonium nitrate fertilizer at 2 levels: low (10) and high (134 kg N ha^{-1}). Water and N treatments were initiated in 1993 to ensure that plants were acclimated to their respective treatments, before data collection was initiated in 1994. The study contained a total of 32 plots from 4 replications of 2 ploidy levels, 2 water levels, and 2 N levels.

Forage samples were collected from plots for nutritive quality analysis at the vegetative, boot, anthesis, and anthesis plus 10-day stages of maturity in 1994, 1995 and 1996. Forages began to grow at different times each year due to variation in accumulated growing degree days; thus, sampling dates were not consistent among years. In 1994, samples were harvested on 4, 16, and 31 May, and 14 June. In 1995, samples were harvested on 10 and 22 May, and 6 and 21 June. In 1996, samples were harvested on 17 and 28 May, and 14 and 26 June. Within years, forage samples were harvested from a different portion of the plot at each sampling date. In September of each year all plots were clipped to a similar height to minimize potential plot effects the following year.

Harvested samples were rinsed in distilled water to remove any contaminating soil, and dried to a constant weight at 55° C in a forced-air oven. All samples were ground through a 1-mm screen before analysis. Samples collected at anthesis and anthesis plus 10-day stages of maturity were separated into leaf, stem and inflorescence tissue before being ground. Inflorescence samples were not analyzed for this study because sample material was limited. Forage samples obtained at vegetative and boot stages of maturity were primarily leaf tissue. Samples were analyzed for P, Ca, K, Mg, S, Cu, Zn, Mn, Fe, aluminum (Al) and sodium (Na) using a plasma emission spectrophotometer.

Data were analyzed using the SAS MIXED procedure (SAS Inst., Inc. 1996) with ploidy, water and N levels fixed and replication, replication x water level, and replication x water x ploidy x N level considered random. Years were treated as repeated measures. Least-squares means for ploidy, water, and N levels were separated by an F-test and means for stage of maturity were separated by the SAS PDIFF option. Data comparisons were considered significant at $P < 0.05$.

Table 1. Main effect and interaction probabilities for leaf tissue minerals of 2 ploidy levels of Russian wildrye, grown at 2 water levels and 2 N fertilizer levels over 3 growing seasons.

Effect	P	Ca	K	Mg	S	Mineral Na	Cu	Zn	Mn	Fe	Al
Ploidy level	0.06	<0.01	0.34	<0.01	0.58	<0.01	0.65	0.21	<0.01	0.29	0.13
Water level	<0.01	0.13	0.09	0.24	0.01	0.12	0.10	0.46	<0.01	0.09	0.19
Nitrogen level	<0.01	<0.01	<0.01	0.41	<0.01	<0.01	<0.01	<0.01	0.18	0.05	0.03
Ploidy x water	0.44	0.13	0.55	0.06	0.16	0.76	0.59	0.80	0.42	0.56	0.21
Ploidy x nitrogen	0.55	0.54	0.14	0.41	0.05	0.77	0.10	0.20	0.92	0.96	0.69
Water x nitrogen	<0.01	0.73	0.10	0.38	<0.01	0.23	0.05	0.90	0.91	0.41	0.87
Ploidy x water x nitrogen	0.55	0.65	0.54	0.19	0.85	0.28	0.49	0.84	0.83	0.23	0.28
Harvest date (HD)	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
HD x ploidy	0.44	<0.01	0.02	0.04	0.19	0.27	0.97	0.18	0.06	0.44	0.13
HD x water	<0.01	<0.01	<0.01	<0.01	0.88	0.97	0.99	0.26	<0.01	0.05	<0.01
HD x nitrogen	0.12	<0.01	0.70	0.05	<0.01	0.10	0.06	0.99	<0.01	0.08	<0.01

Results

Statistical probabilities of main effects and interaction effects are summarized in Table 1 for leaf tissue and Table 2 for stem tissue. Data are presented by main effect, in the following order: ploidy level, water treatment level, N fertilizer, and harvest date.

Ploidy Level

Calcium, Mg, Na, and Mn concentrations were higher in diploid than tetraploid leaf tissue (Table 3). Diploid leaf Ca concentrations were 0.26, 0.23, 0.38, and 0.42% and tetraploid Ca concentrations were 0.24, 0.22, 0.33, and 0.36% for vegetative, boot, anthesis, and anthesis plus 10-day harvest dates, respectively. Significant ploidy level x harvest date interactions for leaf Ca and Mg (Table 1 and Fig. 1 A, B) were due to greater mineral concentration differences between diploid and tetraploid leaf tissues at later harvest dates, but leaf Ca and Mg concentrations were still consistently higher in diploid than tetraploid tissues.

Tetraploid plants had higher stem P concentrations than diploid plants, but diploid plants had higher Ca, K, Na, and Mn concentrations (Table 3). The only ploidy level interaction with these minerals in stem tissue was with water level (Table 2 and Fig. 1C). Diploid and tetraploid stem P did not differ at the 50% water level, but at the 150% water level, tetraploid plants were slightly higher in P than diploid plants. Ploidy level affected relatively few mineral concentrations and most differences were quite small, even when they were significant.

Table 2. Main effect and interaction probabilities for stem tissue minerals of 2 ploidy levels of Russian wildrye, grown at 2 water levels and 2 N fertilizer levels over 3 growing seasons.

Effect	P	Ca	K	Mg	S	Mineral Na	Cu	Zn	Mn	Fe	Al
Ploidy level	0.02	<0.01	0.03	0.53	0.27	0.01	0.57	0.27	0.02	0.91	0.38
Water level	<0.01	0.39	0.93	0.45	0.01	0.63	0.80	0.10	0.04	0.06	0.38
Nitrogen level	<0.01	<0.01	<0.01	<0.01	<0.01	0.14	<0.01	<0.01	0.72	0.37	0.02
Ploidy x water	0.04	0.55	0.19	0.86	0.76	0.45	0.51	0.40	0.97	0.72	0.33
Ploidy x nitrogen	0.72	0.57	0.72	0.59	0.15	0.47	0.66	0.71	0.90	0.69	0.40
Water x nitrogen	<0.01	0.26	0.13	0.09	0.27	0.44	0.58	0.67	0.54	0.38	0.23
Ploidy x water x nitrogen	0.26	0.12	0.94	0.97	0.48	0.06	0.87	0.38	0.86	0.23	0.28
Harvest date (HD)	<0.01	0.01	<0.01	0.36	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.38
HD x ploidy	0.22	0.64	0.16	0.38	0.86	0.17	0.18	0.34	0.74	0.66	0.24
HD x water	0.18	0.99	0.99	0.88	0.88	0.68	0.11	0.04	0.22	0.19	0.61
HD x nitrogen	0.27	0.10	0.50	0.39	0.06	0.47	0.03	0.32	0.90	0.62	0.10

Table 3. Leaf and stem mineral concentrations in diploid and tetraploid Russian wildrye taxa. Values are mean and SE averaged over water level, N level and harvest date.[1]

Ploidy level	P	Ca	K	Mg	S	Na	Cu	Zn	Mn	Fe	Al
	------------(% of DM)------------						------------(ppm dry basis)------------				
Leaf Tissue											
Diploid	0.28	0.32^{a}	3.6	0.25^{a}	0.32	0.13^{a}	7	38	55^{a}	101	62
Tetraploid	0.27	0.29^{b}	3.6	0.23^{b}	0.33	0.11^{b}	7	37	50^{b}	95	59
SE	0.01	0.01	0.1	0.00	0.01	0.01	0	2	1	6	2
Stem tissue											
Diploid	0.16^{b}	0.10^{a}	2.9^{a}	0.10	0.15	0.08^{a}	5	22	20^{a}	39	26
Tetraploid	0.17^{a}	0.09^{b}	2.7^{b}	0.10	0.15	0.07^{b}	5	21	19^{b}	39	25
SE	0.01	0.00	0.1	0.01	0.01	0.00	0	1	1	1	1

[1] Means within a tissue type and mineral with different superscripts differ at $P < 0.05$.

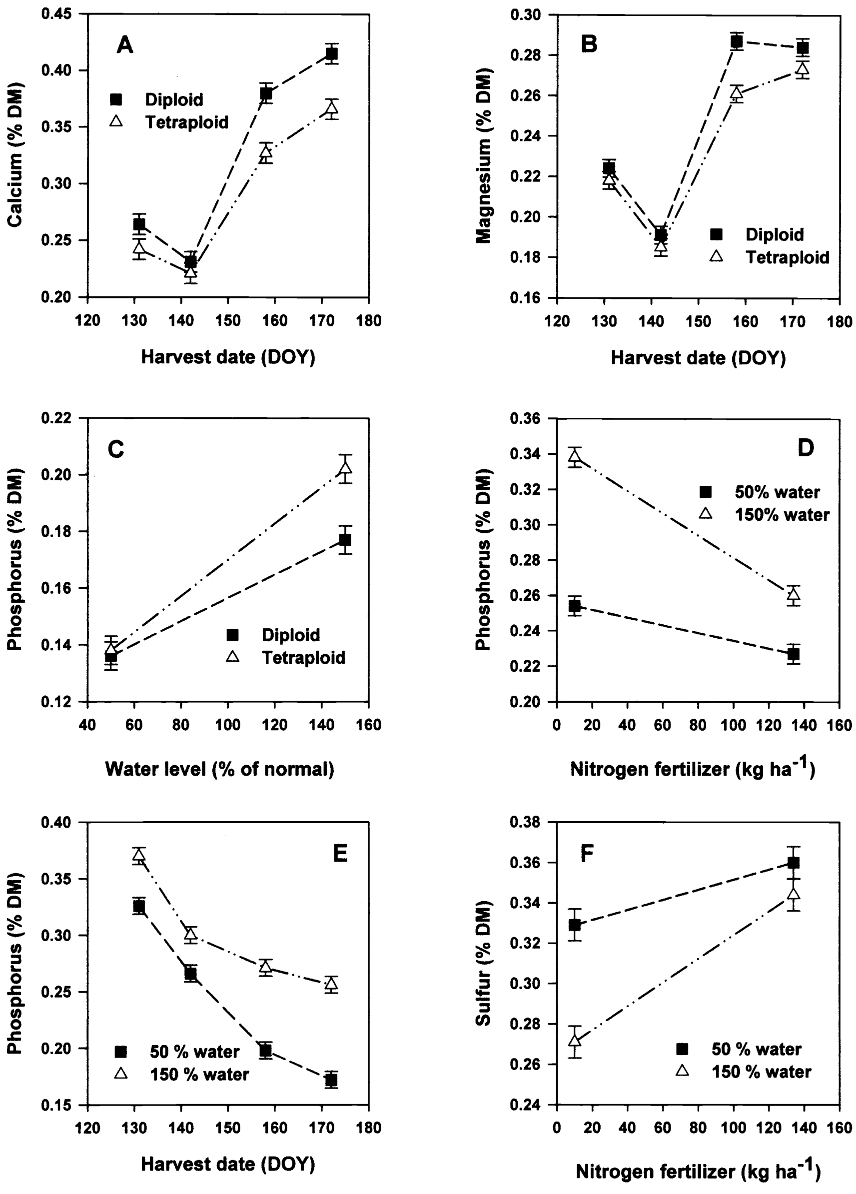

Fig. 1. Interaction effects of (A) ploidy and harvest date on leaf Ca, (B) ploidy and harvest date on leaf Mg, (C) ploidy and water level on stem P (D) water level and N fertilizer on leaf P, (E) water level and harvest date on leaf P, and (F) water and N fertilizer level on leaf S.

Although mineral concentrations in leaf and stem tissues were not statistically compared, concentrations of P, Ca, Mg, S, Zn, Mn, Fe, and Al, in leaf tissue were 50 to 150% higher than levels in stem tissue. Potassium, Na, and Cu concentrations were also higher in leaf tissue, but differences were not as great as they were for the other minerals (Table 3).

Water Treatment

Leaf tissue P, S and Mn were significantly affected by water level, with the 150% water treatment resulting in the highest P concentrations, and the 50% water treatment resulting in the highest S and Mn levels (Table 4). However, water level effects on P were not consistent over the 2 N levels (Fig. 1D). Leaf P increased less between high and low N treatments at the 50% water level than at the 150% water level. There was also a water by harvest date interaction for leaf P, where leaf P levels for the 50% water treatment were lower initially, and declined more rapidly between vegetative and anthesis plus 10-day stages of maturity, than P levels for the 150% water treatment (Fig. 1E).

An interaction between water and N fertilizer levels for leaf S (Fig. 1F) was due to the magnitude of the difference between N effects at 50% and 150% water levels, but S was higher in leaves from high N treatment plants for both water treatments. Differences in Mn concentrations in leaf tissue between 50 and 150% water treatments were not consistent over harvest dates creating an interaction (Fig. 2A). Manganese concentration differences between the 2 water treatments were greater at anthesis and anthesis plus 10-day stages of maturity than at vegetative and boot stages, although Mn concentrations were always higher for the 50% water treatment.

Stem tissue concentrations of P were increased by the 150% water treatment, while Mn concentrations in stem tissue were higher in plants grown at the 50% water treatment, which is consistent with leaf tissue results (Table 4). Stem P levels at the 50% water treatment differed little between low and high N treatments, but at the 150% water treatment P concentrations were substantially higher at the low than at the high N treatment, resulting in a significant interaction (Fig. 2B). Mineral concentrations in either Russian wildrye leaf or stem tissue were relatively unaffected by differences in growing season water levels.

Nitrogen Fertilizer

Nitrogen fertilizer had a greater affect than ploidy or water level on mineral concentrations in both Russian wildrye leaf and stem tissue, with 9 minerals affected in leaf tissue, and 8 in stem tissue (Table 5). Phosphorus levels in leaf tissue were decreased by N fertilization, but Ca, K, S, Na, Cu, Zn, Fe, and Al concentrations were all increased (Table 5). In leaf tissue, only Mg and Mn concentrations were unaffected by N fertilizer.

Water and N treatments interacted with regard to leaf Cu (Fig. 2C), with the 50 and 150% water treatments having the same leaf Cu concentration at the low N level (10 kg ha^{-1}), while at the high N level (134 kg ha^{-1}) leaf Cu was slightly greater for the 150% water treatment. Significant interactions also existed between harvest date and N level, for leaf Ca (Fig. 2D), S, and Al (Table 1). Calcium levels were the same for high and low N treatments at the

Table 4. Leaf and stem mineral concentrations in Russian wildrye grown at 2 water levels. Values are mean and SE averaged over ploidy level, N level and harvest date.[1]

Water level	P	Ca	K	Mg	S	Na	Cu	Zn	Mn	Fe	Al
	(% of DM)						(ppm dry basis)				
Leaf Tissue											
50% of ave.	0.24^{b}	0.32	3.7	0.24	0.34^{a}	0.12	7	38	58^{a}	106	62
150% of ave.	0.30^{a}	0.29	3.6	0.24	0.31^{b}	0.13	7	37	47^{b}	90	59
SE	0.01	0.01	0.1	0.00	0.01	0.01	0	2	1	6	2
Stem tissue											
50% of ave.	0.14^{b}	0.10	2.8	0.10	0.16	0.07	5	22	21^{a}	41	26
150% of ave.	0.19^{a}	0.10	2.8	0.10	0.14	0.08	5	20	18^{b}	37	25
SE	0.01	0.00	0.1	0.01	0.01	0.00	0	1	1	1	1

[1]Means within a tissue type and mineral with different superscripts differ at $P < 0.05$.

first harvest date, but levels were slightly greater at the high N treatment for the other 3 harvest dates. Leaf S was greater for the high N treatment at all 4 harvest dates, and the magnitude of this difference increased from vegetative to anthesis plus 10-day harvest dates.

Stem P levels were also decreased at the high N level while Ca, K, Mg, S, Cu, Zn, and Al increased (Table 5). In contrast to leaf Mg, stem Mg was slightly but significantly increased by N fertilizer, while Na, Mn, and Fe were unaffected by N levels. Stem Cu was higher at anthesis than anthesis plus 10 days, and differences between N treatments were also greater at anthesis, causing a significant interaction (Fig. 2E).

Harvest Date

Concentrations of all 11 minerals in leaf tissue were significantly affected by harvest date, and all minerals except Mg and Al were affected by harvest date in stem tissue (Table 6). Leaf P and Zn levels decreased from vegetative to anthesis plus 10-day stages of maturity, and stem P and Zn declined between anthesis and anthesis plus 10 days. Copper concentrations tended to decline as maturity advanced in both leaf and stem tissue. Calcium, Mg, Na, and Al concentrations in leaf tissue declined from vegetative to boot stages, then increased at anthesis and anthesis plus 10-day stages of maturity. Potassium, S, Mn, and Fe were less consistently affected by stage of maturity. Stem tissue K, S, Mn, and Fe declined significantly between anthesis and anthesis plus 10 days, while Ca and Na increased slightly (Table 6). Stem tissue had fewer harvest date interactions, but there was a harvest date x water level interaction for Zn (Fig. 2F). Stem Zn at anthesis was higher for both the 50 and 150% water levels, but Zn concentration differences between anthesis and anthesis plus 10 days was greater for the 50% water treatment.

Discussion

Ploidy Level

Few differences in mineral concentration occurred between diploid and tetraploid Russian wildrye leaf and stem tissue, but most differences although small favored diploid plants. 'Ruff' a diploid crested wheatgrass cultivar was reported by Vogel et al. (1993) to generally have higher forage quality than 'Nordan', a tetraploid cultivar, although 'Nordan supported higher steer weight gains. Little previous nutritive quality data are available on the tetraploid germplasm used in this study (Berdahl and Barker 1991). Since improvement in seedling vigor was an important selection criteria for this genetic material (Berdahl and Ries 1997), it is fortuitous that mineral concentrations in the new tetraploid germplasm was not adversely affected in the breeding and selection process. Although in this study genetic differences in mineral levels were small, breeding and selection efforts to reduce the incidence of grass tetany, by improving Mg concentrations in tall fescue (Reeder et al. 1986, Sleper et al. 1989), annual ryegrass (Hides and Thomas 1981) and Russian wildrye (Jefferson et al. 2001) have been encouraging.

Water Treatment

Water stress has been shown to have a positive (Vough and Marten 1971, Wilson 1983, Crasta and Cox 1996), negative (Wilson and Ng 1975), or variable (Halim et al. 1989) effect on forage quality. Most water stress data concerns IVDDM, ADF, NDF or N differences in alfalfa (Vough and Marten 1971, Halim et al. 1989, and Deetz et al. 1996) or annual crops (Crasta and Cox 1996). Data assessing the effect of water stress on forage mineral levels is negligible (Buxton and Fales 1994). In this study, growing-season water levels only

Table 5. Leaf and stem mineral concentrations in Russian wildrye grown at 2 N fertilizer rates. Values are mean and SE averaged over ploidy level, water level and harvest date.[1]

Nitrogen	P	Ca	K	Mg	S	Na	Cu	Zn	Mn	Fe	Al
	(% of DM)						(ppm dry basis)				
Leaf Tissue											
10 kg ha^{-1}	0.30^{a}	0.29^{b}	3.5^{b}	0.24	0.30^{b}	0.11^{b}	7^{b}	36^{b}	54	92^{b}	58^{b}
134 kg ha^{-1}	0.24^{b}	0.32^{a}	3.7^{a}	0.24	0.35^{a}	0.13^{a}	8^{a}	39^{a}	52	104^{a}	62^{a}
SE	0.01	0.01	0.1	0.00	0.01	0.01	0	2	1	6	2
Stem tissue											
10 kg ha^{-1}	0.18^{a}	0.09^{b}	2.6^{b}	0.10^{b}	0.13^{b}	0.07	5^{b}	19^{b}	20	38	24^{b}
134 kg ha^{-1}	0.14^{b}	0.11^{a}	3.0^{a}	0.11^{a}	0.17^{a}	0.08	6^{a}	23^{a}	20	40	27^{a}
SE	0.01	0.00	0.1	0.01	0.01	0.00	0	1	1	1	1

[1]Means within a tissue type and mineral with different superscripts differ at $P < 0.05$.

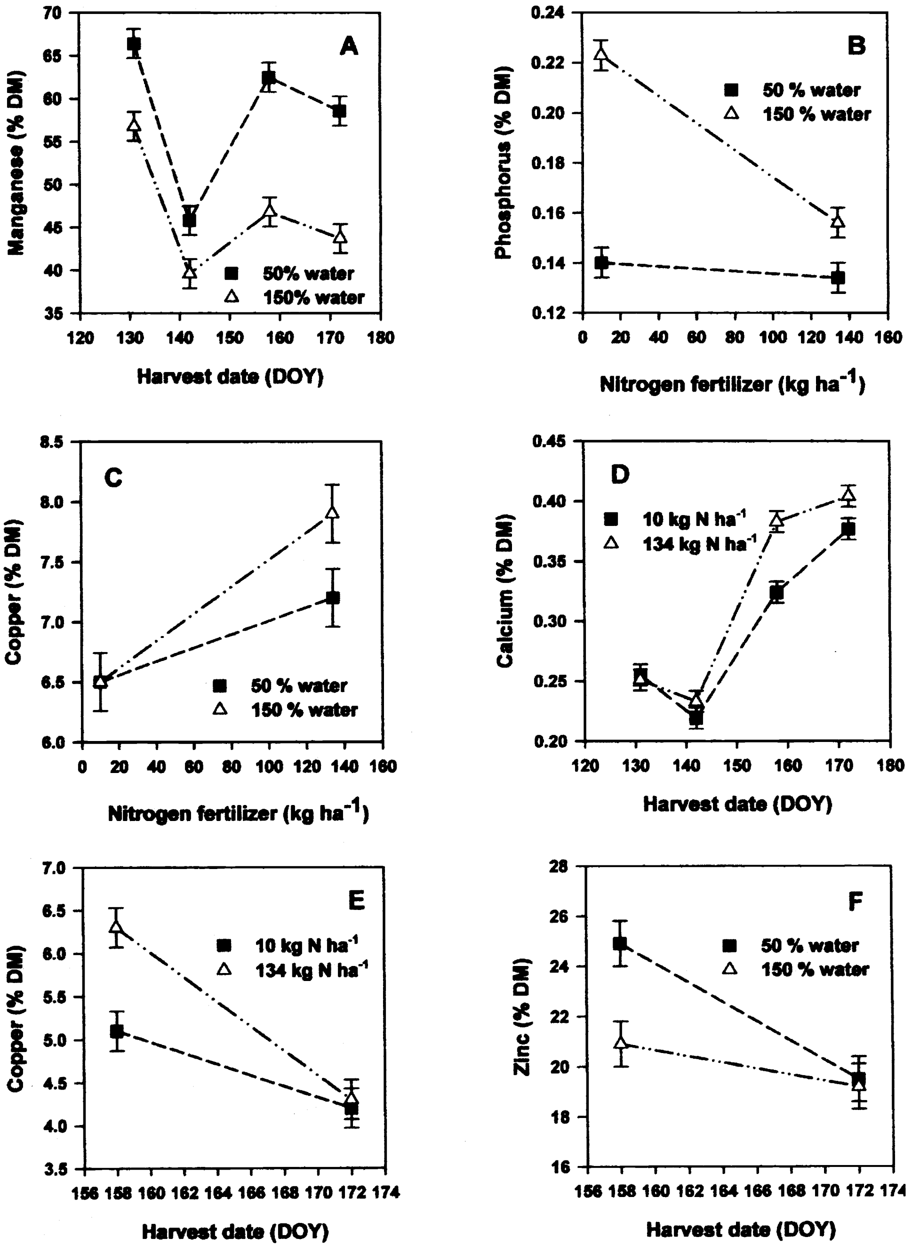

Fig. 2. Interaction effects of (A) water and harvest date on leaf Mn, (B) water and N fertilizer level on stem P (C) water and N fertilizer level on leaf Cu, (D) N fertilizer and harvest date on leaf Ca, (E) N fertilizer and harvest date on stem Cu, and (F) water level and harvest date on stem Zn.

affected concentrations of P, S, and Mn in leaf tissue and P and Mn in stem tissue. The increased phosphorus levels in both leaf (25%) and stem (38%) tissue that occurred with higher water levels (150% of average) is particularly important, because P is generally considered to be deficient for much of the world's grazing livestock (Church et al. 1971). These results are also encouraging because an increase in growing-season water in a semi-arid environment should increase forage yield which often results in a dilution of mineral concentrations. In a previous report of dry matter yields from this study (Frank and Berdahl 1999) the high water treatment (150% of average) only increased Russian wildrye production by 4%, so dilution of mineral concentrations in this study would have been minimal. Main effect results of this research need to be considered in light of several significant interactions with water level and ploidy, nitrogen, and harvest date for various minerals, which indicate the results may not be consistent over all environments.

Nitrogen Fertilizer

Fertilizer N had a greater effect on Russian wildrye leaf and stem mineral concentrations than ploidy or water level. The large effect on mineral concentrations found with N fertilizer is particularly important because Russian wildrye is reported to be prone to causing grass tetany, which is associated with high levels of K and low levels of Ca and Mg (Committee on Mineral Nutrition 1973). Fertilizing with N at 134 kg N ha^{-1}, a relatively high rate, increased K and Ca in both leaf and stem tissue, but had little effect on Mg concentrations. Similar results have been reported previously (Karn et al. 1983). However, data reported by Reynolds and Wall (1982) indicated that lower N rates (67 kg N ha^{-1}), increased forage Mg and decreased K, while N rates similar to ours increased forage K and had little effect on Mg and Ca. Increasing dietary K levels in ruminants (Greene et al. 1983, Wylie et al. 1985) results in decreased Mg absorption, exacerbating a potential grass tetany problem.

In contrast to most other minerals, P concentrations in both leaf and stem tissue were decreased by N fertilizer, probably a dilution effect due to enhanced forage yields. Previously reported forage yields from this study (Frank and Berdahl 1999) showed that fertilizing with 134 kg N ha^{-1} increased forage production by 46% over the 10 kg N ha^{-1} rate. It is interesting to note that increasing water increased forage P, while increasing N had the opposite effect. Although N fertilizer affected several forage mineral levels, we found that overall, forage quality was not adversely affected, and the likelihood of grass tetany was not measurably increased.

Harvest Date

Phosphorus levels in both leaf and stem tissues were adequate (NRC 1996) for beef cows and yearling steers during most phases of their lives. However, stem tissue P levels at anthesis plus 10 days were not adequate for beef cows in early lactation (Table 6). Beef cow Ca needs could have been met by leaf tissue at anthesis or anthesis plus 10 days, but at vegetative and boot stages of maturity Ca would have been inadequate for high milking beef cows in early lactation. Stem tissue Ca was very low (about 0.10%), indicating that if Russian wildrye hay contained 50% or more stem tissue, it would not be adequate in Ca for even moderately milking beef cows (NRC 1996).

Magnesium in leaf tissue ranged from 0.19-0.28%. It has been suggested that

Table 6. Leaf and stem mineral concentrations in Russian wildrye harvested at different stages of maturity. Values are mean and SE averaged over ploidy, water, and N level.[1]

Maturity stage	P	Ca	K	Mg	S	Na	Cu	Zn	Mn	Fe	Al
	(% of DM)						(ppm dry basis)				
Leaf Tissue											
Vegetative	0.35^{a}	0.25^{c}	3.7^{b}	0.22^{b}	0.36^{a}	0.10^{b}	8^{a}	45^{a}	62^{a}	106^{b}	57^{c}
Boot	0.28^{b}	0.23^{d}	3.7^{b}	0.19^{c}	0.29^{d}	0.09^{b}	7^{b}	40^{b}	43d	63^{d}	41^{d}
Anthesis	0.23^{c}	0.35^{b}	3.9^{a}	0.27^{a}	0.32^{c}	0.14^{a}	7^{b}	37^{b}	55^{b}	89^{c}	63^{b}
Anthesis + 10 d.	0.21^{d}	0.39^{a}	3.2^{c}	0.28^{a}	0.34^{b}	0.14^{a}	6^{c}	30^{c}	51^{c}	136^{a}	80^{a}
SE	0.01	0.01	0.1	0.00	0.01	0.01	0	2	1	7	2
Stem tissue											
Anthesis	0.18^{a}	0.09^{b}	3.0^{a}	0.10	0.16^{a}	0.07^{b}	6^{a}	23^{a}	22^{a}	42^{a}	26
Anthesis + 10 d.	0.15^{b}	0.10^{a}	2.6^{b}	0.10	0.14^{b}	0.08^{a}	4^{b}	19^{b}	18^{b}	36^{b}	25
SE	0.01	0.00	0.1	0.01	0.01	0.00	0	1	1	1	1

[1] Means within a tissue type and mineral with different superscripts differ at $P < 0.05$.

forage Mg levels above 0.2% should be adequate to prevent grass tetany (Kemp 1960). However, Mg levels may need to be substantially above 0.2% when forage K levels exceed 3.25% (Metson et al. 1966). Although Mg in Russian wildrye leaf tissue exceeded 0.19% at all stages of maturity, leaf K levels ranged from 3.25 to 3.89% suggesting that Mg levels may have been inadequate to prevent grass tetany at some stages of maturity. The lowest levels of Mg occurred at the vegetative and boot stages when K was near 3.7% (Table 6). In comparison, at anthesis Mg in stem tissue was only 0.1%, while K was near 3.0%. It would appear that Russian wildrye on a whole plant basis, would have been marginal in Mg at all stages of maturity.

Sulfur concentrations in both leaf and stem tissue were at or above levels indicated by McDowell (1997) to be adequate for lactating and growing and finishing cattle. Forage copper levels ranging from 4-6 ppm, with molybdenum (Mo) concentrations below 1.5 ppm provided adequate Cu for cattle in western Australia, but in England, cattle grazing pastures with Cu concentrations of 7–14 ppm and Mo concentrations of 3–20 ppm responded to Cu therapy (Underwood 1977). Copper requirements reported by the NRC (1996) are 10 ppm for cattle in all stages of production. Copper concentrations in Russian wildrye leaf tissue were below 10 ppm, but may have been adequate for all classes of beef cattle, since molybdenum concentrations were below 1.0 ppm (data not shown). Copper concentrations in stem tissue were more marginal. The NRC (1996) recommends 30 ppm Zn and 50 ppm Fe for all classes of beef cattle. These recommendations were easily met by leaf tissue, but were inadequate in stem tissue (Table 6). The Mn recommendation for growing and finishing cattle is 20 ppm; both leaf and stem tissue met or exceeded this level. However, the Mn recommendation for gestating and lactating cows is 40 ppm (NRC 1996). Leaf tissue easily met this recommendation, while stem tissue would provide only about half of the recommended level (Table 6).

Conclusion

Ploidy level resulted in small and relatively minor differences in mineral concentrations in Russian wildrye leaves and stems. This was a beneficial finding, because the tetraploid germplasm was developed without consideration of potential breeding and selection effects on forage quality. Growing-season water level also had minimal effects on mineral concentrations, except for P which was apparently enhanced by higher soil water. Nitrogen fertilizer had both positive and negative effects on forage mineral levels. For example, positive effects include slightly higher levels of Ca, Cu, and Zn, and negative effects included lower P, which is always detrimental to forage fed animals. Higher K concentrations associated with N fertilizer would exacerbate a potential grass tetany problem. There were some important mineral changes due to maturity, with concentrations of P, Cu and Zn tending to decline with maturity and Ca and Mg tending to increase. Phosphorus in whole plants at anthesis and anthesis plus 10 days and Ca and Mg at vegetative and boot stages would have been marginal for high milk producing beef cows during early lactation. Copper levels appear marginal at all stages of maturity in both leaves and stems. Nevertheless, if producers are aware of these potential mineral problems, the variables considered in this research should have little effect on the use of Russian wildrye for spring grazing.

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Wyoming big sagebrush seed production from mined and unmined rangelands

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Abstract

Wyoming Coal Rules and Regulations require shrubs be returned to mined land and that revegetation "...be self renewing." We evaluated seed production and seed quality of Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* (Beetle & Young)) by measuring the effect of mining, herbivory, and environmental modification on seed production at 5 sites on the Dave Johnston Coal Mine near Glenrock, Wyo. Mined-land stands ranged in age from 5 to >20 years. Single sagebrush plants on mined, and adjacent unmined land were treated by: (1) fabric mulch around the base, (2) windbreak on the north and west, (3) both mulch and windbreak, and (4) neither windbreak nor mulch. Plants were fenced and compared with unfenced, untreated, neighboring plants. Seeds were harvested for 3 years and data were collected on seed-stalk numbers, bulk weight of seeds produced, and seed quality. Fenced mined-land plants produced several times more seeds than fenced plants on adjacent unmined land. There was no difference in seed quality. Treatments to modify the plant environment resulted in some benefits but fencing had a greater effect on seed-quality parameters than did planned treatments. We conclude the sagebrush seed-production potential on reclaimed lands such as those of the Dave Johnston Coal Mine is equal to, and often several times greater than that of adjacent unmined lands. However, browsing by wild ungulates can eliminate the mined-land yield advantage.

Key Words: environmental effects, seed quality, big game, soil moisture, ecological restoration

Resumen

El reglamento y normas de explotación de Carbón en Wyoming exige que los arbustos se regresen a la tierra minada y que esa revegetación "sea auto renovable". Evaluamos la producción y calidad de semilla del "Wyoming big sagebrush" (*Artemisia tridentata* Nutt. ssp. *wyomingensis* (Beetle & Young)) midiendo el efecto del minado, la herbivoría y la modificación ambiental en la producción de semilla en 5 sitios en la mina de carbón Dave Johnston situada cerca de Glenrock, Wyo. Las poblaciones en el terreno minado variaron de 5 a más de 20 años. Plantas individuales en el terreno minado y en un terreno adyacente sin minar fueron tratadas con: (1) acolchado con tela alrededor de la base , (2) cortina rompeviento en el norte y oeste, (3) ambos, acolchado y cortina rompeviento y (4) ni acolchado ni cortina rompeviento. Las plantas fueron cercadas y comparadas con plantas vecinas sin cercar y sin tratar. Las semillas fueron cosechadas durante 3 años y se colectaron datos sobre el número de tallos florales, peso bruto de las semillas producidas y calidad de la semilla. Las plantas cercadas en terreno minado produjeron varias veces mas semilla que las plantas cercadas en terrenos adyacentes sin minar. No hubo diferencia en la calidad de la semilla. Los tratamientos para modificar el ambiente de la planta resultaron en algunos beneficios, pero el cercar las plantas tuvo un mayor efecto en los parámetros de calidad de semilla que los tratamientos planeados. Concluimos que el potencial de producción de semilla de "Sagebrush" en terrenos minados, tal como los presentes en la mina de carbón Dave Johnston es igual a, y a veces varias veces mayor, la producida en terrenos adyacentes sin minar. Sin embargo, el ramoneo por ungulados silvestres puede eliminar la ventaja que da los terrenos minados.

Wyoming began legislating the return of woody plants to mined lands in 1973 with the Surface Mining Control and Reclamation Act. The act simply required shrubs be included in reclamation seed mixtures. Current Wyoming law requires 20% of eligible lands be restored to shrub patches not less than 0.02 ha supporting an average density of 1 shrub m^{-2}. It also requires that revegetation "... be self-renewing ..." (DEQ-LQD 1995, WEQC 1995, Federal Register 1996).

Since 1973, attention has been focused on shrub seeding methods, re-establishment densities, and dominant species (WEQC 1995, Booth et al. 1999). Measurement of shrub stand regeneration on mined lands has received little attention. No studies have measured mined-land seed production or quality although surveys by Gores (1995) and Lyford (1995) give some information on seedling recruitment.

We tested the hypothesis that Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* (Beetle & Young) seed production and quality on mined land was not different from that of adjacent unmined land. We also tested environment-modifying treatments as potential mitigation options should mined-land seed production be found deficient.

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Materials and Methods

Site Description

Our study was conducted on the Dave Johnston Coal Mine, 40 km east of Casper, Wyo. (42.992 N, 105.851 W). The mine is at an elevation of 1,646 m, has a mean annual precipitation of 328 mm and a mean annual temperature of 8.8° C (Martner 1986, Owenby and Ezell 1992). The site averages 123 frost-free days per year. Soil parent material is Cretaceous clay shale (Young and Singleton 1977). Five sites were located on the mine where mined-land sagebrush stands were in close proximity to stands of sagebrush on unmined rangeland (Table 1).

Table 1. Description of sagebrush study sites on the Dave Johnston Coal Mine.

	Mined Stand[1]			
Site Name	Age	Slope	Aspect	Comments
	(yrs)			
Fuel Island	>20	gentle	West	Unmined site was grazed
Entry 50	16	gentle	West	Unmined site was grazed
110 School	12	moderate	North	None
60 Badger	10	very gentle	Southwest	Unmined site was mod. sloping
4 School	5	moderate	West	Unmined site was mostly level

[1] Unless otherwise noted, slope, aspect, and livestock grazing are the same for the mined and unmined stands. The distance between paired mined and unmined stands was estimated as ≤ 100 m and elevational differences were estimated at ≤ 56 m.

Treatments and Experimental Design

The study was begun July 1995, by selecting 48 plants of similar size at each site (24 on mined land and 24 on unmined rangeland) (Table 2). Single sagebrush plants were treated as follows: (1) understory plants were cut to ground level and a square, 1 m^2-piece of fabric mulch (Appleton et al. 1990) was installed around the base of the plant, (2) a windbreak of fabric mulch was erected on the north and west side of the plant, (3) both mulch and a windbreak were installed, and (4) neither windbreak nor mulch (control). The experimental design was a split plot, 2 x 2 factorial replicated among the 5 sites with whole plots being land type (mined vs. unmined) and sub-plots being mulch and windbreak treatments with 3 sub-samples (individual plants).

Table 2. Experimental variables used in sagebrush seed production study.

Variable [number and identification]
Sites [5; Fuel Island, Entry 50, 110 School, 60 Badger, 4 School]
Whole plots [2; mined and unmined]
Sub-plots [4 treatments x (3 sub-samples + 3 paired plots) = 24 as indicated below]
Mulch plots with paired untreated and unfenced plots [3 + 3]
Windbreak plots with paired untreated and unfenced plots [3 + 3]
Mulch + windbreak plots with paired untreated and unfenced plots [3 + 3]
Control plots with paired untreated and unfenced plots [3 + 3]

The plants selected for treatment were surrounded by a 1-m^2 x 1 m-high fence of 2.54-cm wire net, then paired with an unfenced and untreated adjacent plant (Table 2). Our test necessarily included an evaluation of herbivory and environmental modification by the wire net because we needed to protect experimental plants and we needed to measure the effect of protective measures.

Soil moisture data were obtained from gypsum blocks buried to 10 cm below the soil surface and beneath the canopy of treated plants. The blocks were read mid-month, May through September, 1996 through 1998. The data were analyzed by month across the 3 years of the study.

Seeds were harvested annually in late October or early November 1996, through 1998. Data collected included number of seed stalks and bulk weight of seeds produced per plant; and seed weight, moisture content at harvest, germination, and seedling vigor. Seed quality tests used 20 seeds per plant or the maximum number of seeds available if <20. Seed moisture at harvest was determined as described by Bai et al. (1997). Seeds were imbibed at 5° C for 4 days followed by incubation at 20° C with 12 hours of light (65.9 microeinsteins $sec^{-1}m^{-2}$ PAR) and germination counted at 7 and 14 days (Booth and Bai 1999). At the end of the test ungerminated seeds were squeezed to determine which were firm or rotten. Firm seeds were counted as dormant. Quality tests were conducted using slant boards (Jones and Cobb 1963) and seed vigor evaluated by measuring seedling axial length after 14 days of incubation (Booth and Griffith 1994).

Statistical Analysis

We used the "Mixed" procedure in SAS to test for differences among variables and the "differences" option to compare least-square means (Littell et al. 1996, SAS 1996). Protective fencing was evaluated in separate analyses as a sub-plot effect (Table 3). Data for each year were analyzed separately in both analyses because differences due to year were expected and separate analyses by year reduces the number of interactions that must be evaluated (Table 3). The analysis for fenced plots compares effects of land, mulch, and windbreak among plants with protective fencing for each of 3 years. The analysis for unfenced plots compares the effect of land and fence (for the same 3 years) using fenced and unfenced control plants (no mulch or windbreak) (Table 3). The separate analyses will be reported under separate headings.

G.D. Booth (1987) observed that "Too often, ...researchers let the simplicity of the statistical test replace their own reasoned thought." Certain situations require a yes or no answer. Often, as in this study, the objective is to measure the degree of influence. To aid readers in judging the relative influence of our test variables and their interactions we report F-statistics as observed significance levels (OSLs) and we give the corresponding degrees of freedom (df). Low sample numbers can lead to concluding that there is no effect when there is, and large sample numbers can result in "significant" differences that have no meaning (Booth 1987).

Results

Seed Stalk Numbers

Fenced

None of the test variables affected seed stalk numbers. (The OSLs for all variables and interactions were $P > 0.20$ except land in 1996 ($P = 0.16$), and mulch ($P = 0.12$) and windbreak ($P = 0.10$)in 1997; df: land = 4, mulch = 104, windbreak = 104.)

Table 3. Example programs, with model statements, as submitted to SAS for fenced, and fenced-vs-unfenced plot analysis.

Fenced

```
proc mixed;
class site land mulch windbreak replication;
model bulk weight =
 land
 mulch
 land x mulch
 land x windbreak
 land x mulch x windbreak;
random site site x land;
lsmeans land  mulch x windbreak
 land x mulch x windbreak / difference;
run;
```

Fenced vs. Unfenced

```
proc mixed;
class site land fence replication;
model bulk weight =
 fence
 land
 land x fence;
random site  site x land;
lsmeans fence land x fence / difference;
run;
```

Unfenced vs Fenced

Fenced plants produced greater seed-stalk numbers than unfenced plants all 3 years (Table 4). (The OSLs for land and the land x fence interaction (48 df) were P > 0.20 for all comparisons.)

Seed Yield per Plant (Bulk Weight)

Fenced

Land affected seed yield all 3 years, windbreak in 2 years, and mulch only in 1996 as part of a 3-way interaction (Table 5).

Unfenced vs Fenced

The OSL for the land x fence interaction (48 df) was P < 0.05 in all 3 years and protected plants on mined land always ranked first, yielding 3 to 6 times more seed than protected plants on unmined land (Fig. 1).

Seed Quality Analysis

Average Seed Weight - Fenced

Average seed weight had some influence of land x mulch in 1997 and mulch in 1998 (Table 6).

Average Seed Weight - Unfenced vs Fenced

Fenced plants produced heavier seeds in 1996 and 1997, but not in 1998 (Table 4).

Seed Moisture - Fenced

Seed moisture at harvest was similar among variables. (Land x mulch (104 df) OSL in 1997 was P = 0.10, for all other effects the OSLs were P > 0.20. Means for the interaction ranged from 5.0% for mined land with mulch, to 6.3% for mined land without mulch.)

Seed Moisture - Unfenced vs Fenced

Fenced plants had higher seed moisture than unfenced plants all 3 years (Table 4).

Seed Germination - Fenced

Ranked means do not suggest any consistent effect on germination or dormancy. Mean germination percentages ranged between 39 and 92% on unmined land, and between 77 and 92% on mined land. (There was a 3-way interaction of land x windbreak x mulch (21 df) in 1996 (P = 0.02). In 1997, the OSLs were all P > 0.18 (df: land = 3, other variables = 21), and in 1998 there was a land x windbreak 2-way interaction (P = 0.02).)

Percentage dormant seeds (those that did not germinate but remained firm through the test period) ranged from 3.5 to 23.7% in 1996, 1.0 to 6.8% in 1997, and 1.2 to 8.4 in 1998. (Land x windbreak in 1996 and 1998, and mulch x windbreak in 1996 had OSLs where P = 0.12; all other effects had OSLs > 0.20 (df the same as for germination).)

Seed Germination - Unfenced vs Fenced

Fencing did not affect germination or the percentage of dormant seeds. (The OSLs were P = 0.12 for a 1998 land x fence interaction (5 df), and P > 0.20 for all others (df:land = 4, others = 5).) Mean germination percentages for main effects (land, fence) ranged from 76 to 90% among the 3 years. The corresponding mean dormancy percentages ranged from 2.0 to 6.6%. OSLs for all effects and all years were > 0.19.

Table 4. Effect of protective fencing on means of sagebrush seed stalks per plant, weight of sagebrush seeds, and seed moisture 1996 to 1998. The observed significance level (OSL) is given for each pair of means.

Variable	1996		1997		1998	
	Fenced	Unfenced	Fenced	Unfenced	Fenced	Unfenced
Number Seed-stalks	22	4	56	10	76	15
OSL (df=48)	P < 0.01		P < 0.01		P < 0.01	
Seed Wt (mg/seed)	0.1507	0.0708	0.2483	0.1422	0.2325	0.1916
OSL (df=48)	P = 0.01		P < 0.01		P = 0.29	
Seed Moisture (%)	3.9	1.3	5.6	3.1	4.0	2.5
OSL (df=48)	P < 0.01		P < 0.01		P = 0.02	

Table 5. Mean bulk weight of sagebrush seeds per plant by year as affected by type of land, mulch, and windbreak[1].

Year	Land Status	Mulch	Wind-break	Bulk Weight Seeds (g)
1996	Mined	yes	no	25.5a
	Mined	no	yes	21.8ab
	Mined	no	no	13.0 b
	Mined	yes	yes	12.7 b
	Unmined	yes	yes	4.3 b
	Unmined	yes	no	3.9 b
	Unmined	no	no	3.1 b
	Unmined	no	yes	2.4 b
1997	Mined	–	no	29.9a
	Mined	–	yes	20.1 b
	Unmined	–	yes	8.6 b
	Unmined	–	no	6.0 b
1998	Mined	–	–	19.1 (P=0.10)
	Unmined	–	–	4.4

[1] Observed Significance Level: 1996 land x mulch x windbreak P = 0.06; 1997 land x windbreak P = 0.07; and 1998 land P = 0.10; df: land = 4, windbreak = 102, mulch = 102, interactions=104. Means within a year followed by the same letter are not different at P < 0.05 as indicated by differences in least-square means within the "Mixed" statistical procedure (SAS 1996).

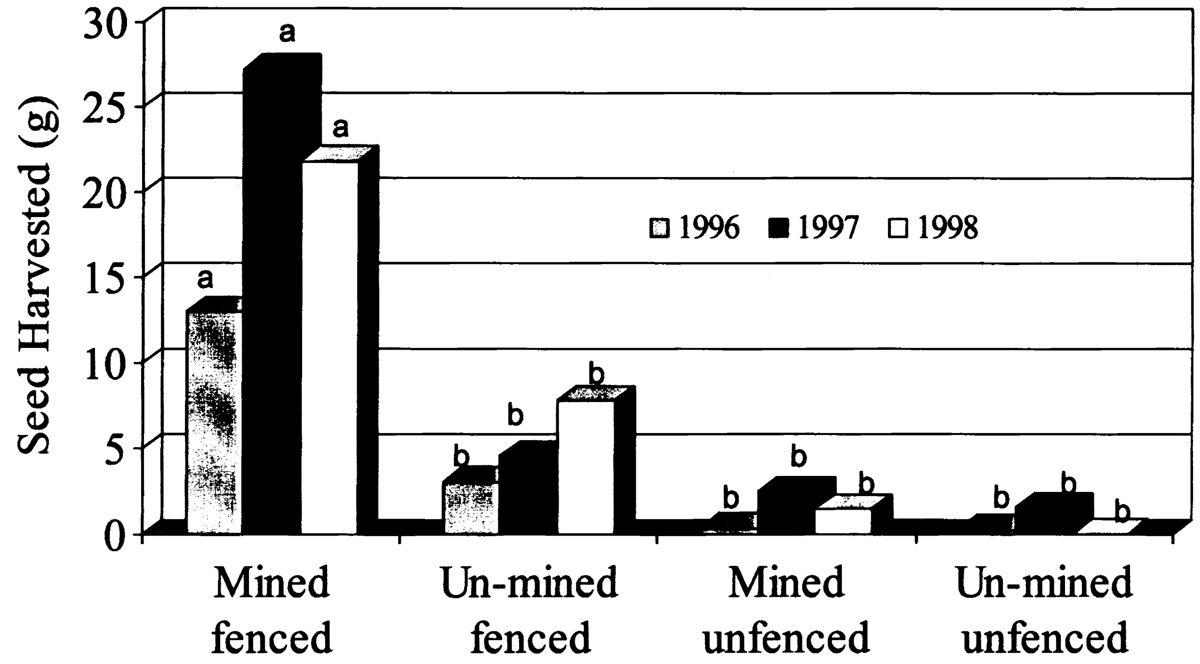

Fig. 1. Mean bulk weight of sagebrush seeds per plant by year as affected by type of land and protective fencing. The OSL for the land x fence interaction was P = 0.03, 0.03, and 0.05 in 1996, 1997, and 1998. Means within a year followed by the same letter are not different at P < 0.05 as indicated by differences in least square means within the "Mixed" statistical procedure (SAS 1996).

Seedling Length - Fenced

Means for axial length ranged from 23 to 34 mm. (The OSLs: 1996, P > 0.20 for all variables; 1997, land x mulch was P = 0.07, mulch x windbreak was P = 0.15, and all others were P > 0.20. In 1998 land x windbreak was P = 0.13, land x mulch x windbreak was P = 0.11, and all others were P > 0.20; df: land=3, mulch and windbreak = 4, and interactions = 13.)

Seedling Length - Unfenced vs Fenced

There were no differences due to land or fencing in 1997 or 1998 (P > 0.57, 2 to 6 df) and in 1996 there were not enough seeds harvested to compare treatments.

Soil Moisture (Fenced Plots Only)

Soil moisture in May was influenced by site x land x mulch (P = 0.05), land x mulch x windbreak (P < 0.01), year x mulch (P < 0.05), year x land (P < 0.01, and year x site (P < 0.01)(df for all variables and interactions = 346 to 354). The interactions with site and year were expected. The 3-way interactions (Table 7) reveal that mined-land soils had soil moisture > that of unmined lands. The greatest soil moisture occurred on mined land with mulch and windbreak.

June soil moisture interactions were site x land (P = 0.02), year x mulch (P = 0.04), and year x site (P < 0.01). The site x land data again indicated that mined-land soil moisture was > that of that unmined lands (Table 8). There were no differences in main effects or interactions for July (P > 0.83); and, year x site was the only significant interaction in August and September (P < 0.01 for both months).

Table 6. Seed quality: mean weight of sagebrush seeds by year as affected by land type and mulch[1].

Year	Land Status	Mulch	Seed Weight (mg/seed)	OSL
1996	Mined	–	0.21	P = 0.22
	Unmined	–	0.11	
1997	Unmined	yes	0.33a	P = 0.09
	Mined	yes	0.28ab	
	Mined	no	0.27ab	
	Unmined	no	0.24b	
1998	–	yes	0.28	P = 0.09
	–	no	0.24	

[1] Multiple means within a year followed by the same letter are not different at P < 0.05 as indicated by differences in least-square means using the "Mixed" statistical procedure (SAS 1996). Degrees of freedom:land = 4, mulch = 104, windbreak = 104, interactions = 104. OSL = Observed Significance Level.

Plant Mortality

There were 3 mined-land plants in the study that died at 110 School (12.5%) and 11 that died at 60 Badger (46%). (Note the high soil moisture for mined land at 60 Badger (Table 8).) All mortality during the 3 years occurred on mined land; there was no mortality at any of the other study sites.

Discussion

Land Status - Mined versus Unmined Land

Seed yields were consistently greater on mined land and the interaction of land x fence resulted in significantly greater seed production than for other treatment combinations. Soil moisture was usually greater under mined-land plants in May and June and that may account for the greater production. Why these soils contained more moisture is a matter for speculation. Conceivably plant density - either of shrubs or of all plants - was lower on mined land. Plant density often affects seed yield and differences in soil moisture may be only 1 aspect of that affect (USDA 1961, Lopez-Bellido et al. 2000, Henderson et al. 2000, Holen et al. 2001).

Table 7. **Mean percentage soil moisture for May averaged over 3 years and as affected by land, mulch, and windbreak.**

Windbreak	Mulch	Mined	Unmined	OSL[1] for Land
		------------ (%)	------------	
Yes	Yes	72.8	62.6	<0.01
Yes	No	59.6	55.6	0.09
	OSL for Mulch	<0.01	<0.01	
No	Yes	69.3	66.5	0.29
No	No	69.7	58.4	<0.01
	OSL for Mulch	0.87	<0.01	

[1] Observed Significance Level

Seed quality as measured by seed weight, seed moisture, germination, and seedling vigor (axial length) was not affected by land status. Thus, we found no reason to question the quality of mined-land seed.

Herbivory - Fenced and Unfenced

It is clear that large herbivores reduced seed production potential by eating seed stalks (Table 4). Wagstaff and Welch (1991) also reported that protected sagebrush plants produce significantly more seed stalks than plants not protected from grazing animals. We recognize that protective fencing modified the environment in favor of the protected plants. However, the report of Gores (1995), and personal observations of the effects of wildlife herbivory on mined-land shrub stands suggest the bias was relatively insignificant and should not be used to under rate wildlife herbivory as a factor limiting seed production of mined-land sagebrush.

Table 8. **Mean percentage soil moisture for June averaged over 3 years as affected by site and land.**

Site	Mined	Unmined	OSL[1] for Land
	------ (%)	------	
Fuel Island	20	16	0.55
Entry 50	36	27	0.66
110 School	31	37	0.36
60 Badger	70	45	<0.01
4 School	35	21	0.03

[1] Observed Significance Level

Environmental Modification

We found that surrounding a sagebrush with wire netting (fenced) resulted in a beneficial modification of its environment as evident by greater seed weights from protected plants (Table 4). This was not expected, especially with the large (2.54 cm) net used. The fencing affect may account for the minimal effect of mulch and windbreak on seed production and quality and the finding may have implications for those who grow and sell big sagebrush seeds. Mulch and windbreak did influence seed production and quality, but these effects were not as consistent as was the effect of land type, herbivory, or fencing. The mulch did not always result in greater soil moisture (Table 7), probably due to its small size ($1\ m^2$). A larger piece of fabric would likely have shown a more consistent benefit to soil moisture (Appleton et al. 1990).

Conclusions and Recommendations

Wyoming big sagebrush on reclaimed mined lands similar to those of the Dave Johnston Coal Mine have the potential to produce more seeds than plants from adjacent unmined land. However, the mined-land seed-production advantage will be realized only when the plants are protected from browsing wildlife. Environmental modification can also improve seed production and some factors of seed quality, but these efforts are viewed as more expensive and less effective than excluding browsing animals.

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Non-selective grazing impacts on soil-properties of the Nama Karoo

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Abstract

Non-selective grazing (NSG) is a relatively novel way of farming livestock in the Nama Karoo of South Africa. Our key question was how heavy grazing under this high-intensity, low-frequency grazing system would impact on certain soil properties. The study was designed to compare the impacts of NSG (treatment) with no grazing (control) in terms of: (1) amount of soil organic carbon (OC); (2) soil microbial respiration rates; (3) soil stability and infiltration properties. The treatment significantly lowered the amount of OC in the topsoil. Microbial respiration rates corresponded with the fertile patch matrix in both treatment and control with significantly higher respiration rates measured under plants compared to open, unvegetated areas. Respiration rates in treatment open areas were significantly higher than in control open areas. There was a trend ($P < 0.1$) for higher aggregate stability, final infiltration rate and cumulative infiltration for treatment open soils compared to controls during an initial rain event of 44 mm hour^{-1} in a rainfall simulator. During a second rain event on sealed soils only aggregate stability was significantly higher for treatment compared to control soils. We conclude that the short-duration, low-frequency, intensive herbivory by livestock under the non-selective grazing system resulted in a more active microbial community, which turned over organic matter more rapidly and led to higher soil stability and infiltration capacity of open, unvegetated soils. We present this as an example of conditions where herding by high densities of large herbivores can have positive impacts on soil quality.

Key Words: grazing system, hoof action, infiltration, intensive herbivory, microbial respiration, semi-arid

Resumen

El apacentamiento no selectivo (NSG) es una forma relativamente nueva de manejar el ganado en el Nama Karoo de Sudáfrica. Nuestra pregunta clave fue como el apacentamiento fuerte bajo este sistema de apacentamiento de alta intensidad baja frecuencia impactaría en las propiedades del suelo. El estudio se diseño para comparar los impactos del NSG (tratamiento) con el no apacentamiento (control) en términos de: (1) cantidad de carbón orgánico en el suelo (OC); (2) tasas de respiración microbiana en el suelo y (3) propiedades de infiltración y estabilidad del suelo. El tratamiento disminuyo significativamente la cantidad de OC en la capa superior del suelo. Tanto en el tratamiento como en el control las tasas de respiración microbiana correspondieron a las de una matriz de parches fértiles y el control con tasas de respiración significativamente mayores bajo las plantas que en los espacios abiertos sin vegetación. Las tasas de respiración en las áreas abiertas del tratamiento fueron significativamente mayores que las tasas de las áreas abiertas del control. Hubo una tendencia ($P < 0.1$) de mayor estabilidad de los agregados, mayor tasa de infiltración final e infiltración acumulada en los suelos abiertos del tratamiento comparados con el control, esto durante un evento inicial de lluvia de 44 mm hora^{-1} realizado con en el simulador de lluvia. Durante un segundo evento de lluvia sobre el suelo sellado solo la estabilidad de los agregados fue significativamente mayor en el tratamiento que en los suelos del control. Concluimos que la corta duración, baja frecuencia y herbívora intensa del ganado bajo el sistema de apacentamiento no selectivo resulta en una comunidad microbiana más activa, la cual actuó más rápidamente sobre la materia orgánica lo que conduce a una mayor estabilidad del suelo y mayor capacidad de infiltración de los suelos abiertos sin vegetación. Presentamos esto como un ejemplo de las condiciones donde el apacentamiento con altas densidades de grandes herbívoros puede impactar positivamente en la calidad del suelo.

Grazing animals primarily affect rangeland soils by direct impacts through trampling and dunging (Smoliak et al. 1972), and indirectly by altering plant community structure (Thurow et al. 1988, Dormaar et al. 1997). Soil quality, or productive potential, as characterized by, amongst others, infiltration rate, nutrient status, and stability (resistance to erosion), determines the flows of nutrients and water between soils and plants (Tongway and Hindley 1995). Management may change these soil qualities, either by ensuring resource conservation (soil, nutrients, water) within the system, or by degrading the system so that resources are lost or "leaked" (Tongway and Hindley 1995). Biologically mediated soil processes such as decomposition, mineralization, production and maintenance of macropores, production of soil aggregates, and fixation, are critical for the maintenance and restoration of soil production potential (Whitford and Herrick 1996). Grazing animals are the "tools" by which the rangeland manager can either maintain or reduce productive potential, depending mainly on stocking rate and grazing systems applied. The correct use of these tools can have long-term economic implications for the livestock operation (Savory 1983, Biondini et al. 1998, Beukes et al. 2002).

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There is an extensive literature on the merits of different stocking rates and grazing systems. Some reviews (e.g. O'Reagain and Turner 1992) suggest that there is little evidence to support rotational grazing in favour of continuous grazing. Others have postulated that grazing systems that combine short periods of high grazing intensity with prolonged periods of rest (high-intensity-low-frequency grazing ≈ non-selective grazing) simulates the herding of wild ungulates and may play an important role in influencing range condition (Acocks 1966). McNaughton et al. (1988) have shown that removal of this type of grazing in the Serengeti grasslands leads to an increase in N immobilized in litter and standing dead biomass, and a reduction in soil microbial turnover rates and net soil N mineralization. This stimulated McNaughton's (1993) grazing optimization theory—grazing stimulates soil and plant processes which, in turn, maximize primary production through plant compensatory growth mechanisms. However, this theory is still being intensively debated (Painter and Belsky 1993, Biondini et al. 1998).

A number of studies have shown that heavy grazing leads to plant compositional changes, a reduction in total organic cover, and changed physical and chemical properties of the topsoil layers with a resultant reduction in infiltration rates (Smoliak et al. 1972, McCalla et al. 1984, Graetz and Tongway 1986, Thurow et al. 1986, Biondini and Manske 1996, Mworia et al. 1997, Biondini et al. 1998). The literature, however, is replete with contradictory results on the effects of grazing on soils, possibly a consequence of the different environments, soils and grazing management systems of the trials (Lavado et al. 1996). One of the reasons for these contradictions is the varied interpretations of "heavy grazing". Although heavy grazing is generally understood to mean that grazing animals are kept in an area (paddock) until they have removed up to 90% of the aboveground biomass (Biondini et al. 1998), this can be achieved by either keeping relatively few animals for a long time in the paddock (which translates into short rest periods) or by stocking high densities for a short time in numerous small paddocks (which translates into longer rests depending on the number of paddocks available). We argue that these differences are important and will result in different impacts on soils and vegetation. We postulate that heavy grazing under a high-intensity-low-frequency/non-selective grazing system would improve soil quality through its concentrated but short duration impacts on ecosystem processes (McNaughton et al. 1988, Savory 1991).

This study was designed to test this hypothesis by comparing the impacts of non-selective grazing (treatment) vs. no grazing (control) on certain soil quality indicators viz: (1) total soil organic carbon (OC); (2) soil microbial respiration rates; (3) aggregate stability, infiltration rate, erodibility, and cumulative infiltration. In each case we predicted that the grazing treatment would increase OC, microbial respiration rates, and soil stability and infiltration.

Materials and Methods

Study Area

Fieldwork was conducted on the farm Elandsfontein (7,000 ha) situated 32 km north-east of Beaufort West in the Nama Karoo (32°15'S/22°45'E). A series of doloritic rocky outcrops run across the farm with the rest of the landscape consisting of level to near-level pediments. Soils are of mixed origin, derived from dolerite weathering products and Karoo System shales or shale-derived pedisediments (Ellis and Lambrechts 1986). The reddish coloured duplex soils have a coarse sandy loam texture, are relatively rich in most plant nutrients (topsoil plant-available P > 20 mg/kg; topsoil exchangeable K > 7%), and have low levels of salts (electrical resistance > 1,000 ohms), exchangeable Na (ESP < 1%), and organic carbon (OC = ± 0.2%).

The mean annual rainfall for the farm for the period 1987–1998 was 212 mm year^{-1} with a CV of 47%. Severe droughts occur regularly in the Nama Karoo with the last one being the 1990–1994 drought when Elandsfontein recorded a mean of 139 mm year^{-1}. Fieldwork at Elandsfontein commenced in the drought-breaking year of 1995 (238 mm) after the very dry 1994 (33 mm). There is a trend for more rainfall, with a higher reliability, to fall during summer months. Frontal systems bring light rain in winter while summer rains are often characterized by brief cloudbursts resulting in rapid run-off. The mean annual A-pan equivalent potential evapotranspiration is 2,400–2,600 mm (Schulze 1997).

The vegetation is classified by Acocks (1975) as veld type 26, Karroid Broken Veld; and by Low and Rebelo (1996) as Central Lower Karoo. This semi-arid grassy shrubland is dominated by grasses, mainly species of *Stipagrostis* and *Eragrostis*, while *Pentzia incana* (Thunb.) Kuntze and *Rosenia humilis* (Less.) Bremer are dominant dwarf shrubs. Rocky sites include a sparse, tall shrub to low tree stratum where the principle genus is *Rhus*. A highly variable ephemeral, and scarce succulent component exists.

Over a period of 30 years the landowner subdivided the farm into many small paddocks. Only since the early 1990's were these paddocks sufficiently small to achieve the high grazing intensities of the non-selective grazing system. Currently the infrastructure on Elandsfontein consists of 147 paddocks arranged in wagon-wheel layouts around 38 permanent watering points. Large mixed herds of Nguni cattle, Merino sheep, and Boer goats (in an average ratio of 1:14:3) are rotated through the paddocks in a non-selective grazing system. The number of herds is reduced as far as possible to concentrate animals and minimize the grazing period (< 14 days). Grazing intensities of 40– 60 Large Stock Unit Grazing Days per hectare (LSU*days/ha where 1 LSU is the equivalent forage intake of a 455 kg steer) are applied (compared to 10– 20 of more conventional group camp systems), after which a paddock is rested for at least a full year. A rumen stimulant in the form of cut saltbush (*Atriplex nummularia* Lindl.) is supplied to improve animals' intake of poorer quality fibre towards the end of a period of occupation.

This non-selective grazing system differs from short-duration grazing (SDG) as summarized by Holechek et al. (2000) in that high grazing intensities are achieved by reducing numbers of herds and paddock sizes and not by increasing stocking rate. With substantially more paddocks non-selective grazing also allows for much longer periods of rest compared to short-duration grazing.

Experimental design

In April 1995, four paddocks (A, B, C and D) on Elandsfontein were subjectively assessed as similar in terms of topography, soils, and vegetation, and were identified as the 4 replicates for this study. Although the paddocks differed in size (A = 34 ha, B = 87, C = 108, D = 32) the treatment, grazing intensity (measured as Large Stock Unit Grazing Days/ha = LSU*days/ha), were kept similar across the replicates by adjusting the grazing period (days). A 5 strand stock fence was used to erect a 50 m x 50 m exclosure in each paddock. The exclosure fences were positioned away from watering points and stock paths, and excluded livestock grazing but not herbivory by indigenous vertebrates steenbok (*Raphicerus campestris*), hares (*Lepus* spp.), tortoises (*Psammobates* spp.), porcupine (*Hystrix austro-africanae*), and invertebrates. The fenced areas were regarded as controls whereas the adjacent 50 m x 50 m areas were regarded as the grazing treatments.

The Treatment

After the exclosures were set up in April 1995, each paddock received a non-selective grazing (NSG) treatment each year thereafter (until 1998) by stocking a combination of Nguni cattle, Merino sheep, and Boer goats at grazing pressures varying from 40 to 60 LSU*days/ha. Grazing intensities varied between years because of food availability, and animal reproductive status and condition, but were always kept as similar as possible across replicates by adjusting the length of the grazing period (days). The treatment was not applied during any particular season, but the aim was always to herd as many animals together as was available, and to keep the grazing period within the maximum of about 2 weeks (it varied between 2 and 16 days). These high grazing intensities were achieved by herding up to 348 LSU in a 32 ha paddock for 5 days (1998 treatment). To extend the period of occupation by a few days, and thereby force the animals to ingest more fibrous, less palatable material, they were supplied with 1.5–2 tonnes of cut saltbush (*Atriplex nummularia* Lindl.) every alternate day. The woody portion (> 50%) of the saltbush shoots does not get utilized and remains on the land as litter. The leaf material with an average 22% protein, helps to maintain rumen function and improves intake of low quality fibre (Barnard 1986). Care was taken not to deposit the saltbush on or nearby the 50 m x 50 m treatment areas. For experimental purposes the treatment was applied annually, but under normal circumstances a paddock would receive a rest period of more than a year (147 paddocks at ± 9 days per paddock converts into a theoretical rest period of 3–4 years).

Soil organic carbon (OC)

In June 1998, within a month after the treatment, 3 of the 4 replicate paddocks were selected for collecting soil samples for OC measurements. Owing to financial constraints, OC measurements were taken in only 3 (A, C and D) of the 4 experimental paddocks. One, 5 m x 5 m plot was randomly positioned inside the control and treatment areas of each paddock. Care was taken to avoid stock paths. Each plot was subdivided into a grid with 100 cells each measuring 0.5 m x 0.5 m. Using this grid, 100 soil samples (top 5 cm) were systematically collected in each plot. After passing each soil sample through a 2 mm sieve to remove larger fractions, the OC content (%) was determined using the Walkley and Black method (Nelson and Sommers 1982).

Soil microbial respiration rates

Every year since 1996, within a month after the treatment had been applied, soil samples were collected from control and treatment areas of the 4 replicate paddocks for measuring microbial respiration rates. Samples were randomly taken from the top 5 cm of open, unvegetated areas between shrub and grass clumps (intermound), as well as from mound soils underneath shrubs (mainly *Pentzia incana* (Thunb.) Kuntze). Samples were passed through a 2 mm sieve, moistened with 10 g water per 100 g air-dry soil, and stored in a polythene bag for 1 week. Bags were shaken every day to aerate the soil. After the incubation period of 1 week, CO_2 release as a result of microbial respiration was determined using NaOH to react with the CO_2 in respiration flasks. After approximately 1 week (the exact time was noted) in the respirometers, the free NaOH was titrated with HCl. Titrations were standardized against a control respirometer with sand instead of soil. The water content of the moist soil at the time the respirometers were set up was determined by drying sub-samples overnight at 105° C. Soil microbial respiration rates were expressed as g CO_2 g^{-1} air-dry soil $second^{-1}$ (for more detail see Rowell (1994) pp. 117 –119).

Aggregate stability, infiltration rate, erodibility, and cumulative infiltration

Soil sample collection and preparation

In June 1998, within a month after the grazing treatment, 20 kg soil samples were collected from the top 10 cm of open, unvegetated areas in treatment and control areas of all 4 paddocks. The collected samples were air-dried and crushed to pass a 4 mm sieve.

Rainfall simulation

Infiltration, runoff and interrill erosion were measured by using a rainfall simulator with a rotating disk, such as those developed by Morin et al. (1967). Three replicates of a soil were packed 20 mm deep in 300 mm x 500 mm boxes, over an 80 mm deep layer of coarse sand. The boxes were placed in the rainfall simulator at a slope of 5%. The soil was first saturated from the bottom with tap water and then exposed to simulated rainfall of distilled water with an electrical conductivity value of 1.0 mS m^{-1}. The mechanical parameters of the applied rain were: instantaneous application rate of 44 mm $hour^{-1}$; water drop average diameter of 19 mm; median drop velocity of the rain event, 6.02 m $second^{-1}$; and the kinetic energy was 18.1 J mm^{-1} m^{-2}. The volumes of water percolating through the soil were recorded at 2-minute intervals during an event of 2 hours. Timed runoff samples were collected at 2-minute intervals during the 2-hour event, weighed, oven dried at 105° C, and reweighed to determine runoff rate, sediment concentration, and sediment yield. During the first storm seal formation occurred (a thin wet layer of low hydraulic conductivity that forms at the soil surface during a storm) as a result of physical and chemical processes initiated by the multiple impacts of the raindrops (Levy 1988).

After the first storm, the trays with soil were removed from the rain simulator and dried at room temperature to form a crust (hard setting of seal with drying). The dried soil was then again subjected to a second storm similar as the first storm where similar soil parameters were measured.

Calculations

Cumulative infiltration and final infiltration rate

In many arid and semi-arid region soils, the amount of water that infiltrates the soil is determined by the hydraulic conductivity of a seal at the soil surface (Ben-Hur et

Table 1. Summary statistics for soil organic carbon (%) measurements from 3 paddocks (A, C, and D) at Elandsfontein in June 1998.

	Paddock					
	A		C		D	
Statistic	Treatment	Control	Treatment	Control	Treatment	Control
	(%)					
Mean (n = 100)	0.26	0.31	0.42	0.43	0.58	0.63
Standard Deviation	0.13	0.12	0.11	0.11	0.24	0.25

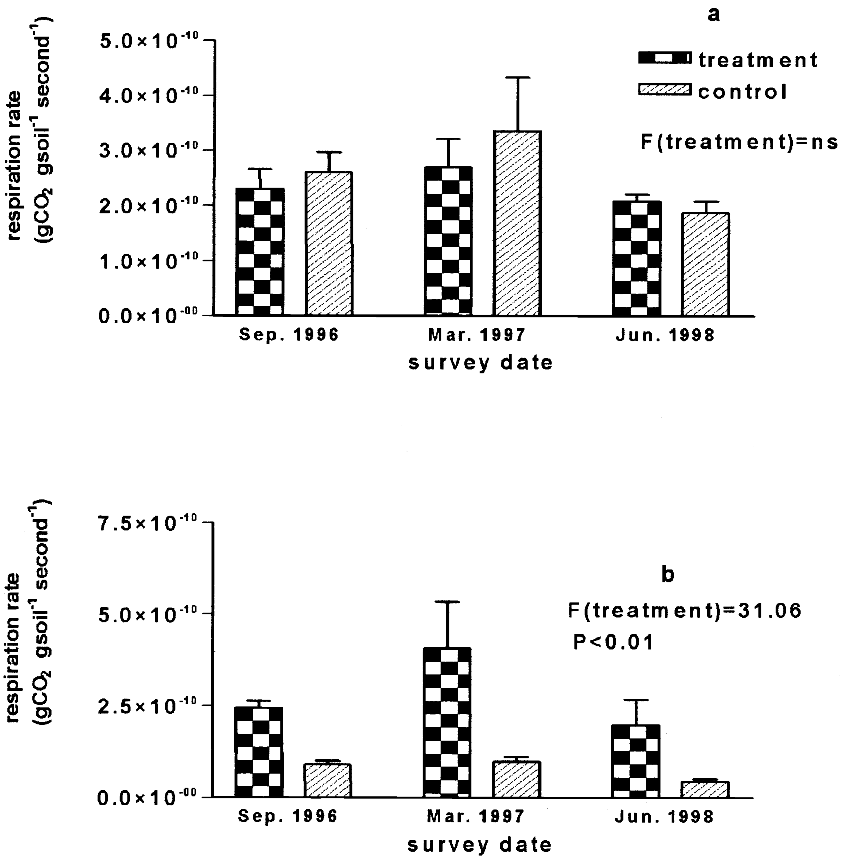

Fig. 1 Soil microbial respiration rates for mound soils (a), and intermound soils (b).

al. 1985, Singer and Warrington 1992). A rainfall simulator was used to determine infiltration and runoff as other methods like infiltrometers in the field and permeameters in the laboratory ignore the negative influence of a seal formation (Morin and Benyamini 1977, Sidiras and Roth 1987). Final infiltration rate (mm hour^{-1}) is measured directly from a graph of infiltration rate vs. cumulative rainfall (mm) when infiltration rate is constant 3 consecutive times. Cumulative infiltration (mm) is calculated as the amount of rain that infiltrates the soil until the final infiltration rate occurs.

Aggregate stability

Sealing, crusting, water infiltration, runoff and erosion result from aggregate breakdown. The detachment of soil fragments by rain, and the susceptibility of soil to these processes is inferred from measurements of aggregate stability (Morin and Benyamini 1977, Stern et al. 1991, Le Bissonnais 1996). Le Bissonnais (1996) reviewed the 4 main mechanisms (i.e. slaking, breakdown by differential swelling, mechanical breakdown by raindrop impact and physico-chemical dispersion) of aggregate breakdown, and the existing methods for the assessment of aggregate stability. According to Nearing and Bradford (1985), the main cause of structural degradation at the soil surface is raindrop impact. Therefore, the stability of aggregates was determined from the approach of mechanical breakdown by raindrop impact by using a rainfall simulator. The measure of seal formation employed in this study was the infiltration rate calculated by a Hortonian type equation describing the curve relating infiltration rate (I_t) to elapse time (t):

$$I_t = I_f + (I_i - I_f)\, e^{-Ypt} \qquad (1)$$

in which I_i is the initial infiltration rate, I_f is the final infiltration rate, Y is a curve-fitting parameter related to the stability of the soil aggregates and p is rain intensity (Van der Watt and Valentine 1992). The parameter values were transformed using 1-*x* so that aggregate stability would follow the same trend as infiltration.

Erodibility

Interrill erosion was estimated based on the area and total runoff from each tray and the calculated sediment concentration. The interrill erodibility coefficient related to soil properties (K_i in kg second^{-1} m^{-4}) was calculated from Kinnell (1993);

$$K_i = q_{si} / I \cdot Q \cdot L \cdot S_f \qquad (2)$$

where q_{si} is the rate of soil discharge from an interrill area (kg m second^{-1}); I the intensity of the rainfall (m second^{-1}); Q the rate of runoff discharge from an interrill area (m second^{-1}); L the down slope length of the interrill area; and S_f a non-dimensional slope adjustment factor that is calculated from $S_f = 1.05 - 0.85\exp^{(-4\sin(S))}$, where S is the slope (Kinnell 1993).

Statistical analysis

The amount of OC was analysed using 2-way analysis of variance with "treatment" and "paddock" as the 2 factors.

Microbial respiration rates were measured on more than 1 occasion (1996, 1997 and 1998). An analysis of variance for repeated measurements was performed to test the null hypothesis that the change over time in the measured parameter would not differ significantly between treatment and control.

For the rainfall simulator results on aggregate stability, final infiltration rate, erodibility and cumulative infiltration paired t-tests (2-tailed) were used to test the null hypothesis that there was no significant difference in the values of the observed variable between treatment and control.

Results

Soil organic carbon (OC)

Both treatment ($P = 0.009$) and paddock ($P < 0.001$) had a significant effect on OC amount while the interaction between these 2 factors was not significant ($P > 0.05$). Non-selective grazing generally resulted in lower OC of the topsoil; more so in paddocks A and D (Table 1).

Soil microbial respiration rates

In control areas respiration rates were always significantly higher in mound soils compared to intermound soils. Treatment had no significant impact on microbial activity in mound soils, but resulted in a significant increase in microbial respiration rates in intermound soils (Fig. 1). The time effect and the time x treatment interaction were not significant.

Aggregate stability, infiltration rate, erodibility, cumulative infiltration

There was a trend for soils from grazed

Table 2. Characteristics (mean ± SD) of soils collected from open areas in control and grazing treatment paddocks (n = 4) in June 1998. Soils were subsequently subjected to a 44 mm hour^{-1} rainfall event using a rainfall simulator. Results of paired t-tests (two-tailed) are shown.

	Treatment	Control	t-value	P
Initial rain shower on disturbed soils (first storm)				
Parameter related to aggregate stability	0.9747 ± 0.017	0.9519 ± 0.009	2.41	0.09
Final infiltration rate (mm hour^{-1})	16.88 ± 8.95	4.2 ± 0.13	2.83	0.07
Erodibility (x 10^6) (kg second^{-1} m^{-4})	1.55 ± 0.19	1.61 ± 0.31	0.37	0.74
Cumulative infiltration (mm)	28.98 ± 11.23	8.48 ± 2.85	2.96	0.06
Second rain shower on sealed soils (second storm)				
Parameter related to aggregate stability	0.9702 ± 0.005	0.9606 ± 0.006	11.26	0.002
Final infiltration rate (mm hour^{-1})	5.28 ± 2.72	2.48 ± 0.74	1.68	0.19
Erodibility (x 10^6) (kg second^{-1} m^{-4})	1.219 ± 0.33	1.404 ± 0.08	1.07	0.36
Cumulative infiltration (mm)	14.95 ± 9.09	5.6 ± 0.08	2.04	0.13

areas to be more stable, and with a better water infiltration capacity compared to control soils when a rain event was simulated on sieved (disturbed) soils (Table 2). There was no significant difference in erodibility. When a rain event was simulated on sealed soils, which is closer to field conditions most of the time, the treatment soils showed a significantly higher aggregate stability compared to the control soils. With this second rain event there were no significant differences in erodibility or infiltration capacity.

Discussion and Conclusions

Our results do not support the initial hypothesis that non-selective grazing would increase organic carbon (OC). The trend was for soils of grazed areas to have lower OC values compared to ungrazed areas. The visible coarse litter after a non-selective grazing event was not reflected in the OC readings probably because soil samples were passed through a 2 mm sieve before recording OC content, or there was not sufficient time for the coarse litter to be fragmented. It would appear that the concentrated hoof action concomitant with non-selective grazing did not promote the process of fragmentation. In a study of short-duration grazing (SDG) impacts on range soils in Alberta, Canada, Dormaar et al. (1989) also found that hoof action did not significantly increase incorporation of litter into the soil. The reduced OC of the topsoil as a result of the non-selective grazing treatment is in accordance with the results of several workers (e.g. Graetz and Tongway 1986, Thurow et al. 1986, Willms et al. 1990, Dormaar et al. 1997) who found that heavy grazing reduced the plant biomass and litter base, and therefore OC of the soils. Since organic matter input is related to standing plant biomass (Garcia-Miragaya and Cáceres 1990), it is possible that with the removal of >50% of the forage with non-selective grazing, organic matter input over time was lower in the grazed compared to ungrazed areas.

Another explanation for the trend of lower OC in the grazed areas is related to the significantly higher microbial respiration rates recorded in the intermounds of the grazed areas (Fig. 1). Soil respiration rate (CO_2 production) depends on the activities of microbial organisms which is controlled by organic matter content, O_2 supply, temperature, soil water content, and nutrient supply (Rowell 1994). The pulsed input of organic matter from intensive feeding and trampling and the thorough mixing and aeration of the topsoil by hoof action resulted in a highly active soil biotic community, which rapidly turned over soil OC (McNaughton et al. 1988, Tongway and Ludwig 1996). This grazing impact was not as pronounced in mound soils because of the already loose and friable structure of these soils.

Since soil samples for the rainfall simulator measurements were collected from intermound areas, it is possible to relate the rainfall simulator results to microbial respiration rates of intermound soils. We postulate that the pulsed input of litter and dung together with mixing and aeration of the top layers of non-selective grazing soils led to a rapid increase in soil biotic processes. These soil biotic processes are largely responsible for aggregate creation and stabilisation (Whitford and Herrick 1996). The trend for higher final infiltration rate and cumulative infiltration of the treatment compared to the control soils could be related to the greater aggregate stability of the treatment soils (Greene and Tongway 1989). Furthermore, the increased infiltration in the treatment soils induced a higher water content, which fed back to further promote microbial activities.

The trend for both treatment and control soils to seal, and thereby reduce infiltrability, after an initial rain event (Table 2) is important in confirming field observations that intermound soils become hard and devoid of life when grazed areas are rested for too long (Savory 1983). The longer these unvegetated areas are exposed to raindrop impact and the sun, the more their physical structure can be expected to deteriorate. The challenge is therefore for the manager to avoid returning animals to a paddock too soon, and thus impact negatively on plant productivity, or wait too long and thus reduce rainfall effectiveness.

Holechek et al. (2000) summarized the current knowledge on the merits of short-duration grazing. The evidence they assimilated suggests that short-duration grazing, with its large numbers of animals on small areas for short periods of time, does not benefit soil health but rather results in degradation. Our results point to situations and conditions where high-density grazing might indeed improve water infiltration mainly due to a more active soil biota. This tentative result warrants a reassessment of the positive impacts of high-density grazing systems on soil quality as perceived by amongst others Savory (1983) and McNaughton et al. (1988). There are particularly 3 aspects that we recommend receive further attention: (a) The role of grazing frequency as a factor in determining the impact of large herbivores on soils. The longer rest periods between herding events of non-selective grazing compared to short-duration grazing might be an important difference in terms of soil impacts. The infrequent but heavy grazing of non-selective grazing ensures a pulsed but adequate belowground input of organic matter as a substrate for soil organisms, while soils are loosened and aerated but not compacted; (b) The role of soil type. Our study was conducted on dolerite derived soils with high levels of sesqioxides, high base status and favourable soil structure (Ellis pers comm. 2002). The outcome of herding on more compact soils (e.g. shale) might be completely different; (c) The impacts of infrequent, intensive grazing on soil microbial activities and therefore OC dynamics, nutrient cycling and water infiltration. We believe that any grazing system which enhances soil biotic activities will improve overall ecosystem condition and therefore productivity and sustainability.

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Book Reviews

Keepers of the Wolves. By Richard P. Thiel. 2001. University of Wisconsin Press. Madison. 227 p. US$50.00 cloth, US$19.95 paper. ISBN 0-17470-0 cloth, 0-299-17474-3 paper.

The timber wolf was essentially extinct in the state of Wisconsin by the mid-Twentieth Century. Hunters, trappers, and haters of wolves had killed off all but a few in the surrounding forests. *Keepers of the Wolves* by Richard P. Thiel is a blow-by-blow depiction of the search for these remaining wolves. In writing this book, Thiel shows the reader the behind-the-scenes work of a wolf biologist and an avid fan of wolves. He provides "factual information on the aspects of the biology of the wolf living in the frontier of its North American range," as well as information on government efforts to preserve the species.

Chapter 1 begins with Dr. Thiel describing his early interest in the wolves, and their absence in Wisconsin. He then takes his love for wolves and combines it with an education and a degree gained in field studies of wolf biology. He receives a job as the director of a wolf project conducted by the Wisconsin Department of Natural Resources.

The book consists of 14 chapters that describe the trials and tribulations of Richard Thiel and his group of researchers in their search for the nearly extinct Wisconsin timber wolf. The first set of tracks that was positively identified was followed by many more throughout the remainder of his initial study. Once wolves were found, officials were skeptical of radio telemetry; therefore, the only form of tracking involved going out and getting dirty. Snowshoeing and driving took up much of the research time. Soon after the first wolves were physically tracked, Thiel again proposed the use of radio telemetry. With backing and promotion by various other researchers, the idea was finally accepted. Radio telemetry allowed progress to continue at a much faster rate than during the previous work.

The book explains the biology of the wolves, their traveling behaviors, details of tracking them, and the pack behaviors of the Wisconsin timber wolf populations. Wolves are difficult to track because they have many features similar to other canids, including coyotes, feral dogs, and domestic dogs.

Scat is one of the major tools in wolf identification. Wolf scat is easily identified by deer hair, rabbit fur, and particles of other such prey that are found in it. Another way to distinguish wolf signs from those of other canids is by looking at the size of the tracks themselves. Wolves tend to have larger paws, and "stretch a good four to five inches" (p. 7).

The book goes on to document the many sightings and the trackings of wolves throughout the forests of Wisconsin. At the beginning of this research, the wolves were nearly extinct. With protection under the Endangered Species Act, the wolves were soon recovering. As Thiel continued his research, the wolves became more and more plentiful, leaving the story, at least for now, with a happy ending; the wolf populations of Wisconsin, and the bordering state of Minnesota, had successfully rebounded, leaving the wolves with many packs and the potential for more.

Keepers of the Wolves is an excellent, well-written book. Not only is it easy to follow, but also the content of the book itself is both interesting and educational. This book teaches the reader more about wolves and the ways of the wolf than many other similar books due to its skillful presentation. The research it presents is appealing, was apparently well conducted, and was well documented throughout. Overall, this book significantly increased my knowledge of the subject, and my interest in the subject of wolves.—*Amy Hobbs*, University of Montana, Missoula, Montana.

Global Rangelands: Progress and Prospects. Edited by A. C. Grice and K. C. Hodgkinson. 2002. CABI Publishing, New York, N.Y 320p. US$120.00 cloth. ISBN 0-85199-523-3.

Throughout the years rangeland has been studied, the concept of declining productivity due to use and overuse has been of major interest. *Global Rangelands: Progress and Prospects* goes beyond this single concept. Four major themes are woven together to outline the modern-day challenges of range managers. These themes are multiple use, sustainability, the relative importance of socio-economic versus biophysical factors, and the importance of interactions with non-rangeland systems.

The papers in *Global Rangelands: Progress and Prospects* are compiled from papers of the VI International Rangeland Congress. Twenty-two chapters by contributing authors describe current ideas, statistical models, and prospective outcomes for rangelands. Chapters 1–3 focus on some people involved with rangelands in different parts of the world. These chapters discuss how the perceptions—both individual and communal— impact rangeland and societies. The 5 following chapters (4–8) address the scientific knowledge that is currently known about soils, plants, and biodiversity. Chapters 9–13 discuss the tools, models, grazing strategies, mining strategies, and water resources for rangelands. Chapters 14–17 examine communication and decision-making related to rangelands. Some personal perspectives on the future of rangelands are offered in Chapters 18-18-20. The 2 closing chapters weave together the preceding chapters, and attempt to pass on the key, take-home messages.

Chronologically, the book has a good sequence of subjects. First, people are considered. Many rangelands may not be used correctly, but the early chapters make clear that there are many uses of rangelands, and what is arguably right in one case is not right for all.

Second, the book addresses the biological issues of soils, plants and biodiversity. These issues too relate to people, because people are concerned with soil condition, plant community condition, and biodiversity. Description and assessment of these concepts involves determining which variables will be monitored, what data will be collected, and what records will be kept. Our scientific knowledge about rangelands is obtained from these procedures.

The third step in this sequence involves analysis and discussion of the data collected. Decisions are made about the best plan of action for an area of rangeland. A plan of management is implemented.

In some respects, *Global Rangelands: Progress and Prospects* failed the test of enticement for reading, even though its papers are fairly easy to read. Literary and editorial qualities were sound, but some of the papers seemed short on creative ideas, and were routine in presentation. In some cases, many words said very little, and the reading was uneventful. Since each paper had different authors, maintaining a unifying theme proved difficult, and tracking one was challenging.

The VI International Rangeland Congress brought together people from around the world to discuss new ideas and progress in range management. With reasonable success, *Global Rangelands: Progress and Prospects* presents these proceedings as a somewhat chronological, historical summary. It does serve as a generally effective summary of the current state of the world's rangelands.—*Richard Lindgren*, Washington State University, Pullman, Washington.

A Poverty of Reason: Sustainable Development and Economic Growth. By Wilfred Beckerman. 2003. The Independent Institute, Oakland, CA. 96p. US$17.95 paper. ISBN 0-945999-85-2.

There is no gainsaying the fact that in contemporary times, "sustainable development" has become one of the most bandied about and at the same time one of the least clearly understood concepts. Given this state of affairs, it makes perfect sense to ask what the notion of sustainable development actually means. This is, in fact, the central question that this book asks. Specifically, the author uses the 7 chapters of this book "to identify the key planks in the sustainable-development platform and [then subjects] them to critical analysis" (p. ix). In the remainder of this review, I shall sample selectively from the various chapters and thereby give the reader a flavor for the intellectual contributions of this book.

In Chapter 1, the author correctly points out that even though there are many meanings of sustainable development, it is useful to think of this concept in terms of a "strong" definition and a "weak" definition. The strong definition essentially requires us to maintain the environment exactly as we find it today. In contrast, the weak definition recognizes the possibility of substituting between natural and man-made resources. Consequently, the weak definition allows us to deplete some resources "as long as adequate compensation is provided by increases in other resources..." (pp. 2-3).

Are the prospects for continued economic growth hindered by the potential finiteness of natural resources? This interesting question is explored in Chapter 2. The author's basic point here is that before we ask members of the present generation to make sacrifices to benefit future generations, we must first take into account the possibility that future generations will be far richer than the present generation. Although this point may well-be true, it is still possible to quibble with parts of the author's analysis. Here are 2 examples. First, the author says that if a specific natural resource such as coal were to become scarce then its price would rise and that this "process would take place very gradually, allowing time for economies to adapt" (p. 14). The part about the price rising makes economic sense but it is not necessarily the case that the relevant process will be gradual. Second, the author goes on to say that increases in human capital account for the current high levels of income and output in the modern world. He then claims that "there is no physical limitation on the growth of this human capital" (p. 17). Once again, it is not obvious that there are no physical constraints whatsoever on the acquisition of knowledge, training, and skills.

Chapter 3 discusses the notion that economic growth is leading to great diminution in the world's biological diversity. The author spends some time discussing the contention that this diminution "deprives the human race of an essential input into our welfare, notably as a source of future medicinal remedies" (p. 25). This notwithstanding, recent research in ecological economics—see the 1995 Cambridge University Press book *Biodiversity Loss,* edited by C. Perrings et al. and the 1999 paper titled "Contemporary Research in Ecological Economics: Five Outstanding Issues" by Amitrajeet A. Batabyal in the International *Journal of Ecology and Environmental Sciences*—has clearly shown that the main reason why we should care about biodiversity is not because of its potential medicinal value but because biodiversity contributes positively to an ecological-economic system's resilience and from the standpoint of the management of ecological-economic systems, resilience is a desirable property. The author appears to be oblivious of this literature because he does not ever mention it. Instead, he continues to hammer away at the salience of the less important link between biodiversity and the procurement of potential medicinal benefits. On p. 25, the author asserts that there are virtually no "precise measurements" of the extent of contemporary deforestation. In this regard, it may never be possible to have measurements that are precise enough for the author. Even so, as the work of Norman Myers—see the 1992 W.W. Norton book The Primary Source—and John Terbogh—see the 1997 Oxford University Press book Last Stand edited by R. Kramer et al.—has shown, it is possible to have a pretty good idea about the extent of and the rate of change in deforestation.

The precautionary principle is the subject of Chapter 5. In this chapter, the author casts doubt on the validity of this principle, finding thinking associated with this principle to be responsible for all manner of ills including a paucity of research on biotechnology and genetically modified crops. Although this is generally an interesting and well written chapter, there are a few warts. Here are 2 examples. First, the author criticizes the precautionary principle on the grounds that "in following [this] principle there is a danger that terrible mistakes might be made" (p. 44). Although this is certainly a possibility, the author's criticism isn't particularly useful because one could credibly claim that by not following the precautionary principle, terrible mistakes might be made. Indeed, this latter line of reasoning would be particularly relevant when there are potential irreversibilities to contend with. Second, without any supporting evidence, the author blames the precautionary principle for the "increasing bureaucratization of human activities..." (p. 45).

The general subject of Chapter 7 is the ethics of sustainable development. In this chapter, the author conducts a reasonably detailed analysis of the practical implications and the ethical foundations of sustainable development. In particular, the author first argues that in order to justify a preference for sustainability over the maximization of per capita welfare over time, one has to appeal to some ethical value other than welfare. In particular, if future generations can be shown to have rights to a level of per capita welfare that is no lower than that attained by any earlier generation, then such rights would indeed trump simple welfare maximization. He then goes on to show that "the general proposition that future generations cannot have anything, including rights, follows from the meaning of the present tense of the verb *to have*" (p. 68). In addition, the author approvingly borrows from Derek Parfit's prominent 1984 book *Reasons and Persons* and points out that "even people who do exist cannot have rights to anything unless, in principle, the rights can be fulfilled" (p. 68). This is a fine chapter. It intelligently discusses some reasonably complicated issues and it is, without a doubt, the best chapter in this slim book.

In sum, *A Poverty of Reason* is very much a mixed bag. Parts of this book are very good and in these parts, the author does a good job of analyzing the issues and, in the process, he debunks some of the more extreme contentions of environmentalists. On the other hand, a perusal of other parts of this book suggests that the author has occasionally let his zeal get the better of him. This notwithstanding, I would recommend this book to readers who wish to learn more about whether it is right to ask (some very poor) members of the present generation to make sacrifices for future generations who obviously do not exist at the present and who, according to the author, have no rights.—*Amitrajeet A. Batabyal*, Rochester Institute of Technology.

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