Journal of Range Management

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Grazing impacts on selected soil parameters under short-term forage sequences

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Abstract

Long-term cultivation is known to change soil physical and chemical properties, but little is known about whether short-term agricultural practices, such as rotational grazing, can initiate such changes. This study investigated the impacts of 3 grazing intensities (heavy, medium, and light) and 4 forages on selected soil physical and chemical parameters of a Typic Haplustoll at Lacombe, Alberta. Measurements were conducted on soil samples collected at the beginning (1993) and the end (1996) of the study. Two perennial forages, smooth brome grass (*Bromus inermis* cv. 'Carlton') and meadow brome grass (*Bromus riparius* cv. 'Paddock'), and 2 annuals, a mixture of triticale (*X Triticosecale* Wittmack cv. 'Pika') and barley (*Hordeum vulgare* L. cv. 'AC Lacombe') and triticale alone were used for the study. Grazing intensity or forage species did not affect carbon-to-nitrogen ratio. Grazing intensity influenced changes in available water holding capacity for the 0–5 cm interval, soil nitrogen for the 30–45 cm interval, soil pH for the 5–15 cm interval and electrical conductivity for all depth intervals except for the 0–5 cm interval ($P \leq 0.05$). Forage species affected changes in soil carbon in the 0–5 cm interval, soil pH between 0 and 15 cm, and electrical conductivity between 5 and 45 cm ($P \leq 0.05$). Soil electrical conductivities for all grazing levels and forage treatments were within the range (i.e. 0–2 dS m⁻¹) considered to have negligible effects on plant growth. The minimal effects of grazing and plant species on soil parameters in this study may have been due to the resilient intrinsic properties of the soil and/or the short study length.

Key Words: Carbon, electrical conductivity, nitrogen, potassium, soil pH

Cultivation accelerates mineralization of organic matter (Broersma 1991) and may consequently alter water retention properties, and carbon (C) and nitrogen (N) content of the soil. Yearly cultivation in annual cropping systems may pulverize soil particles and thus weaken soil structure and render the soil more vulnerable to erosion. Although long-term cultivation is known to change many soil physical and chemical properties (Johnston et al. 1971) as little as 5 years of cropping can initiate such changes (Dormaar et al. 1989, Dormaar and Willms 1990).

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Resumen

Se sabe que el cultivar los terrenos por un largo tiempo cambia la propiedades físicas y químicas del suelo, sin embargo pero poco se sabe acerca de que si la practicas agrícolas de corto plazo, tales como el apacentamiento rotacional, puede iniciar dichos cambios. En este estudio se investigo el impacto de 3 intensidades de apacentamiento (alta, media y ligera) y 4 especies forrajeras en los parámetros físico-químicos de un suelo "Typic Haplustoll" en Lancombe, Alberta. La mediciones se realizaron en muestras de suelo colectadas al inicio (1993) y al final (1996) del estudio. En este experimento se utilizaron dos especies perennes, "Smooth brome grass" (*Bromus inermis* cv. 'Carlton') y "Meadow brome grass" (*Bromus riparius* cv. 'Paddock') y dos especies anuales, una mezcla de triticale (*X Triticosecale* Wittmack cv. 'Pika') y cebada (*Hordeum vulgare* L. cv. 'AC Lamcombe') y triticale solo. Ni la intensidad de apacentamiento ni las especies vegetales afectaron la relación carbón-nitrógeno. La intensidad de apacentamiento indujo cambios en la capacidad de retención de agua disponible del estrato de 0-5 cm, en el nitrógeno del suelo del estrato 30-45 cm, en el pH a la profundidad de 0-15 cm y en la conductividad eléctrica de todos los estratos, excepto el de 0-5 cm ($P \leq 0.05$). Las especies vegetales afectaron el carbón del suelo a la profundidad de 0-5 cm, el pH del estrato 0-15 cm y la conductividad eléctrica del estrato de 5-45 cm ($P \leq 0.05$). Las medidas de conductividad eléctrica del suelo para todas las intensidades del apacentamiento y especies vegetales estuvieron dentro del rango (esto es 0-2 dS m⁻¹) que se considera no detrimental para el crecimiento de las plantas. El efecto mínimo de la intensidad de apacentamiento y especies vegetales en los parámetros del suelo medidos en este estudio se pudo deber a las propiedades intrínsecas del suelo para soportar situaciones de disturbio o a que el período de tiempo que comprendió el estudio fue muy corto.

The combined effect of dung and urine depositions with cattle grazing may alter soil acidity (Johnston et al. 1971) and salinity (Chaneton and Lavado 1996), and may also increase the loss of nitrogen via volatilization (Holland and Detling 1990). Furthermore, heavy grazing is known to increase surface soil bulk density (Krenzer et al. 1989, Mapfumo et al. 1999) which may in turn hinder root growth.

Perennial forages reduce soil erosion due to the maintenance of protective cover, improved soil structure and aggregate stability and increased litter on the soil surface. Indeed, most studies of the grazing impacts on soil physical and chemical properties have been conducted on perennial grasses. In many parts of the aspen

parkland of Alberta, however, pasturing annual crops by swath grazing is being used to extend the grazing season (Lagroix-McLean and Naeth 1997), with annuals such as winter triticale and barley becoming common pasture species (Baron et al. 1993). However, little is known about the direct impacts of grazing of annual forages on soil parameters.

Our working hypothesis considered that grazing differentially impacts particular soil parameters and the extent of impact is related to the intensity of grazing and the type of forage being grazed. The objective of this study was to investigate the effects of heavy, medium and light intensity grazing of annual and perennial forages on soil parameters over a relatively short period of time.

Materials and Methods

Experimental Design

The study was conducted at the Lacombe Research Station, Alberta, Canada on a Typic Haplustoll derived from glacio-lacustrine parent material. On average the soil (0–15-cm depth) contained 15% clay, 34% silt, and 51% sand. The experimental design was a randomized complete block with 3 grazing treatments, 4 plant species and 4 replicated blocks, for a total of 48 plots. Plots, 33 × 9 m, were established in 1992 by tilling a 15-year old growth pasture which had been under extensively managed grazing. The old-growth pasture was composed of smooth brome grass (*Bromus inermis* L.), Kentucky bluegrass (*Poa pratensis* L.), quackgrass (*Agropyron repens* L.), bluegrass (*Poa* spp.) with common occurrences of dandelion (*Taraxacum officinale* L.).

Plant Species

The 4 forage species used to seed plots included 'Carlton' smooth brome grass (*Bromis inermis*), 'Paddock' meadow brome grass (*Bromus riparius* Rehm.), 'Pika' triticale (*X Triticosecale* Wittmack), or a mixture of 'Pika' triticale/'AC Lacombe' barley (*Hordeum vulgare* L.). Perennials (i.e. smooth brome grass and meadow brome grass) were seeded on 31 May 1993. Smooth brome grass was seeded at 11.2 kg ha⁻¹ and meadow brome grass at 16.8 kg ha⁻¹. Before seeding the experimental area received a broadcast application of 8, 14, 26, and 5 kg ha⁻¹ of N, P, K, and S, respectively. In subsequent years, perennial and annual plots were fertilized at the same time. Each spring 100, 22, and 41 kg ha⁻¹ of N, P, and K, respectively were broadcast over the experimental area. Annual plots were rototilled each spring to

a depth of 10 cm, and seeded to triticale at 135 kg ha⁻¹ in 2 passes, or triticale at 90 kg ha⁻¹ and barley 50 kg ha⁻¹ in separate operations. Plant residue remaining after the last grazing of the previous season was left in place until spring (end of April) seeding. The herbicide, MCPA (2-methyl-4-chlorophenoxyacetic acid), was applied to annual plots after the crop emerged at rates of 600 g a.i. ha⁻¹ in 1994 to 1996. No weed control was used in perennial plots.

Grazing Systems

Beginning in 1994, up to 6 animals were placed on a treatment at 1 time, depending on the intensity of grazing desired. Each grazing event was less than 24 hours. Forage height was used to define grazing intensity. Forage heights were determined using a disk meter (Bransby et al. 1977) and the average of 10 disk heights was calculated. Averaged over 3 grazing years, the number of grazing events per season for perennials were 7, 5, and 3 for heavy, medium and light grazing, respectively, whereas comparable figures for annuals were 4, 4, and 2 for heavy, medium and light grazing, respectively (Table 1). Averaged over 3 years, mean cow-days per season for perennials was 37, 20, and 16 and for annuals 19, 11, and 8 for heavy, medium and light grazing, respectively. Mean residue levels for perennials averaged over 3 years were 0.89, 1.71, and 2.57 Mg ha⁻¹ and for annuals 0.91, 1.22, and 2.23 Mg ha⁻¹ for heavy, medium and light grazing, respectively.

Soil Sampling

Soil sampling was conducted prior to grazing in September 1993 using a hand

auger to a depth of 60 cm. Sampling at the end of the study was conducted in October 1996 to the same depth using a tractor-mounted hydraulic auger. For both samplings, three samples per plot were taken and separated into increments of 0–5, 5–15, 15–30, 30–45, and 45–60 cm. All samples were air-dried and ground to pass a 2-mm sieve. Before determination of physical and chemical properties, the 3 samples from the same depth interval and within each plot were mixed to form a composite sample.

Soil Physical and Chemical Properties

Water retention properties were determined on these disturbed soils using pressure plates (Topp et al. 1993). Field capacity was the gravimetric moisture content retained at a pressure of 0.033 MPa and wilting point was moisture content retained at 1.5 MPa. Available water holding capacity (AWHC) was the difference between field capacity moisture and wilting point moisture.

Electrical conductivity (EC) was determined using the saturation extract method (Janzen 1993). Soil pH was determined using distilled water in a soil: water ratio of 1:2. Total C in soil was determined using the Leco carbon analyzer. Initial soil tests did not indicate the presence of free carbonates. Soil samples for determinations of total N were digested using the standard Kjeldhal method with concentrated sulfuric acid (McGill and Figuerido 1993). Total N concentration was then determined using the autoanalyzer (Technicon Autoanalyzer II). Extractable K using extractant solution of 1N NH₄OAC adjusted to pH 7 with NH₄OH

Table 1. Number of grazings, cow-days for each grazing season and the total number of cow-days for each grazing intensity and plant species for the entire study period.

Grazing Level	Number of Grazings			Cow-days			Total Cow-days
	1994	1995	1996	1994	1995	1996	
Smooth brome grass							
Heavy	7	7	6	34.8	45.0	32.5	112.5
Medium	6	5	4	21.7	21.7	16.3	59.7
Light	3	3	3	15.5	18.5	15.5	49.5
Meadow brome grass							
Heavy	8	6	5	43.3	36.8	27.0	107.1
Medium	6	5	4	23.8	19.3	15.5	58.6
Light	3	3	3	15.0	15.3	13.5	43.8
Barley/Triticale							
Heavy	5	3	3	23.3	16.5	15.8	55.6
Medium	4	4	3	11.3	11.3	9.8	32.4
Light	2	2	2	6.5	9.8	5.8	22.1
Triticale							
Heavy	5	4	3	25.5	18.8	12.5	56.8
Medium	4	4	3	13.5	10.0	8.5	32.0
Light	2	2	2	9.8	9.3	6.3	25.4

or acetic acid (Hendershot et al. 1993) was determined using atomic absorption spectrophotometry.

Statistical Analysis

To test for significant ($P = 0.05$) changes in soil parameters, pre- versus post-treatment, a paired t-test was used for each combination of grazing intensity, plant species and soil depth. For individual depths, we tested for significant effects of grazing intensity and plant species on soil parameters with a 2-way ANOVA using the SAS institute generalized linear models procedure (SAS Institute 1989). Change (post-treatment–pre-treatment) in available water holding capacity, organic carbon, total soil nitrogen, extractable potassium, soil pH, and electrical conductivity were dependent variables. Where the F-test indicated a significant ($P = 0.05$) effect, means were separated using the least significance difference (LSD) test (Gomez and Gomez 1984).

Results

Water Retention

For all species and grazing intensities, water contents at field capacity (FC) for soil depths between 0 and 30 cm ranged between 21 and 31 g 100 g⁻¹ of soil, whereas water contents at wilting point (WP) ranged between 11 and 18 g 100 g⁻¹ of soil. For depth intervals between 30 and 60 cm, FC ranged between 15 and 22 g 100 g⁻¹ of soil, whereas WP ranged between 7 and 10 g 100 g⁻¹ of soil. Change in available water holding capacity (AWHC) after 3 years of grazing was not significantly different among species. For the 0–5 cm depth interval the heavy grazing intensity had a significantly lower AWHC after 3 years of grazing (Table 2). Change in AWHC for medium and light grazing in the 0–5 cm interval was positive and significantly greater than that for the heavy grazing. Water retention in light and medium grazing may have increased relative to heavy grazing, possibly because the former treatments had greater organic matter input and incorporation into the soil compared to the latter. In fact results from a concurrent study indicate that the average litter (all dead plant material) mass measured in the fall over 3 years of grazing were 2.8, 3.4, and 5.4 Mg ha⁻¹ for heavy, medium, and light grazing, respectively (Baron et al. 1999). Litter masses measured in spring for the respective grazing treatments were 1.6, 2.5, and 4.2 Mg ha⁻¹. It is also possible that surface soil

Table 2. Change in available water holding capacity (g 100 g⁻¹) after 3 years relative to corresponding pre-grazing values under different grazing intensities at different soil depths. Values pooled over plant species.

Depth Interval (cm)	Grazing intensity		
	Heavy	Medium	Light
	(g 100 g ⁻¹)		
0–5	–1.25 *b	1.26 a	1.86 *a
5–15	0.12 a	–1.64 *a	–0.15 a
15–30	2.37 *a	0.28 a	0.25 a
30–45	0.49 a	0.03 a	0.61 a
45–60	–0.57 a	–0.13 a	–0.33 a
Average	0.23	–0.04	0.45

Means followed by an asterisk are significantly ($P = 0.05$) different than their corresponding pre-grazing values (t-test). Row means followed by different small letters indicate significant differences among grazing intensities (LSD test).

compaction observed in a concurrent study (Mapfumo et al. 1999) may have reduced macro-porosity and thus AWHC at low moisture tension.

Chemical and Nutrient Properties

Total soil nitrogen content in all depths and treatments ranged between 0.06 and 0.50 g 100 g⁻¹ of soil. Species did not affect soil N content. Generally grazing altered soil N content between 0 and 30 cm ($P = 0.05$) (Table 3). Averaged over all depths the change in N content was positive in all 3 grazing treatments.

Table 4. Change in potassium content (mg kg⁻¹) after 3 years relative to corresponding pre-grazing values for different grazing intensities, plant species and soil depths.

Depth Interval	Depth (cm)	Grazing intensity		
		Heavy	Medium	Light
		(g 100 g ⁻¹)		
Smooth brome	0–5	63 aA	18 aA	139 aA
Meadow brome		64 *aA	15 aA	–22 aA
Barley/triticale		121 aA	–6 aA	100 aA
Triticale		40 aA	25 aA	12 aA
Smooth brome	5–15 cm	30 aA	119 aA	32 aA
Meadow brome		57 aA	10 aA	41 aA
Barley/triticale		35 aA	28 aA	85 *aA
Triticale		7 aA	71 *aA	11 aA
Smooth brome	15–30 cm	–17 aA	4 aA	25 aA
Meadow brome		30 aA	–12 aA	–11 aA
Barley/triticale		–3 aA	–2 aA	20 aA
Triticale		14 aA	4 aA	–4 aA
Smooth brome	30–45 cm	–7 aB	6 aA	3 aB
Meadow brome		22 aA	0 bA	0 bB
Barley/triticale		0 bB	1 bA	25 aA
Triticale		3 aB	0 aA	2 aB
Smooth brome	45–60 cm	1 aA	8 aA	4 *aA
Meadow brome		0 aA	–2 aA	15 aA
Barley/triticale		5 aA	5 aA	6 aA
Triticale		9 aA	2 aA	4 aA

Means followed by an asterisk are significantly ($P = 0.05$) different than their corresponding pre-grazing values (t-test). Row means followed by different lower case letters indicate significant difference among grazing intensities (LSmeans, $P = 0.05$) within species. Column means followed by upper case letters indicate significant difference among species (LSmeans, $P = 0.05$) within grazing intensity.

Table 3. Change in nitrogen content (g 100 g⁻¹) after 3 years relative to corresponding pre-grazing values under different grazing intensities at different soil depths. Values pooled over plant species.

Depth Interval (cm)	Grazing intensity		
	Heavy	Medium	Light
	(g 100 g ⁻¹)		
0–5	0.043 *a	0.035 a	0.043 *a
5–15	0.046 *a	0.068 *a	0.051 *a
15–30	–0.018 b	0.049 *a	0.003 ab
30–45	–0.011 a	0.001 a	–0.026 a
45–60	–0.004 a	0.001 a	0.003 a
Average	0.011	0.031	0.015

Means followed by an asterisk are significantly ($P = 0.05$) different than their corresponding pre-grazing values (t-test). Row means followed by different small letters indicate significant differences among grazing intensities (LSD test).

Extractable K content ranged between 73 and 650 ppm for the depths between 0 and 30 cm, whereas for intervals between 30 and 60 cm, K content ranged between 68 and 97 ppm. Change in extractable K content was significantly affected by the interaction between grazing and species only for the 30–45 cm interval (Table 4). For heavy grazing, meadow brome grass had the largest change in K content compared to other forages. For the medium grazing treatment, change in extractable K content was similar among all species. However, the light grazing barley/triticale

Table 5. Change in carbon content (g 100 g⁻¹) after 3 years relative to corresponding pre-grazing values under different plant species at different soil depths. Values pooled over grazing intensities.

Depth interval (cm)	Smooth brome-grass	Meadow brome-grass	Barley/ Triticale	Triticale
0–5	0.12 a	0.08 a	-0.29 *b	-0.39 *b
5–15	0.21 a	-0.12 a	0.12 a	-0.04 a
15–30	0.22 a	-0.36 a	-0.09 a	-0.31 a
30–45	-0.10 a	-0.48 *a	-0.42 *a	-0.29 a
45–60	-0.05 a	-0.17 a	0.00 a	-0.09 a
Average	0.08	-0.21	-0.14	-0.22

Means followed by an asterisk are significantly (P = 0.05) different than their corresponding pre-grazing values (t-test). Row means followed by different small letters indicate significant differences among grazing intensities (LSD test).

treatment had the largest change in K content compared to other treatments.

Soil carbon content generally ranged between 3 and 6 g 100 g⁻¹ of soil for depth intervals between 0 and 30 cm, and from <1 to 2 g 100 g⁻¹ of soil for intervals between 30 and 60 cm. Change in soil carbon (C) content after 3 years of grazing was not significantly affected by grazing intensity, but was affected by forage species only for the 0–5 cm depth interval (Table 5). Soil carbon content under perennials slightly increased after 3 years of grazing whereas under annuals soil carbon content decreased. These differences may be attributed to a combination of opposing factors; yearly cultivation of annuals which likely promoted organic matter decomposition, and accumulation of litter under perennials which likely increased soil carbon. In perennials, annual cultivation was not conducted such that rate of litter incorporation into the soil carbon pool was most likely greater than the rate of organic matter breakdown. In spite of the differences in change in carbon content among species, grazing intensity or forage species did not affect the change in carbon-to-nitrogen (C:N) ratio. For all grazing intensities, forage species and soil depths, C:N ratios ranged between 9:1 to 18:1.

Electrical conductivities (EC) ranged between 0.16 and 0.75 dS m⁻¹ for depth intervals between 0 and 30 cm and between 0.12 and 0.30 dS m⁻¹ for depths between 30 and 60 cm. Change in EC was significantly influenced by forage species for the 5–15, 15–30, and 30–45 cm intervals. Barley/triticale had a greater increase in electrical conductivity compared to meadow brome-grass (Table 6). However smooth brome-grass had a similar change in EC to meadow brome-grass, barley/triticale and triticale. Grazing intensity also influenced change in EC for all depth intervals between 15 and 60 cm. The heavy grazing treatment had a significantly greater increase in EC than medium or light grazing. Averaged over all depths the

increase in EC for heavy grazing was five times greater than that for medium and light grazing.

Soil pH ranged between 5.1 and 6.4 for depth intervals between 0 and 30 cm, and ranged between 6.6 and 7.0 for depth intervals between 30 and 60 cm. The change in pH after 3 years of grazing was significantly different among forage species for the 0–5 and 5–15 cm intervals (Table 7). Under both smooth brome-grass and meadow brome-grass changes in pH were greater than that for barley/triticale, but were not different from soil pH change under triticale. Grazing intensity affected soil pH change for the 5–15 cm depth interval. Under heavy grazing soil pH change was significantly greater (and negative) than that for medium and light grazing. Overall soil pH change for all depths, grazing intensities and forage species, did not exceed 0.2 units; such a change unlikely influenced plant growth and soil chemical and microbial processes.

Table 6. Change in electrical conductivity (dS m⁻¹) after 3 years relative to corresponding pre-grazing values under different plant species (pooled over grazing intensities) and under different grazing intensities (pooled over different plant species) at different soil depths.

Depth interval (cm)	Smooth brome-grass	Meadow brome-grass	Barley/ Triticale	Triticale
0–5	-0.09 a	-0.27 *a	-0.25 *b	-0.08 *a
5–15	0.22 *ab	0.11 *b	0.27 *a	0.15 *b
15–30	0.20 *ab	0.11 *b	0.27 *a	0.18 *ab
30–45	0.19 *ab	0.11 *b	0.23 *a	0.15 *b
45–60	0.10 *a	0.06 *a	0.14 *a	0.09 *a
Average	0.12	0.02	0.13	0.10

Depth interval (cm)	Heavy	Grazing intensity Medium	Light
0–5	-0.03 *a	-0.25 *a	-0.23 *a
5–15	0.36 *a	0.12 *b	0.08 *b
15–30	0.29 *a	0.17 *b	0.11 *b
30–45	0.24 *a	0.12 *b	0.14 *b
45–60	0.16 *a	0.06 *b	0.07 *b
Average	0.20	0.04	0.03

Means followed by an asterisk are significantly (P = 0.05) different than their corresponding pre-grazing values (t-test). Row means followed by different small letters indicate significant differences among plant species and among grazing intensities (LSD test).

Discussion

The small differences in water retention among grazing treatments generally reflect the minimal impacts of grazing, regardless of grazing intensity, on soil parameters evaluated in this study. Results from a concurrent study also indicate minimal grazing effects on soil bulk density, relative compaction (Mapfumo et al. 1999) and water-stable aggregate size distribution (Mapfumo 1997).

The carbon:nitrogen ratio reflects the potential for soils to mineralize and immobilize N. Generally a C:N ratio less than 20:1 indicates a potential for net mineralization whereas C:N ratio greater than 30:1 indicates potential immobilization (Tisdale et al. 1993). In our study, for all grazing levels, plant species and years, C:N ratios were less than 20:1, suggesting that N release through mineralization likely occurred. This process results in increased mineral nitrogen (NH₄-N and NO₃-N) which may contribute to increased solute concentration and hence electrical conductivity (EC) of the soil solution.

Extractable K includes soil solution K as well as K that is adsorbed onto exchange sites on the clay surfaces (exchangeable K). It is difficult to ascertain why grazing and forage species had an interactive effect only for the 30–45 cm interval. However, processes such as leaching, fixation by micaceous clays, weathering of feldspars and crop uptake occur concurrently and are known to affect exchangeable K (Tisdale et al. 1993). Changes in

Table 7. Change in soil pH after 3 years relative to corresponding pre-grazing values under different plant species (pooled over grazing intensities) and under different grazing intensities (pooled over different plant species) at different soil depths.

Depth interval	Smooth brome	Meadow brome	Barley/Triticale	Triticale
(cm)				
0–5	0.16 *a	0.12 *a	–0.06 *b	0.04 *ab
5–15	0.04 *a	0.03 *a	–0.18 *b	0.04 *a
15–30	0.18 a	0.20 a	0.13 a	0.18 a
30–45	0.04 *a	0.11 *a	–0.01 *a	0.04 *a
45–60	–0.06 *a	0.00 *a	–0.23 *b	–0.12 *ab
Average	0.07	0.09	–0.07	0.04

Depth interval	Heavy	Grazing intensity Medium	Light
(cm)			
0–5	0.08 *a	0.02 *a	0.11 *a
5–15	–0.17 *b	0.05 *a	0.07 *a
15–30	0.13 a	0.18 a	0.21 a
30–45	–0.04 *a	0.07 *a	0.10 *a
45–60	–0.15 *a	–0.04 *a	–0.12 *a
Average	–0.03	0.06	0.07

Means followed by an asterisk are significantly ($P = 0.05$) different than their corresponding pre-grazing values (t-test). Row means followed by different small letters indicate significant differences among plant species and among grazing intensities (LSD test).

soil macroporosity and rooting patterns might influence preferential flow paths and fertilizer distribution. Annuals might uptake more K before it leaches very far.

Changes in soil pH among grazing treatments within species were small (0.20 units), and soil depth seemed to have more influence on pH than either plant species or grazing level. However, the decrease in soil pH after 3 years of heavy grazing obtained for the 5–15 cm interval may be due to increased $\text{NH}_4\text{-N}$ from dung and urine depositions, which through nitrification produced $\text{NO}_3\text{-N}$ plus hydrogen ions. In fact results from a concurrent study indicate that both mineral N and $\text{NO}_3\text{-N}$ levels were greater under heavy compared to medium and light grazing (Baron et al. unpublished data). Estimates of urine loading rates from that study were 18,615, 10,075 and 7,919 $\text{L h}^{-1} \text{yr}^{-1}$ for heavy medium and light grazing, respectively with dung loading estimates for the respective grazing intensities of 1489, 806 and 634 $\text{kg DM ha}^{-1} \text{yr}^{-1}$. The lack of soil pH differences among grazing intensities for the surface (0–5 cm) interval can be partly attributed to $\text{NH}_3\text{-N}$ loss from fresh cattle wastes through volatilization which some researchers have reported to be more than 50% only three days after deposition (Westerman et al. 1985). Despite the observed changes after 3 years of grazing, the soil pH remained within the non-restrictive range for growth of annual or perennial grasses. Overall, if we assume a constant rate of change of pH over time it would take at least 15 years to effect a unit change in soil pH.

Electrical conductivity in all treatments was between 0 and 2 dS m^{-1} , which is the range within which salinity has negligible effects on plant growth (Bernstein 1975). The greater increase in EC under heavy compared to medium and light grazing treatments for depth intervals between 15 and 60 cm, may have been due to a combination of yearly application of fertilizer, increased urine and dung loading rates as well as organic-N mineralization to produced mineral N. These processes are known to increase total solutes in soil solution which is directly related to electrical conductivity.

In general, grazing intensity nor the type of forage grazed has insignificant effects on the soil parameters measured after three years of grazing. These early results may be refined after comparisons are made following 10 to 20 years of treatments.

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Vegetation response to stocking rate in southern mixed-grass prairie

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Abstract

Stocking rate directly influences the frequency and intensity of defoliation of individual plants which, in turn, impacts energy flow and plant succession in grazed ecosystems. The objective of this study was to determine the effect of stocking rate on standing crop dynamics and plant species composition of a southern mixed-grass prairie over a 7-year period (1990 through 1996). Long-term (30-year) mean precipitation has been 766 mm per year. Growing conditions were generally favorable for the study period. Yearling cattle (initial weight 216 kg, SD = 12 kg) grazed at 6 stocking rates, ranging from 23 to 51 AUD ha⁻¹, from 14 April to 24 September (162 days). The currently suggested year-long stocking rate is 25 AUD ha⁻¹. Herbage standing crop was measured in July and September every year while species composition was determined in July in even years. Total and dead standing crop declined as stocking rate increased but live standing crop was not related to stocking rate. Slopes of regression lines relating standing crop and stocking rate were constant over years, indicating no response for plant productivity. The major vegetation components, sideoats grama [*Bouteloua curtipendula* (Mich.) Torr.], shortgrasses, and forbs were not affected by stocking rate over years. Tallgrasses responded by increasing at the lower stocking rates over the study period. However, these grasses contributed less than 5% of the total standing crop. Red and purple threeawn (*Aristida longiseta* Steud. and *A. purpurea* Nutt.) increased at all stocking rates from 1990 to 1996 but the increase was greater at the lower stocking rates. This mixed-grass vegetation showed little response to stocking rate over the 7-year study period. The vegetation may have been in equilibrium with previous heavy stocking rates so that little change would be expected at those rates. Increases in grazing sensitive species at lighter stocking rates may occur over longer time intervals.

Key Words: standing crop, plant succession, grazing impacts, *Bouteloua*, *Aristida*

Vegetation dynamics on Great Plains grasslands are a function of grazing, fire, climate, and soils. Of these factors, managers can

Resumen

La carga animal influye directamente en la frecuencia e intensidad de defoliación de las plantas individuales, lo cual a su vez, impacta en el flujo de energía y la sucesión vegetal de los ecosistemas bajo apacentamiento. El objetivo de este estudio fue determinar, durante un período de 7 años (1990 a 1996), el efecto de la carga animal en la dinámica de la producción de forraje en pie y la composición botánica de un pradera de zacates mixtos del suroeste. La media de precipitación a largo plazo (30 años) ha sido de 766 mm por año. Durante el período de estudio, las condiciones de crecimiento para las plantas generalmente fueron favorables. Ganado de año (peso inicial 216 kg, SD = 12 kg) apacentó bajo seis cargas animal que variaron de 23 a 51 UAD ha⁻¹, el período de apacentamiento fue del 14 de Abril al 24 de Septiembre (162 días). La carga animal que actualmente se recomienda es de 25 UAD ha⁻¹. La producción de forraje en pie se midió en Julio y Septiembre de cada año, mientras que la composición botánica se determinó cada dos años en Julio. La cosecha total de forraje en pie y la cantidad de forraje muerto disminuyó conforme la carga animal aumento, pero el forraje vivo en pie no se relaciono con la carga animal. Las pendientes de las líneas de regresión que relacionan la cosecha en pie y la carga animal fueron constantes a través de los años, indicando una falta de respuesta en la productividad de las plantas. Los componentes principales de la vegetación, "Sideoat grama" [*Bouteloua curtipendula* (Mich.) Torr.], zacates cortos y hierbas no fueron afectados por la carga animal a través de los años. Durante el período de estudio, los zacates altos respondieron incrementandose en las cargas animal bajas. Sin embargo, estos zacates contribuyeron con menos del 5% del total de forraje en pie. Los zacates "Red threeawn" y "Purple threeawn" (*Aristida longiseta* Steud. y *A. Purpurea* Nutt.) se incrementaron en todas las cargas animal evaluadas, pero el aumento fue mayor en las cargas animal bajas. La vegetación de zacates- mixtos mostró poca respuesta a la carga animal durante el período de estudio de 7 años. La vegetación pudo haber estado en equilibrio con cargas animal altas previas al periodo de estudio de tal manera que se esperarían solo cambios menores con las cargas animal altas. El aumento de especies sensitivas a la carga animal que se registró con cargas animal bajas puede ocurrir en períodos de tiempo mas largos.

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exert a major influence on grazing and fire. Over the great majority of these grasslands, grazing is currently the primary management factor. The fundamental principle of grazing management is to control the frequency and intensity of defoliation of individual

plants (Heitschmidt and Walker 1996). The primary method for controlling the frequency and intensity of defoliation has been to control the stocking rate or the number of animals present per unit land area for a specified time.

Mixed-grass vegetation in west central Kansas changed considerably as stocking rate increased (Launchbaugh 1967) but little change was observed in western Nebraska (Burzlaff and Harris 1969). Differences between studies can be attributed to weather, the levels of stocking rate included, the length of the study, and the particular mix of plant species at a location (Hart and Norton 1988). If the range of stocking rates is wide enough in mixed prairie, midgrasses are generally more abundant at lower stocking rates while shortgrasses are more abundant at higher stocking rates (Launchbaugh 1967, Sims et al. 1976, Thurrow et al. 1988, Fuhlendorf and Smeins 1997). The specific objective of this study was to measure the effect of cattle stocking rate on standing crop dynamics and species composition of a southern mixed-grass prairie.

Materials and Methods

Study Area

The study area is located 15 km southwest of Clinton, Okla. on the Marvin Klemme Range Research Station (35° 50' N, 99° 8' W), a unit of the Oklahoma Agricultural Experiment Station. The study area is characterized by rolling uplands (2–15% slopes) dissected by moderately deep, steep-walled drainages. The mean elevation is 490 m. The predominant soil of the experimental pastures is the Cordell silty clay loam (Loamy, mixed, thermic Lithic Ustochrepts). Cordell soils are shallow with a depth of 25 to 36 cm (Moffatt and Conradi 1979). Rocky outcrops of hard red siltstone make up 0–25% of Cordell mapping units.

The nearest reporting station for long-term climatological data (1961–1990) is located at Clinton, Okla. (35° 22' N, 99° 04' W), 14 km northeast of the research station. The climate is continental with cool winters and hot summers. The mean annual precipitation is 766 mm, ranging from 510 to 817 mm. The mean precipitation from April through September is 518 mm or 68% of the annual precipitation. The mean frost-free growing period is 206 days from April to October. The mean temperature is 16.1°C with January as the coldest month (mean 8.9°C) and July as the hottest month (mean 28.4°C).

Red Shale ecological sites dominate the study pastures. This site supports mixed-grass prairie as the potential natural vegetation with mean forage production of 1,050 kg ha⁻¹. Major grass species include sideoats grama [*Bouteloua curtipendula* (Michx.) Torr.], blue grama [*B. gracilis* (Willd. ex Kunth) Lag. ex Griffiths], hairy grama [*B. hirsuta* Lag.], buffalograss [*Buchloe dactyloides* (Nutt.) Englem.], silver bluestem [*Bothriochloa saccharoides* (Sw.) Rydb.], red threeawn [*Aristida longiseta* Steud.], purple threeawn [*A. purpurea* Nutt.], and little bluestem [*Schizachyrium scoparium* (Michx.) Nash]. Major forbs include western ragweed [*Ambrosia psilostachya* DC.] and curlycup gumweed [*Grindelia squarrosa* (Pursh) Dun.]. Scattered populations of the half-shrub broom snakeweed [*Gutierrezia sarothrae* (Pursh) Britt. & Rusby] are found on shallow sites.

Approximately 30% of the Klemme Station was previously cultivated. Old fields (3 to 27 ha) are scattered across all study pastures. About two-thirds of these old fields were reseeded to mixtures of native grasses 25 to 35 years ago. The exact seed mixtures used are not known but likely included sand bluestem [*Andropogon hallii* Hack.], little bluestem, indiagrass [*Sorghastrum nutans* (L.) Nash], sideoats grama, and blue grama. The reseeded fields are now dominated by sideoats grama. The remaining fields revegetated naturally and supported mixed-grass vegetation.

Grazing management on the study pastures is not documented prior to 1988. Livestock have grazed the pastures since at least 1900. Stocking rates since 1965 are estimated to have been moderately heavy to heavy.

Methods

Stocking rates of 23, 26, 34, 41, 48, or 51 AUD ha⁻¹ were randomly allocated to 6 pastures. The currently recommended sustainable stocking rate is 25 AUD ha⁻¹ (SCS 1960). Average pasture area was 65 ha. The pastures were continuously stocked with mixed breed yearling beef steers (*Bos taurus* x *Bos indicus*; maximum 1/8 *B. indicus*) typical of commercial stocker cattle originating in the southeastern U.S. Herd size varied from 10 to 25 steers depending on stocking rate. During the 7-year study period (1990 through 1996), the mean start and end of the grazing season was 15 April and 24 September.

Initial body weight of the steers averaged 216 kg (SD = 12 kg). We attempted to equalize average body weight of steers

among treatments. To do this, steers were first classified into weight groups based on 23 kg increments. We then calculated the number of steers required from each weight group for each treatment based on proportional representation of all weight groups within each treatment. Finally, specific steers from each weight group were randomly allocated to treatments. The steers had access to a free-choice mineral supplement during the grazing season. All procedures for animal care and management were in accordance with accepted guidelines (Consortium 1988).

Herbage standing crop was measured each year around 20 July and 24 September. For each sample date, 50 quadrats were clipped to ground level to determine total standing crop in each pasture. Quadrat area was 0.1 m². Quadrats were systematically spread across each pasture along pace transects. The same approximate transects were sampled on each date. In each pasture, 2 to 3 samples of pure live and dead herbage were collected to determine ratios of live and dead tissue in the total herbage (Gillen and Tate 1993).

Species composition was determined around mid-July every other year from 1990 to 1996. Species composition was measured using the dry-weight rank method (Gillen and Smith 1985) with 100 quadrats per pasture (50 of which were also used for standing crop sampling). The 0.1 m² quadrats were systematically distributed across the pastures along pace transects. Species groups were: sideoats grama, shortgrasses (buffalograss, blue grama, and hairy grama), silver bluestem, threeawns (red and purple threeawn), tallgrasses (little bluestem and sand bluestem), other perennial grasses, annual grasses, forbs, and broom snakeweed.

For the statistical analysis, we used an analysis-of-covariance model (Littell et al. 1991). The model contained terms for stocking rate, year, and the stocking rate x year interaction. Year was a classification variable while stocking rate was a quantitative covariate. Since stocking rate varied slightly in a given pasture over years because of differences in the length of the grazing season or initial steer weight, we used the mean stocking rate over the 7-year study period. Dependent variables were standing crop or relative species composition.

The analysis-of-covariance model fit a linear regression between the dependent variable and stocking rate for each year. For instance, if the stocking rate effect was significant for July standing crop,

there was a linear relationship between July standing crop and stocking rate. If the year effect was significant, the intercept for the regression lines was different between some years. If the stocking rate x year interaction was significant, the slope of the line relating the July standing crop and stocking rate was different for some of the years in the analysis. If the stocking rate x year interaction was not significant, the slope of the regression relating July standing crop and stocking rate was constant over years.

We initially fit a full covariance model to our data for standing crop and relative species composition. If the stocking rate x year interaction was significant in the initial model, we examined all regression coefficients for the full model. We then dropped all coefficients that were not significant ($P > 0.10$) and fit a reduced regression model. If the stocking rate x year interaction was not significant ($P > 0.10$), we fit a reduced model containing only stocking rate and year. If year was significant in the reduced model, we made pair-wise comparisons of least squares means between years ($P = 0.05$).

With this procedure, we essentially fit a linear regression between a dependent variable and stocking rate for different years, for instance 1990 and 1996 as a simplified example. We then compared the lines for the 2 years. If the slopes of the lines for 1990 and 1996 were different, stocking rate had a significant effect over years. If the slopes of the lines for 1990 and 1996 were not different, stocking rate had no effect over years, regardless of the relationship in 1990. We assumed any significant relationship present between species composition and stocking rate in July 1990 to be a chance relationship. This was the first year of the study and we would not expect stocking rate to have an effect on plant populations within 3 months. To address our research objective, we emphasized interactions of stocking rate with year. Significant effects of stocking rate were not considered important unless they changed over years.

Results and Discussion

Precipitation

Means of annual and growing season precipitation during the study were 6% and 14% above the long-term means, respectively (Table 1). The most stressful conditions occurred in 1994 when growing season precipitation was 69% of the mean. This was offset by high precipitation in

Table 1. Precipitation during the study period and 30-year average precipitation (1961–1990) at Clinton, Okla.

Year	Precipitation	
	Annual (mm)	Apr. through Sep. (mm)
1990	670	514
1991	733	535
1992	774	484
1993	709	496
1994	575	361
1995	1195	935
1996	817	781
Study average	813	591
30-year average	766	518

1995 and 1996 although much of the growing season precipitation in 1995 fell in large intense storms with considerable runoff. Overall growing conditions were average to favorable during the study period.

Standing Crop

Total Standing Crop. Total standing crop, averaged over stocking rates and years, was similar in July (1,920 kg ha⁻¹) and September (1,870 kg ha⁻¹, $P = 0.96$). Total standing crop was only different among months ($P < 0.05$) in 1991, with 2,460 and 1,880 kg ha⁻¹ present in July and September, respectively. Herbage growth and consumption were in rough balance in the later portion of the growing season.

Total standing crop and stocking rate had an inverse relationship because of greater total forage demand at higher stocking rates (Table 2, Fig. 1). Averaged over months, standing crop decreased approximately 17.5 kg ha⁻¹ for every AUD ha⁻¹ increase in stocking rate. We found no interaction between stocking rate and year (Table 2). This suggests stocking rate did not affect the herbage production potential of the pastures over the term of the study.

Table 2. P-values from analyses of variance for standing crop components in July and September from a 7-year stocking rate study on mixed-grass prairie in western Oklahoma.

Item	Stocking rate	Year	Stocking rate x year
<u>Total Standing Crop</u>			
July	<0.01	<0.01	0.31
September	<0.01	<0.01	0.55
<u>Live Standing Crop</u>			
July	0.96	<0.01	0.92
September	0.43	<0.01	0.08
<u>% Live Standing Crop</u>			
July	<0.01	<0.01	0.20
September	<0.01	<0.01	0.24
<u>Dead Standing Crop</u>			
July	<0.01	<0.01	0.08
September	<0.01	<0.01	0.48

Live Standing Crop. Averaged over stocking rates and years, live standing herbage averaged 930 kg ha⁻¹ in July and 720 kg ha⁻¹ in September. Live standing crop in July was not related to stocking rate and there was no stocking rate by year interaction (Table 2). Live standing crop varied among years, ranging from 630 kg ha⁻¹ in 1995 to 1,410 kg ha⁻¹ in 1992.

There was a stocking rate by year interaction for live standing crop in September. From 1990 to 1995, live standing crop in September was not affected by stocking rate (Fig. 2). In 1996, live standing crop was negatively related to stocking rate. Precipitation for the July to September period in 1996 totaled 294 mm, 40% above the long-term mean, and was well distributed. The favorable precipitation regime may have delayed transfer of herbage from the live to the dead component and allowed an accumulation of live herbage as stocking rates decreased.

Percentage live standing crop was significantly related to stocking rate in both July and September (Table 2). Averaged over sample dates and years, percentage live standing crop ranged from 42% at 23 AUD ha⁻¹ to 52% at 51 AUD ha⁻¹. Percentage live standing crop increased by 0.4% for each increase of 1 AUD ha⁻¹ ($P = 0.05$), a relationship that was constant over sample dates and years. Percentage live standing crop was similar ($P = 0.96$) for July and September at 48% and 46% of total standing crop, respectively, when averaged over stocking rates and years. Live standing crop ranged from a low of 28% in September 1990 to a high of 67% in July 1992.

Dead Standing Crop. Dead standing crop was related to stocking rate ($P < 0.01$) in both July and September (Table 2, Fig. 3). As stocking rate increased, the standing crop of dead herbage decreased.

Fig. 1. Total standing crop of herbage in July and September as affected by stocking rate. Points are averages of 7 years. For July, standing crop = $2483 - 15.2$ (stocking rate). For September, standing crop = $2458 - 14.4$ (stocking rate). For the combined regression model, $R^2 = 0.59$, $P = 0.06$. Slope and intercept terms for July and September are not different ($P > 0.90$).

Fig. 2. Standing crop of live herbage in September as affected by stocking rate. For 1990-95, standing crop = $721 + 1.4$ (stocking rate). For 1996, standing crop = $2222 - 21.0$ (stocking rate). For the combined model, $R^2 = 0.92$, $P < 0.01$. Intercepts and slopes are different between sets of years (intercepts $P < 0.01$, slopes $P = 0.02$).

The only exception to this relationship occurred in July 1990, the first year of the study. On that date, there was no relationship between dead standing crop and stocking rate. Grazing treatments had been imposed for about 3 months at that time and had not exerted a measurable impact on dead standing crop. By the end of the first year in September of 1990, a relationship had been established between dead standing crop and stocking rate and this relationship remained constant over the following years and sample dates. Dead standing crop declined 17.4 kg ha^{-1} for each increase of 1 AUD ha^{-1} ($P < 0.01$).

Standing crop of dead herbage averaged $1,660 \text{ kg ha}^{-1}$ in July and 1560 kg ha^{-1} in September ($P = 0.85$).

Effects of stocking rate on standing crop components were manifest in the dead herbage component. This suggests the amount of herbage transferred from the live to the dead component was greater at lower stocking rates because more herbage would reach physiological maturity and move into the dead component. Conversely, at higher stocking rates a portion of this herbage would be consumed before it could transfer to the dead compartment. In north central Texas, a high

stocking rate reduced both live and dead standing crop of the grass component (Heitschmidt et al. 1989).

With 2 minor exceptions, the relationship between standing crop and stocking rate did not change over the 7-year study period. This suggests the impact of stocking rate was simply increased herbage consumption due to greater numbers of livestock as stocking rate increased. There is no evidence of an effect on plant productivity at the community level. If plant productivity had declined over years at the higher stocking rates, the slope of standing crop versus stocking rate would have become more negative.

Table 3. Coefficients and statistics of regression models describing response of species composition (%) to stocking rate between 1990 and 1996. Year is coded 0 for 1990 and 1 for 1996. Stocking rate is AUD ha^{-1} .

Period	N	Intercept	Year	Stocking rate	Year x Stocking rate	R^2	C.V.	MSE
Sideoats grama	12	14.8** (2.8) ¹		0.1+ (0.8)		0.27	13.0	6.7
Shortgrasses	12	37.4** (4.9)		-0.3* (0.1)		0.39	18.0	21.1
Silver bluestem	12	1.0 (2.0)		0.1* (0.05)		0.41	31.0	3.8
Threeawns	12	5.8** (0.7)	11.7** (2.7)		-0.14+ (0.07)	0.84	20.5	3.0
Other grasses	12	9.8** (1.1)				0.00	39.4	14.8
Annual grasses	12	2.7** (0.3)	-2.7** (0.4)			0.81	51.8	0.5
Forbs	12	22.1** (1.5)				0.00	23.7	27.5
Broom snakeweed	12	4.4** (0.7)				0.00	58.0	6.7

**, *, + significant at the 0.01, 0.05, and 0.10 levels respectively.

¹Standard error of estimate.

Fig. 3. Standing crop of dead herbage as affected by stocking rate. For 1990, slopes are not different from 0 ($P > 0.96$) and are not different between July and September ($P = 0.83$). For 1991 to 1996, July standing crop = $1655 - 18.0$ (stocking rate); September standing crop = $1640 - 16.8$ (stocking rate). For the combined model, 1991 to 1996, $R^2 = 0.82$, $P < 0.01$. Intercept and slope terms for July and September are not different ($P > .67$).

Species Composition

Sideoats grama was the most abundant single species, comprising approximately 20% of the vegetation, and was not affected by stocking rate. While the relative composition of sideoats grama was greater at the higher stocking rates, this positive relationship was already present in 1990 at the initiation of the study and did not change over 7 years (Table 3, Fig. 4). This was unexpected because sideoats grama is often considered a decreaser in mixed-grass prairie (SCS 1960, Taylor et al. 1997). Heitschmidt et al. (1985, 1989) also reported the composition of sideoats grama was not influenced by stocking rate in mixed-grass prairie. In central Texas, sideoats grama increased as stocking rate was decreased but changes were not immediate and were mediated by soil depth (Fuhlendorf and Smeins 1997, 1998). Sideoats grama declined slightly on all pastures in 1994 but returned to initial levels in 1996 (Table 4).

The shortgrasses were prominent in all pastures, contributing approximately 25%

of the vegetation. Buffalograss was the major species in this category. As with sideoats grama, shortgrasses did not respond to either stocking rate or year (Tables 3 and 4, Fig. 4). Other studies have reported increases in the relative composition of shortgrasses as stocking rate increased (Klippel and Costello 1960, Launchbaugh 1967, Thurow et al. 1988, Heitschmidt et al. 1989).

Silver bluestem was most abundant at the higher stocking rates (Table 3, Fig. 4). This relationship was present at the beginning of the study and remained constant over years indicating no effect of stocking rate on silver bluestem. There was also no relationship with year (Fig. 4). Silver bluestem percentage composition averaged 6% and remained unchanged over the 7 years of the study. Silver bluestem is also a secondary species in Texas mixed-grass prairies and increased slightly as stocking rate was decreased (Fuhlendorf and Smeins 1997) or else was not affected by stocking rate (Heitschmidt et al. 1989).

There was no relationship between threeawns and stocking rate in 1990. By 1996, threeawns were more abundant at the lower stocking rates (Table 3, Fig. 4). The response of threeawns to stocking rate has been variable in other studies. Studies in Texas found either little response of perennial threeawns to stocking rate (Heitschmidt et al. 1989, Taylor et al. 1997) or higher abundance of threeawns at intermediate stocking rates (Fuhlendorf

Table 4. Relative composition (%) for species or species groups over years, averaged over stocking rate from a 7-year stocking rate study on mixed-grass prairie in western Oklahoma.

Species	Year			
	1990	1992	1994	1996
	----- (%) -----			
Sideoats grama	20.8 ^{ab1} (2.9) ²	22.5 ^a (3.0)	17.6 ^c (3.6)	19.1 ^{bc} (2.8)
Shortgrasses	27.1 (6.5)	22.4 (2.9)	26.7 (5.3)	23.9 (4.6)
Silver bluestem	6.8 (2.7)	5.2 (1.5)	5.6 (1.5)	5.6 (2.0)
Threeawns	5.2 ^c (2.1)	6.0 ^c (3.0)	9.0 ^b (2.7)	11.7 ^a (1.9)
Tallgrasses	2.0 (0.8)	3.1 (1.6)	3.2 (2.4)	2.5 (1.9)
Other perennial grasses	11.2 (3.4)	10.7 (4.4)	7.8 (3.6)	8.3 (4.0)
Annual grasses	2.7 ^a (1.0)	2.4 ^a (0.7)	0.8 ^b (0.2)	0.0 ^c (0.0)
Forbs	20.2 (6.3)	19.0 (2.4)	21.8 (3.8)	24.0 (3.5)
Broom snakeweed	3.9 ^c (1.7)	8.6 ^a (2.9)	7.5 ^{ab} (3.3)	5.0 ^{bc} (3.3)

¹Means within a row followed by different letters are different using protected pair-wise t-tests, $P < 0.05$.

²Standard deviation.

Fig. 4. Relative composition of vegetation components as affected by stocking rate in 1990 and 1996. Regression models for each component are found in Table 4. A single line indicates no difference between years.

and Smeins 1997). In contrast, threeawns decreased at higher stocking rates in short-grass prairie in northeastern Colorado (Klippel and Costello 1960). Later work at the same site found heavy grazing after June was generally detrimental to red threeawn (Hyder et al. 1975).

Threeawns are classified as increasers or invaders on virtually all ecological site descriptions used by the Natural Resources Conservation Service in western Oklahoma. This means threeawns should increase in abundance as stocking rates increase. Results from the current and previous studies suggest this classification should be reconsidered. These grasses appear to remain unchanged or decrease as stocking rate increases. Threeawns are unpalatable and are often

the last plants to be grazed as stocking rates increase (Klippel and Costello 1960). As the more palatable plants are grazed, threeawns become more visually prominent. This may explain why they have been considered increasers.

Threeawns increased at all stocking rates from 1990 to 1996 (Table 4) but the increase was greater at the lower stocking rates (Fig. 4). The reason for this general increase is not known. Red threeawn appeared to be favored in wet years but reduced in dry years in shortgrass prairie (Hyder et al. 1975). The increase in threeawns in this study cannot be easily attributed to weather since precipitation was well above average only in years 6 and 7 of the study while threeawns increased between years 3 and 5 (Table 4).

Tallgrasses were negatively related to stocking rate but there was an interaction of stocking rate and year. In the first year of the study (1990), tallgrasses were not related to stocking rate (Fig. 5). By 1992, there was a negative relationship between the tallgrass component and stocking rate. This relationship remained constant through 1996. Although tallgrasses increased at the lower stocking rates, they still contributed no more than 5 to 6% of the total herbage. Descriptions of the potential natural community for the Red Shale ecological site suggest that little bluestem could be co-dominant on this site with sideoats grama (SCS 1960). More than 7 years of moderate stocking rates would be required for little bluestem to increase to such levels. It may be that the initial response of tallgrasses was due to the short-term process of increasing the size of existing plants while further increases in relative composition must wait for the long-term process of establishing new plants.

Other perennial grasses were about 10% of the vegetation. Hairy tridens [*Erioneuron pilosum* (Buckl.) Nash], tall dropseed [*Sporobolus asper* (Michx.) Kunth], and windmillgrass [*Chloris verticillata* Nutt.] were the major grasses in this category. This component was not affected by stocking rate or year and there was no interaction between stocking rate and year (Table 3, Fig. 4). Different responses among species could have prevented any discernible group response.

The annual grass category was primarily Japanese brome [*Bromus japonicus* Thunb.]. This component was not prominent in the study pastures. The annual grasses were not affected by stocking rate (Table 3, Fig. 4) but declined significantly from 2.8% to less than 0.1% over the study period (Table 4). Japanese brome fluctuates greatly over years in response to favorable winter and spring precipitation (Launchbaugh 1967).

Forbs were one of the larger vegetation categories, contributing 20 to 24% of the herbage. Forbs were not affected by stocking rate or year (Table 3, Fig. 4). This supports the results of previous studies, which reported no difference in forb abundance due to stocking rates (Sims et al. 1976, Hart et al. 1988, Heitschmidt et al. 1989). Launchbaugh (1967), in contrast, found that forbs decreased as stocking rate increased. This is contrary to much popular opinion that holds that forbs increase as stocking rates increase. Differences in the effect of stocking rate on forb composition among studies may be attributable to indi-

Fig. 5. Relative composition of tallgrasses as affected by stocking rate. Intercept coefficients are 0.9, 7.1, 9.7, and 6.3 for 1990, 1992, 1994, and 1996, respectively. Slope coefficients are 0.03, -0.11 , -0.17 , and -0.10 for 1990, 1992, 1994, and 1996, respectively. For the combined model, $R^2 = 0.60$, $P = 0.02$. Coefficients for 1990 are different from 1992–1996 ($P < 0.05$), which are not different from each other ($P > 0.24$).

vidual species responses. Species within this group should probably be studied individually for a better understanding of the influence of stocking rate on their relative composition (Heitschmidt et al. 1985).

The half-shrub broom snakeweed was not affected by stocking rate (Table 3, Fig. 4). Broom snakeweed composition more than doubled from 1990 to 1992 before declining back to near initial levels in 1996 (Table 4). These changes over years were independent of stocking rate. Klipple and Costello (1960) reported that broom snakeweed was not affected by stocking rate and was cyclic in nature. In addition, broom snakeweed populations fluctuated dramatically in response to weather in New Mexico (McDaniel et al. 1993).

Conclusions

Stocking rate had few impacts on our experimental pastures over the course of this study. Effects on herbage standing crop can be attributed to the simple fact that livestock demand for forage increased

as stocking rate increased rather than to long-term impacts on plant vigor. Stocking rate affected the relative species contribution of only 2 vegetation components, threeawns and tallgrasses. There may be potential for further changes in tallgrasses over longer time periods. Broom snakeweed fluctuated over time, but this effect was independent of stocking rate. The vegetation was, for all practical purposes, unchanged at the end of this study.

Several hypotheses could be advanced to explain the moderate vegetation response. First, the stocking rates studied may have been too light to cause significant effects. We place lesser weight on this hypothesis because the stocking rates used were substantially higher than the recommended rates. The impact of these stocking rates was further compounded because all of the grazing occurred during the growing season.

Second, weather conditions during the study period may have ameliorated the impact of stocking rate. Both annual and growing season precipitation were above average for the study period. However,

precipitation during the last 2 years of the study was much greater than in the earlier years. During the first 5 years, annual precipitation was 85% of average and growing season precipitation was 81% of average. These precipitation levels would not constitute a severe drought but were below average. We expected these precipitation levels in combination with high stocking rates to trigger vegetation changes but the mixed-grass vegetation was resistant under the observed stocking rates and weather conditions.

A third hypothesis considers the influence of initial conditions. Significant changes may have already occurred in the 80 years the pastures were grazed at high stocking rates before the study began and the vegetation may have already been in equilibrium with the higher stocking rates used in our study. In that case, little change would be observed at high stocking rates but change could potentially occur at lower stocking rates. This is suggested by the slight increase in tallgrasses at the lower stocking rates. Since this component was at low levels initially, increases might take many more years to be practically significant. A similar situation has been reported from central Texas (Fuhlendorf and Smeins 1997). Additionally, grazing sensitive species may not increase immediately because lower stocking rates alone are not enough of a disturbance to cause grazing resistant species to relinquish resources (Fuhlendorf and Smeins 1998). Increases in grazing sensitive species may be delayed until a climatic stress reduces the grazing resistant species and opens space for colonization. We believe this third hypothesis best fits the observed vegetation responses from this study.

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Effects of roundups on behavior and reproduction of feral horses

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Abstract

Roundups are used to maintain feral horse populations in balance with rangeland grazing capacity, but little is known about short-term and long-term effects of roundups on horses. We evaluated the effects of roundups on behavior and reproduction of feral horses. The study was conducted near Challis, Ida. during 1994–1995, and repeated near Lander, Wyo. during 1995–1996. Horses were randomly assigned to 3 different treatment groups. One group (ADOPTED) was gathered by a Bureau of Land Management roundup crew using a helicopter. These horses were removed and placed in the Adopt-A-Horse Program. The second group (SIMULATED) consisted of horses that were gathered by helicopter, but these horses evaded capture and remained in the study area after the roundup. Horses in the third group (CONTROL) were not herded by helicopter. Horse behavior was monitored in the SIMULATED and CONTROL groups before and after roundups. Behavioral variables analyzed were the percentage of time spent resting, feeding, vigilant, traveling, and engaged in agonistic encounters. Neither foraging or social behavior of feral horses was affected by roundups in either study area ($P > 0.10$). Reproduction was monitored within the SIMULATED, CONTROL, and ADOPTED groups during the year following roundups. The percentages of mares with live foals did not differ ($P > 0.10$) among the 3 treatment groups in Idaho or Wyoming. Foaling success rates in Idaho were 29%, 31%, and 43% for CONTROL, ADOPTED, and SIMULATED mares, respectively. In Wyoming, foaling success rates were 29%, 42%, and 48% for CONTROL, ADOPTED, and SIMULATED groups, respectively. We found no evidence that roundups had deleterious effects on behavior or reproduction of feral horses.

Key Words: wild horses, *Equus caballus*, Adopt-A-Horse Program, foraging behavior, social behavior

About 46,000 feral horses (*Equus caballus*) live in the western United States (USDI-BLM and USDA-FS 1993). The Wild Free-Roaming Horse and Burro Act, Public Law 92-195 (U.S. Code 1988), obligates the Bureau of Land Management (BLM) and the U.S. Forest Service to protect feral horses on public lands of the western United States from unauthorized capture or killing. These agencies must also maintain these populations in balance with rangeland carrying capacity (USDI-BLM and USDA-FS 1993). Uncontrolled horse populations lead to excessive grazing, in turn

Resumen

Las redadas se utilizan para mantener las poblaciones de caballos silvestres en balance con la capacidad de apacentamiento, pero poco se sabe acerca de los efectos a corto y largo plazo de las redadas en los caballos. Evaluamos el efecto de las redadas en el comportamiento y reproducción de los caballos silvestres. El estudio se condujo cerca de Challis, Ida. durante 1994 y 1995 y se repitió cerca de Lander Wyo. durante 1995 y 1996. Los caballos se asignaron aleatoriamente a tres grupos de tratamiento. Un grupo (ADOPTADO) fue reunido y removido por una cuadrilla de redadas del Buro de Manejo de Tierras la cual utilizó un helicóptero. Estos caballos fueron después colocados en el programa "Adopta un Caballo". El segundo grupo, (SIMULADO) consistió de caballos que fueron reunidos con helicóptero, pero estos caballos evadieron la captura y permanecieron en el área de estudio después de la redada. El tercer grupo (CONTROL), fueron caballos que no se pastorearon con helicóptero. El comportamiento de los caballos se monitoreo en los grupos SIMULADO y CONTROL antes y después de las redadas. Las variables de comportamiento se analizadas fueron el porcentaje de tiempo utilizado en descanso, alimentación, vigilancia, viajar, y encuentros agonísticos. Las redadas no afectaron ni el comportamiento de alimentación ni el comportamiento social de los caballos salvajes en el área de estudio ($P > 0.01$). Al año siguiente de las redadas se monitoreo la reproducción dentro de los grupos SIMULADO, CONTROL y ADOPTADOS. El porcentaje de yeguas con potros vivos no difirió entre los tres tratamientos ($P > 0.10$) y los resultados fueron similares en Idaho y Wyoming. Las tasas de potros vivos en Idaho fueron 29%, 31% y 43% para los tratamientos CONTROL, ADOPTADO y SIMULADO respectivamente. En Wyoming los porcentajes de potros vivos fueron 29%, 42% y 48% para los tratamientos CONTROL, ADOPTADO y SIMULADO respectivamente. No encontramos evidencia de que las redadas tuvieran un efecto nocivo en el comportamiento o la reproducción de los caballos salvajes.

causing rangeland degradation (Smith 1986). Roundups remove excess animals, after which horses are placed in private ownership via the Adopt-A-Horse Program. Roundups obviously disturb the daily routine and behavior of feral horses, but little is known about short-term and long-term effects of roundups on horses. When perturbations occur, horses may shift their behavior to minimize the effects. For example, feral horses alter their habitat use to seek refuge from biting insects (Keiper and Berger 1982). Behavioral responses to perturbations also may include increased time spent in agonistic encounters with other horses, such as when mares enter new areas and encounter resident mares (Tyler 1972). Perturbations may also induce stress that decreases

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reproduction. For example, forced copulation by invading males may induce abortion in females unprotected by their resident stallion (Berger 1983), and abortions may occur in response to male harassment or other stresses imposed by changes in a herd's social structure (Berger 1983). The purpose of this study was to document the effects of roundups on the foraging behavior, social behavior, and reproductive success of feral horses. Our specific null hypotheses were: 1) behavior does not differ between horses rounded up and horses not rounded up; and 2) reproductive success does not differ among horses rounded up, horses not rounded up, and horses placed in the Adopt-A-Horse Program.

Study Area

The study was conducted in 2 separate areas, one in central Idaho about 3 km southwest of Challis, Ida., and one in central Wyoming about 32 km north of Jeffrey City, Wyo.

Idaho Study Area

The Idaho study area was 150-km² of public land administered by the BLM, located north of Spar Canyon Road, east of State Highway 75, and west of U.S. Highway 93. Elevations ranged from 1,675–2,745 m. Annual precipitation averages 18 cm, with about 50% occurring as snow during November through March (Perrich 1992). Major plant species present were bluebunch wheatgrass (*Agropyron spicatum* (Pursh.) Scribn. & Smith), western wheatgrass (*Agropyron smithii* Rydb.), Sandberg bluegrass (*Poa sandbergii* Vasey), Idaho fescue (*Festuca idahoensis* Elmer), and Wyoming big sagebrush (*Artemisia tridentata wyomingensis* Beetle & Young). Limber pine (*Pinus flexilis* James), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and curlleaf mountain mahogany (*Cercocarpus ledifolius* Nutt. ex. Torr. & Gray) occurred at higher elevations within the study area.

Soils ranged from a loamy-skeletal, mixed frigid Xerollic Haplargid (Dawtonia) at the lower elevations to a loamy skeletal, mixed Calcic Cryoborol (Gany) at the highest elevations. The dominant range site for the study area was Gravelly Loamy (20–30 cm precipitation) with associated range sites of Gravelly Loam (33–40 cm precipitation) and Flagstone (20–28 cm precipitation). The habitat type was Wyoming big sagebrush/bluebunch wheatgrass at lower ele-

vations and Douglas-fir/Idaho fescue at the highest elevations (BLM-SCS 1979).

Wyoming Study Area

The Wyoming study area was in Muskrat Basin, 202-km² of public land administered by the BLM, located between State Highways 789 and 136. Vegetation was dominated by Wyoming big sagebrush, bluebunch wheatgrass, western wheatgrass, Sandberg bluegrass, Idaho fescue, and needle-and-thread grass (*Stipa comata* Trin. & Rupr.). Elevations ranged from 1,820–2,100 m. Annual precipitation averages 25 cm with about 50% occurring during May and June, and 50% occurring during November through March in the form of snow (Perrich 1992). Soils were a loamy-skeletal, mixed (calcareous), frigid, shallow Ustic Torriorthent (Cragosen) in most of the area, and a fine, montmorillonitic Borollic Paleargid (Milren) on the lower sites.

The dominant range site for this study area was Loamy (24–35 cm precipitation) with associated range sites of Shallow Sandy (24–35 cm precipitation) and Sandy (25–35 cm precipitation) (Soil Conservation Service 1988).

Methods

This experiment was conducted in Idaho from July 1994 to July 1995 and in Wyoming from July 1995 to July 1996. Field procedures and statistical methods were identical for both study areas.

Roundups

Horses in each study area were randomly assigned to 3 different treatment groups. One group (ADOPTED) was gathered by a BLM roundup crew using a helicopter. These horses were removed and placed in the Adopt-A-Horse Program. The second group (SIMULATED) consisted of horses that were gathered by helicopter, but these horses evaded capture and remained in the study area after the roundup. Horses in the third group (CONTROL) were not herded by helicopter. In the Idaho study area, the ADOPTED, SIMULATED, and CONTROL groups were composed of 12, 3, and 4 bands (i.e., social subgroups) of horses, respectively. The number of bands in the ADOPTED, SIMULATED and CONTROL groups in Wyoming were 10, 8, and 5, respectively. Bands contained 2 to 10 adult horses, and all bands were photographed to document their membership. Individual members of each band were also photographed, and physical character-

istics of each horse were recorded to aid their identification. In Idaho, the SIMULATED, CONTROL, and ADOPTED groups totaled 14, 14, and 39 mares, respectively. In Wyoming, there were 33, 14, and 34 mares, respectively, in the SIMULATED, CONTROL, and ADOPTED groups. In each study area the roundup and simulated roundup occurred the same day, on 27 August 1994 in the Idaho study area and 13 August 1995 in Wyoming.

Horse Behavior

Horse behavior was monitored in the SIMULATED and CONTROL groups for 3 weeks immediately before and 3 weeks after the simulated roundups. Monitoring before the simulated roundup occurred from 25 July through 26 August 1994 on the Idaho study area and 10 July through 12 August 1995 for the Wyoming area. Data following the simulated roundup was collected from 28 August through 20 September 1994 for the Idaho area and 14 August through 28 August 1995 for the Wyoming area. Behavioral observations spanned more than 600 hours during each year of the study.

We recorded the percentage of time that a band of horses spent in the following activities: feeding (primarily grazing with little or no travel other than to move to a new feeding station); resting (both recumbent and standing); traveling (including incidental grazing while walking); aggression within the band (defined as threat postures, striking with the feet, or biting); aggression between bands; and vigilance (head and neck erect, ears forward, actively looking around). Data were recorded every 10 minutes during 4-hour observation periods using instantaneous scan sampling (Altmann 1974). Each band of horses was observed 3 times before and 3 times after the simulated roundups, with one of the 3 observation periods each occurring in early morning (0700–1100 hours), mid-day (1100–1500 hours), and early evening (1500–1900 hours).

Reproduction

Adopted Groups. A veterinarian drew 10 ml of blood from each mare in the ADOPTED groups. These 10-ml samples were immediately frozen, and later in the laboratory blood serum was separated from plasma. Blood serum samples were then sent to the Veterinary School at the University of California-Davis for analysis. Mares were considered pregnant if estrogen blood serum levels were 7 ng/ml or greater and progesterone levels were 6 ng/ml or greater. In July of the year fol-

lowing roundups, each adopter of a mare was sent a questionnaire asking for foaling information. Non-respondents were contacted in a follow-up survey by telephone. A 100% response rate was achieved.

Simulated and Control Groups. Horses in the SIMULATED and CONTROL groups were observed about 10 months after the roundups. The number of mares and foals in each band was counted on 30 June and 1 July 1995 on the Idaho site and 1 July through 5 July 1996 on the Wyoming site.

Statistical Analysis

A completely random experimental design was used. Data from the Idaho and Wyoming sites were analyzed separately. All differences were considered significant at $P = 0.10$. For the behavioral data, a band of horses was the experimental unit. Individual horses within the bands were subsamples. Behavioral data were transformed using arcsine transformation to meet conditions for normality. Each behavioral variable (feeding, resting, traveling, aggression within the band, aggression between bands, and vigilance) was analyzed using analysis of covariance (Johnson and Wichern 1992). Observations collected before the simulated roundups were the covariables (e.g., vigilance before the simulated roundups was the covariable when analyzing vigilance after the simulated roundups). Data were then analyzed collectively using multivariate analyses. Data from the Wyoming site were analyzed using multivariate analysis of covariance (MANCOVA). Dependent variables in the MANCOVA were the behavioral variables vigilance, feeding, traveling, resting, and aggression between bands following the simulated roundup. The independent variable used was group (i.e., SIMULATED or CONTROL). Covariables used were vigilance, feeding, traveling, resting and aggression between bands before the simulated roundup. For the Idaho site there were too few degrees of freedom to allow the observations before the simulated roundup to be used as covariables, so these data were analyzed using multivariate analysis of variance. Aggression within the band was not used as a variable or covariable in the multivariate analyses because no agonistic encounters within bands were recorded.

The percentage of mares with live foals in the SIMULATED, CONTROL, and ADOPTED groups was compared with chi-square analysis (Johnson and Wichern 1992).

Table 1. Mean percentage ($\pm$ SE) of time that bands of feral horses spent in each behavioral activity following simulated roundups.

Activity	Idaho Site		Wyoming Site	
	Simulated	Control	Simulated	Control
	----- (%) -----			
Vigilance	12.9 $\pm$ 0.8a ¹	8.3 $\pm$ 0.4a	1.3 $\pm$ 0.7a	1.8 $\pm$ 0.9a
Feeding	58.5 $\pm$ 17.3a	71.4 $\pm$ 9.4a	46.9 $\pm$ 5.9a	38.0 $\pm$ 5.3a
Traveling	24.0 $\pm$ 17.0a	17.4 $\pm$ 10.1a	5.5 $\pm$ 1.7a	18.7 $\pm$ 3.8a
Resting	4.6 $\pm$ 3.0a	2.9 $\pm$ 2.0a	46.1 $\pm$ 6.4a	41.3 $\pm$ 0.1a
Aggression within bands	0.0 $\pm$ 0.0a	0.0 $\pm$ 0.0a	0.0 $\pm$ 0.0a	0.0 $\pm$ 0.0a
Aggression between bands	0.0 $\pm$ 0.0a	0.0 $\pm$ 0.0a	0.1 $\pm$ 0.0a	0.2 $\pm$ 0.0a

¹Within each study area, values within rows followed by the same lowercase letter are not different ($P > 0.10$).

Results

Horse Behavior

Individually, none of the behavioral variables differed between SIMULATED and CONTROL treatments in either study area (Table 1). Multivariate analyses also found no differences between the SIMULATED and CONTROL groups in either the Idaho study area ($P = 0.67$) or the Wyoming study area ($P = 0.58$).

Reproduction

The percentage of mares with live foals did not differ ($P > 0.10$) among the 3 treatments in either study area. By July 1995 in the Idaho study area, 29%, 31%, and 43% of the mares had live foals in the CONTROL, ADOPTED, and SIMULATED groups, respectively. In the Wyoming study area, by July 1996 the percentage of mares with live foals in the CONTROL, ADOPTED, and SIMULATED groups was 29%, 42%, and 48%, respectively.

At the time of roundup, 27 of 39 mares (69%) were pregnant in the Idaho ADOPTED group, and 18 of 34 mares (53%) were pregnant in the Wyoming ADOPTED group. Successful pregnancies numbered 12 of 27 (44%) and 14 of 18 (77%) for Idaho and Wyoming ADOPTED groups, respectively.

Discussion and Conclusions

Roundups did not increase agonistic behavior among feral horses, nor did roundups cause feral horses to reallocate their time spent in various daily activities. Feral horses in our study allocated their time similarly to undisturbed free-roaming horses in southern France (Duncan 1980), western Alberta (Salter and Hudson 1979), and central Wyoming (Crane et al. 1997). Feeding was the primary activity.

Domestic horses are usually able to maintain their pregnancies despite hor-

monal changes induced by stressful conditions (Traub-Dargatz et al. 1988, Baucus et al. 1990a, 1990b, Colburn et al. 1991, Ferlazzo et al. 1991, Wong et al. 1992). Similarly, in our study roundups did not decrease reproductive rates of feral horses. Foaling rates of the SIMULATED, CONTROL, and ADOPTED mares all compared favorably with a 10-year average of 35% documented within a feral horse herd in Montana (Garrott and Taylor 1990). The ADOPTED mares experienced the most perturbation but had an overall foaling rate of 33%.

Feral horses in our study apparently adapted easily to any stress caused by roundups. We found no evidence that roundups had deleterious effects on behavior or reproduction of feral horses.

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Rotational stocking and production of Italian ryegrass on Argentinean rangelands

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Abstract

The decreased carrying capacity of Argentinian Flooding Pampa rangelands through the reduction of density of C_3 grasses may be partially attributed to continuous stocking. The objective of this study was to evaluate the effectiveness of rotational vs. continuous stocking to improve winter forage production by incrementing the density of Italian ryegrass (*Lolium multiflorum* Lam.). Under rotational stocking, ryegrass seedlings established almost 2 months earlier in the fall and tiller density was 3-fold higher in winter than under continuous stocking. Aerial net primary productivity of C_3 grasses was approximately 2-fold greater under rotational compared with continuous stocking in the first and second years. This substantial increase in winter productivity supported almost 2-fold increase in stocking rate (from 0.6 to 1.0 AU ha⁻¹).

Key Words: winter forage production, temperate-humid rangeland, grazing systems, *Lolium multiflorum*.

The native temperate grasslands of the Argentinean Flooding Pampa occupies 5,000,000 ha in the eastern portion of central Argentina. This region is characterized by a mild, humid climate with low fertility soils (Soriano et al. 1991). This vast forage resource is utilized by cow-calf operations to produce yearlings that are weaned in autumn and fattened on cultivated pastures in the dryer Western Pampa. Frequent flooding prevents the replacement of native grasslands by cultivated pastures or crops. These grasslands support C_3 and C_4 grasses during the cool and warm seasons, respectively. Since the productivity of C_4 grasses is 3-fold greater than C_3 grasses (Sala et al. 1981), forage production follows a seasonal pattern. During fall and spring, C_3 and C_4 grasses vegetate coincidentally. Early in the fall, C_3 grasses start to grow while C_4 grasses end their growing period with a great quantity of accumulated biomass.

Continuous stocking of these grasslands by domestic herbivores since the last century has resulted in degradation (Deregibus and Cahupé 1983). Grazing progressively reduced C_3 grasses such as *Stipa neesiana* Trin, *Melica brasiliana* Arduinus and *Piptochaetium montevidense* Par. (León and Oosterheld, unpublished), which magnifies the seasonality of forage production.

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Resumen

La reducción de la receptividad de los pastizales naturales de la Pampa Deprimida (Argentina) como consecuencia de la disminución de la densidad de gramíneas C_3 ha sido atribuida al pastoreo continuo. El objetivo de este estudio fue evaluar la capacidad del pastoreo rotativo con respecto al continuo de incrementar la producción invernal de forraje mediante la promoción de ryegrass anual (*Lolium multiflorum* Lam.). Bajo pastoreo rotativo, las plántulas de ryegrass se establecieron dos meses más temprano en el otoño y la densidad de macollos fue 3 veces más alta en invierno que bajo pastoreo continuo. La productividad primaria neta aérea de las gramíneas C_3 fue aproximadamente 2 veces más alta bajo pastoreo controlado que bajo pastoreo continuo. Este significativo incremento en la productividad invernal permitió duplicar la carga animal (de 0.6 a 1 EV ha⁻¹).

This restriction may be overcome by incrementing the density of Italian ryegrass (*Lolium multiflorum* Lam.), an annual grass with high quality forage, native to the Mediterranean region. This species, together with wheat (*Triticum aestivum* L. em Tell.), has become widespread in Flooding Pampa grasslands since the beginning of this century.

Italian ryegrass seeds disperse late in spring and germinate the following autumn. During autumn and spring, competitive interactions among C_3 and C_4 grasses occur. The intensity is controlled by the availability of resources. Light quality, determined by canopy density, plays an important role in these interactions (Deregibus et al. 1983, Casal et al. 1985, 1986). Soil moisture and temperature allow the onset of the germination of Italian ryegrass seeds exposed on soil surface (Rodriguez et al. 1998), and if it is irradiated by direct sunlight, the germination is increased (Deregibus et al. 1994). This occurs whenever the canopy is intensively defoliated through high stocking rate at the end of the summer. As a consequence it would be possible to increase winter forage production through a grazing strategy designed to promote Italian ryegrass germination and seedling establishment (as shown in experiment I/II). The aim of this study was to evaluate the effectiveness of rotational vs. continuous stocking to improve winter Italian ryegrass production.

Methods and Materials

Study area

The study sites were located on 2 commercial farms of the Flooding Pampa region. Each farm consisted of approximately

Table 1. Monthly precipitation registered in the study site during the experimental period.

First period	Precipitation	Second period	Precipitation
	(mm)		(mm)
Mar 89	105	Mar 90	65
Apr 89	226	Apr 90	372
May 89	105	May 90	10
Jun 89	126	Jun 90	46
Jul 89	5	Jul 90	0
Aug 89	0	Aug 90	7
Sep 89	72	Sep 90	12
Oct 89	109	Oct 90	36
Nov 89	191	Nov 90	109
Dec 89	50	Dec 90	28
Jan 90	72	Jan 91	51
Feb 90	34	Feb 91	51
TOTAL	1,095	TOTAL	787

1,200 ha of native grasslands for cow-calf operations. Annual precipitation (average from 1958 to 1988) is 920 mm evenly distributed throughout the year. Monthly temperatures (average from 1958 to 1988) range from 6.8°C in July-August to 21.8°C in January. Because of the flat relief and the occurrence of a high water table, soils belong to the halo-hydromorphic complex and associations (INTA 1977). Studies were conducted in a hydromorphic community, where dominant C₄ grasses were *Paspalum paludivagum* (Hitchc. et Chase) Parodi and *Leersia hexandra* Sw.; dominant C₃ grasses were *Chaetotropis elongata* (H.B.K.) Björkm. and *Lolium multiflorum* Lam.; and dominant spring-summer dicots were *Alternanthera philoxeroides* (Mart.) Griseb., *Leontodon nudicaulis* L. and *Mentha pulegium* L.

During the experimental period (March 1989–February 1991) precipitation was recorded monthly (Table 1).

Research layouts

Two experiments were conducted simultaneously. Experiment I was located on a farm (35°30'S, 57°15'W) 160 km south of Buenos Aires. It was designed to study whether the increment of Italian ryegrass germination under rotational stocking led to an earlier and denser establishment of ryegrass than did continuous stocking. Experiment II was conducted on a farm (36°25'S, 59°05'W) 240 km southwest of Buenos Aires with the objective of determining whether rotational stocking was able to improve winter Italian ryegrass productivity compared to continuous stocking.

Grazing treatments

Grasslands of both farms had been continuously stocked at 0.65 cows ha⁻¹ by

Angus and Hereford cow/calf pairs for more than 25 years. The mean weight of cows was 420 kg, the breeding season occurred from November to January and calves were weaned during April at 6 to 8 months of age with an average weight of 170 kg. Because the physiological status of herds changed throughout the year, the stocking rate gradually decreased from 0.8 animal unit (AU) ha⁻¹ in March when cows weaned calves in the last month of lactation to 0.5 AU ha⁻¹ in winter (from May to July) after weaning of calves. Since March 1989, this grazing method was replaced by rotational stocking on both farms except for paddocks that were maintained under continuous stocking as a control treatment. Rotational stocking was performed by concentrating the cow-calf herd and moving it through a series of 10–12 paddocks with an average size of 45 ha. The annual average stocking rate was 1 AU ha⁻¹, varying between 1.3 AU ha⁻¹ in March to 0.8 AU ha⁻¹ in winter (from May to July). This represented an increase of 54% in the average stocking rate compared to continuous stocking. Occupation period in each paddock varied between 3 to 15 days and rest period between 25 to 90 days according to the growth rate of forage species. During the occupation period imposed in early autumn, nearly all the available biomass was removed to increase Italian ryegrass germination followed by about 90 days rest to allow seedling development. During the occupation periods imposed in spring only around 50% of the available biomass was grassed. This allowed the cattle to make the selection and the ryegrass plants to flower and seed.

Germination and establishment of Italian ryegrass.

In late summer (end of February), approximately 2 months after seed shed,

15 frames (10 x 20 cm) were placed randomly beneath the canopy in 50 ha paddocks that were either continuously or rotationally stocked (3 paddocks per treatment). To determine Italian ryegrass seed bank, a soil sample (20 x 10 x 5 cm) was taken next to each frame. These 15 samples were gathered to obtain a composite sample for each paddock and Italian ryegrass seeds were extracted by sieving. Immediately after this, a 4-day grazing period was implemented on rotationally stocked paddocks, during which cattle removed nearly all the available biomass. At the end of this period, canopy height inside each frame was measured. Italian ryegrass seedling and tiller densities were recorded after approximately 4, 45, 75, and 120 days from the end of the grazing period on rotationally stocked paddocks. Measurements on continuously stocked paddocks were performed on the same sampling dates. The experiment was performed in 1989 and repeated in 1990.

Regression analysis was performed between the seed bank and seedling density recorded during autumn in 1989 and 1990. To analyze the response curves of seedling density over time under different grazing treatments and years, a nonparametric split-plot analysis using the Kruskal-Wallis rank analysis to test the among-experimental-units source of variation and the Friedman statistic for the within-experimental-unit variation was utilized (Potvin and Lechowicz 1990). Data recorded in the first 3 sampling dates were analyzed as repeated measures. In the fourth sampling date, when Italian ryegrass plants were tillering, tiller density was recorded and compared using Tukey's test ($P < 0.05$).

C₃ and C₄ grass productivity

This experiment was performed using a single replicate per grazing treatment, rotationally or continuously stocking, in 40 and 60 ha paddocks respectively.

Total aboveground biomass was harvested from March 1989 to May 1991 before and after each occupation period in the rotationally stocked paddock. Thirty 0.25 m² areas were randomly located and clipped to ground level on each date. In the continuously stocked paddock, thirty, 1 m² cages were randomly placed to avoid the access of large herbivores. Biomass samples were obtained inside each 0.25 m² cage and outside by clipping to ground level whenever the rotationally stocked paddock was grazed. After each clipping, cages were moved to a new location. Those 30 samples were composited then

separated randomly in 3 new groups. These samples were hand separated into 6 components (green and standing dead material of C₃ and C₄ grasses, dicots and grasslikes), oven dried at 70°C and weighed. Within the C₃ component, dry matter of Italian ryegrass was weighed separately.

Above-ground net primary productivity (ANPP) of C₃ and C₄ grasses in rotationally stocked paddocks was estimated as the difference between the accumulated green biomass for each component at the end of each rest period and the remnant biomass left after the previous occupation period, divided by the number of days of the rest period. In the continuously stocked paddock, ANPP was similarly calculated as the difference between the green biomass accumulated within the cages and the existing biomass when the cages were placed, divided by the number of days of the period. To reduce the masking effect in the estimation of senescence in the productivity of each group of grasses, any daily increment of standing dead biomass for both compartments was added to the respective green productivity value (Sala et al. 1981). Annual production was estimated as the summation of the ANPP of each period multiplied by the duration of the corresponding period.

To analyze the overall pattern of ANPP of C₃ and C₄ grasses over time and the differences in their trends between grazing treatments, the multivariate procedure for repeated measures experiments proposed by Gurevitch and Chester (1986) and the correction method for unequally spaced measurements proposed by Robson (1959) were employed. This procedure was applied for the first (26 April 1989–10 December 1989) and the second (13 April 1990–7 January 1991) sampling period of C₃ grasses and for the first (12 July 1989–18 March 1989) and second (28 August 1990–25 March 1991) sampling period of C₄ grasses. A Tukey's test ($P < 0.05$) was applied to compare annual production of C₃ and C₄ grasses and total forage production.

Results and Discussion

Germination and establishment of Italian ryegrass.

The seed bank of Italian ryegrass recorded in late summer ranged from 13,500 to 31,800 seed m⁻² and showed a low association ($-0.23 > r > 0.35$) with seedling density recorded during autumn.

The pattern of Italian ryegrass seedling

Fig. 1. Pattern of ryegrass seedling appearance during autumn under continuous or rotational stocking.

density is plotted in Figure 1. As the repeated measures analysis showed that the factor "Year" and the interactions "Year x Grazing" and "Year x Time" were not significant (Table 2), each point in

Table 2. Non-parametric split-plot analysis of ryegrass seedling density over time under different grazing treatments and years.

Sources	Statistic	P
Among experimental units		
Year	0.0256	0.8728
Grazing	8.3077	0.0039
Year x Grazing	0.0476	0.8273
Within experimental units		
Time	8.101	0.0411
Year x Time	6.001	0.1116
Grazing x Time	0.606	0.8981

Figure 1 is the average of data recorded in the corresponding sampling dates of 1989 and 1990. The highly significant effect of factors "Grazing" and "Time" (Table 2) indicates that grazing treatments modified the pattern of Italian ryegrass seedling appearance. In rotationally stocked paddocks seedlings established earlier and in a greater abundance than in continuously stocked paddocks (Fig. 1). This was partially due to the promotion of germination obtained through the removal of the dense C₄ grass canopy to a 3.5 cm stubble height ($CV = 12\%$) during the grazing period performed in early autumn, because canopies shorter than 5 cm height allow sunlight illumination of Italian ryegrass seeds (Deregibus et al. 1994). Conversely in continuously stocked paddocks a canopy of 8.3 cm stubble height ($CV =$

73%) during early autumn shaded a great proportion of seeds. These seeds would germinate only when their period of light-sensitivity is over in late autumn (Rodriguez et al. 1998), therefore maximum germination was achieved 1 month later than in rotationally stocked paddocks (Fig. 1).

The earlier establishment of Italian ryegrass seedlings under rotational stocking may account for the large differences in ryegrass tiller density between grazing treatments found in early winter (end of June), 3,094 seedlings m⁻² in rotational stocking compared to 1,173 seedlings m⁻² in continuously stocking. Similar values of tiller density were previously reported (Jacobo et al. 1995). Those seedlings, established earlier under rotational stocking, developed under low competition without being disturbed by grazing during the following rest period (90 days). This occurred in the wet, temperate autumn season. Nevertheless, a long fall rest (135 days) without removal of the canopy is not enough to increase Italian ryegrass density (Hidalgo and Cahuepé 1991).

C₃ and C₄ grass productivity.

Grazing treatment resulted in different patterns of ANPP for C₃ grass (Fig. 2). Different linear trends were found for the first (26 April 1989–10 December 1989) and the second (13 April 1990–7 January 1991) sampling period (Table 3). The greater ANPP values obtained from April to September for rotational stocked paddock in 1989 and 1990 (Fig. 2) resulted in almost 2-fold greater annual production (1,377 and 1,135 kg dry matter ha⁻¹ in the first and second growing period respec-

Table 3. ANOVA's for linear to fifth degree contrasts generated from data of ANPP of C₃ and C₄ grasses under rotational or continuous stocking.

ANPP of C ₃ grasses during the first sampling period (26 Apr 89 – 10 Dec 89)													
Source	df	1 st order		2 nd order		3 rd order		4 th order		5 th order		Total	
		MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
Grand mean	1	382	0.58	134558	3.94	4146	0.24	2806	0.01	1354817	3.20		
Trat.	1	11516	17.56 *	66760	1.95	7489	4.70	18590	0.07	1095149	2.58	1317458	1.19
Error	4	656		34182		17616		252266		424004		1106985	
ANPP of C ₃ grasses during the second sampling period (13 Apr 90 – 7 Jan 91)													
Source	df	1 st order		2 nd order		3 rd order		4 th order		5 th order		Total	
		MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
Grand mean	1	23	0.00	588560	2.85	38939	0.89	43713	0.87	289945	1.03		
Trat.	1	93041	7.18 *	59	0.00	41897	0.96	44537	0.89	286730	1.02	48391	0.01
Error	4	12954		206446		43694		50093		281197		6503847	
ANPP of C ₄ grasses during the first sampling period (12 Jul 89 – 18 Mar 90)													
Source	df	1 st order		2 nd order		3 rd order		4 th order		5 th order		Total	
		MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
Grand mean	1	105790	3.54	275956	2.88	10098	0.40	11228	0.10	276905	0.04		
Trat.	1	28173	9.42 *	189949	1.98	30441	4.86	3754	0.03	2150509	0.31	436567	0.30
Error	4	2992		95843		25035		110595		7047056		1465951	
ANPP of C ₄ grasses during the second sampling period (28 Aug 90 – 25 Mar 91)													
Source	df	1 st order		2 nd order		3 rd order		4 th order		5 th order		Total	
		MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
Grand mean	1	3657	4.61	44961	2.25	1039	0.08	462	0.01	106682	0.10		
Trat.	1	12757	16.07 *	9655	0.48	13618	1.10	1814	0.04	409367	0.40	255242	0.20
Error	4	794		19994		12424		43428		1017524		1199511	

tively) compared to continuous stocking (610 and 731 kg DM ha⁻¹). Under both grazing treatments, Italian ryegrass was the major component of this group of grasses (avg. 77%). In view of these

results, we conclude that earlier seedling establishment and an increase in Italian ryegrass density obtained under rotational stocking, are the major determinants of the substantial increase in winter production.

This result shows that rotational stocking may overcome the major negative effect of continuous stocking in these grasslands.

Patterns of ANPP of C₄ grasses were different between grazing treatments (Fig. 3), as significantly different linear trends

Fig. 2. Aboveground net primary productivity of C_3 grasses under continuous or rotational stocking.

were found for the first (12 July 1989–18 March 1989) and the second (28 August 1990–25 March 1991) sampling period (Table 3). The lower values of ANPP observed under rotational stocking (Fig. 3) resulted in a decrease in annual production of C_4 grasses (2,127 and 1,088 kg DM ha⁻¹ in the first and second year) respective to continuous stocking (3,250 and 1,846 kg DM ha⁻¹). This decrease may be a consequence of the increasing competition from the greater population of Italian ryegrass during spring, when ryegrass biomass increases exponentially because of reproductive growth.

Because the increase of C_3 grass production was accompanied by a reduction in C_4 grass production under rotational stocking, total annual production of all grasses was similar among treatments in

the first (3,504 and 3,860 kg DM ha⁻¹) and in the second year (2,223 and 2,577 kg DM ha⁻¹). Therefore, grazing treatment had no relevant impact on overall ANPP, a well documented fact in grazing system literature (Van Poollen and Lacey 1979, Hart et al. 1989, O'Reagain and Turner 1992, Biondini and Manske 1996). The reduction of annual production under both grazing treatments in 1990 (Table 3) was due to the lower precipitation registered in that year (Table 1).

The distribution of total forage productivity (C_3 and C_4 grasses) was affected by rotational stocking as the changes in C_3 and C_4 grass production reduced seasonal variability in forage on offer. This contrasts with Heitschmidt et al. (1987) who reported no difference between rotational and continuous stocking in herbage distribution.

Fig. 3. Aboveground net primary productivity of C_4 grasses under continuous or rotational stocking.

Although the scope of this experiment must be considered very carefully due to limited replication, the results are useful because it is the first comparison of ANPP under rotational and continuous grazing in this region.

We conclude that the earlier establishment of Italian ryegrass and the consequent greater winter forage production explains the increase of stocking-rate supported under rotational stocking compared to continuous stocking (1.0 vs 0.6 average AU ha⁻¹). Under rotational stocking the period of low forage availability may be overcome earlier, so cows may lose less weight during winter supporting improved body condition prior to breeding.

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Flow processes in a rangeland catchment in California

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Abstract

Emerging hydrology-related issues in California grasslands have directed attention towards the need to understand subsurface water flow within a complex, dynamic system. Tensiometers and neutron probes evaluated the subsurface hydrology of a rangeland catchment. Hydrological processes within the catchment varied both in space and time. Spatial variability was evident along the vertical profile and between the catchment slopes. Temporal variability in processes coincided with the seasons (i.e., wet winter, dry summer, and spring). From a water-balance equation developed for the catchment, we determined that there was significant variability both spatial and temporal in the amount of soil moisture lost to evapotranspiration and deep seepage. During the 16 month monitoring period there was a total of 50 cm of rainfall that fell in the catchment of which 9–55 cm was lost to evaporation and 37–79 cm to deep seepage. A simple deduction of the losses (evaporation and deep seepage) from the input (rainfall) shows that all monitored locations had a substantial decrease in the amount of water that was stored in the soil profile.

Key Words: California rangelands, subsurface flow, water budget

A common omission in rangeland hydrology studies has been a rigorous treatment of the subsurface component of the hydrologic cycle. A need exists for the understanding of flow path dynamics (surface and subsurface) and the spatial and temporal variations in the hydrology of rangelands.

The movement of soil water in semiarid and arid climates has been investigated since at least 1949 when Maxey and Eakin attempted to measure ground water recharge in the desert basins of Nevada. By assuming basin recharge to equal basin discharge they concluded that in areas with less than 20 cm yr⁻¹ of precipitation, recharge was essentially negligible. Nixon and Lawless (1960) monitored the movement of soil moisture from rainfall up to depths of 6.0 m in a region 250 km northwest of Los Angeles, California. Using a neutron probe and a nest of sparsely distributed tensiometers (up to a depth of 1.0 m), they concluded that 31% of the rainfall migrated to the deep profile over a period of 240 days following the last rainfall event. Holmes and Colville (1970), while investigating the water balance of a grassland in southern Australia with lysimeters and neutron probes, determined that less than 10% of the 63 cm of precipitation recorded in 5 years recharged a low lying water table.

Resumen

Los problemas que están surgiendo en relación a la hidrología de los pastizales de California, se han enfocado hacia la necesidad de entender el flujo subterráneo del agua dentro de un sistema complejo y dinámico. En una área de captación del pastizal se evaluó la hidrología subterránea mediante el uso de tensiómetros y dispersores de neutrones. Los procesos hidrológicos dentro del área de captación variaron en espacio y tiempo. La variabilidad espacial fue evidente a lo largo del perfil vertical y entre las pendientes del área de captación. La variabilidad temporal de los procesos coincidió con las estaciones (esto es, invierno húmedo, verano y primavera secos). A partir de una ecuación del balance hídrico desarrollada para esta área de captación, determinamos que hubo una variabilidad temporal y espacial significativa en la cantidad de humedad del suelo perdida por evaporación y filtración. Durante los 16 meses del período de monitoreo la precipitación recibida en el área de captación fue de 50 cm de los cuales de 9–55 cm se perdieron por evapotranspiración y de 37–39 cm se perdieron por filtración. Un simple substracción de las pérdidas (evapotranspiración y filtración) de lo recibido (lluvia) muestra que todas las localidades monitoreadas tuvieron un decremento un substancial en la cantidad de agua que fue almacenada en el perfil del suelo.

In recent years both physical and chemical methods have been used to estimate recharge in arid and semiarid regions. Physical methods have included both direct and indirect measurements. While direct measurements of deep seepage have mainly involved the use of lysimeters (Allen et al. 1991, Gee et al. 1993), indirect physical methods have included the use of soil water balances (e.g. Rushton and Ward 1979), the zero flux plane method (Wellings 1984), and estimates of water fluxes from solutions to either Darcy's law or Richards' equation (Sophocleous and Perry 1985, Stephens and Knowlton 1986). Johnston (1987) and Sharma and Huges (1985) demonstrated the considerable variation in the rates of local recharge over a scale of a few meters in many soil types. Assessment of this spatial variability in recharge has been attempted with frequency-domain electromagnetic (EM) or transient electromagnetic methods (Allison et al. 1994). Table 1 summarizes some estimates of deep seepage for semiarid regions.

This paper presents results from the investigation of the subsurface hydrology of a rangeland watershed in California. The central thesis presented is that seasonal changes in the hydrologic cycle cause important variations in the flow dynamics in rangeland catchments in California. In this paper, observations of soil moisture content and associated energy levels are used to develop a water balance for a catchment dominated by annual grasses.

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Table 1. Estimates of deep seepage in semi-arid regions. Source Stephans et al. 1986.

Author	Method	Location	Estimate recharge rate
Enfield et al. 1973	Soil water potential	Washington state (south central)	1 cm yr ⁻¹
Klute et al. 1972	Neutron moisture logging	High Plains, Colorado	0 cm yr ⁻¹
Dincer et al. 1974	Tritium tracer	Saudi Arabia	25% annual precipitation
Allison et al. 1985	Chloride concentration	South Australia	1.4 cm yr ⁻¹
Meyboom 1966	Water level hydrographs	Saskatchewan, Canada	7.5% annual precipitation
Boyle and Salem 1979	Temperature profiles	Illinois (north west)	7.8–31 cm yr ⁻¹
Maxey and Eakin 1949	Steady State flow	Nevada	0 cm yr ⁻¹
Watson et al. 1976	Steady State flow	Nevada	3.4% annual precipitation
Sammis et al. 1982	Hydraulic gradients	Phoenix, Arizona	18 cm yr ⁻¹
Sammis et al. 1982	Temperature profiles	Phoenix, Arizona	9 cm yr ⁻¹
Sammis et al. 1982	Tritium tracer	Phoenix, Arizona	40 cm yr ⁻¹
Stephen and Knowlton 1986	Hydraulic gradients	Socorro, New Mexico	4 cm yr ⁻¹

Materials and Methods

Study Site

Soil water potential and content was measured within a watershed in north-central California over a period of 16 months. The data was used to identify processes influencing the hydrology of the catchment, and to determine quantitatively, the moisture status along vertical soil profiles at specific locations.

The watershed is located within the Russell Tree Farm, a 115-hectare (ha) research station located, in Contra Costa County (Lat. 37° 54' N, Long 122° 03' W), California (Fig. 1). The amphitheater-shaped catchment has an area of 20 ha,

with elevations ranging from 230 m above mean sea level (msl) in the valley bottom to nearly 360 m above msl on the ridge top. The slopes range from 2 to 75%, and the catchment contains at least 2 perennial springs. Annual grasses dominate the vegetation cover in the catchment. Sporadic clusters of predominantly coyote bush shrubs (*Baccharis pilularis*, D.C.) are found scattered throughout the catchment. The other major vegetation type is the California oak, which is restricted to the higher elevations close to the ridge and is dominated by coast live oak (*Quercus agrifolia*, Nee). The Mediterranean climate of the region results in warm to hot summers and winters that are relatively mild. Precipitation occurs as rainfall main-

ly in the winter months. While most climatic parameters remain relatively constant from year to year, precipitation in the region shows variability both within and between seasons (Fig. 2).

Thirteen sites were located along the slopes for measurement of soil moisture content and potentials. These sites were selected to represent the 3 dominant vegetation types found in the catchment (annual grasses, baccharis shrubs, and oak trees) and 3 broad elevations viz. low, medium, and high.

Water content of soils was determined by the neutron-probe method (Gardner 1986). A Campbell Pacific Nuclear Model 503 with a 50 millicurie americium-beryllium source neutron probe was used. The probe was calibrated by a gravimetric analysis that utilized in situ samples from the access tube holes.

Thirteen neutron probe access tubes (Sites 1–13) were installed in February 1993. In most cases, the depth of augering was limited by bedrock. The deeper profiles monitored ranged from 3.75 to 5.70 m in depth and included 5 sites (6–9, and 13) located on the southeast corner of the catchment. Of the 7 shallow profiles, Sites 1 and 2 extended to 2.00 m, while the remaining were restricted to 1.20-m depths. During installation of the access tubes for the neutron probe, a 0.05-m diameter hole was augered, into which a 0.04-m inner diameter, schedule 40 PVC pipe was inserted. The PVC pipe in each hole extended 0.15 m above the ground surface. Bentonite clay was poured around the PVC pipe, 0.10 m below the surface to prevent surface run-off water from flowing down the sides of the tube.

Soil water potential along the catchment slopes was determined using tensiometers. Thirteen nests of tensiometers (Sites 1–13) were installed at a distance of about 1.0-m from the neutron probe access tubes (Fig.

Fig 1. Location of the Russell Tree Farm with monitored sites.

Fig. 2. (a) Annual rainfall at Walnut Creek located 10 Km east of Russell Tree Farm. (b) Variability in monthly rainfall 10 Km east of study site.

3a). A 0.10-m diameter soil auger was used to create the hole into which tensiometers were inserted. The soil removed during augering was collected in 0.15-m sections and stored in sealed plastic bags. The area around the ceramic tip of each tensiometer was back-filled with native soil removed from that particular depth.

This soil was repacked to a density similar to that of the undisturbed native soil and filled to approximately 0.10 m above the center of the ceramic tip (The original packing density was achieved by reintroducing the augered soil from the 0.15 m sections back into the same zone). Above this backfill, bentonite (as a mixture of

powder and pellets) was packed to a height of 0.10 m and wetted to provide a vertical hydraulic seal. Above this seal native soil was packed to the original density. Water was injected into the tensiometers through narrow diameter tubing which extended down to the ceramic cup.

At each site, tensiometers were installed in nests such that the ceramic tips were located at approximately 0.25-m intervals down to a depth of 1.0 m from the surface. Between 1.0 and 2.0 m, tensiometers were installed at 0.5 m intervals, and at greater depths the interval was increased to approximately 1.0 m (Fig. 3b). Of the 13 locations, 6 had tensiometers located at depths greater than 3.0 m (Sites 6–9, 12, and 13). The shallowest nest, Site 3, extended to a depth of 1.0 m, and the deepest, Site 6, extended to a depth of 6.0 m.

Hydraulic head measurements were determined as the sum of gauge pressure at the ceramic tip and the elevation of the ceramic tip relative to the ground surface at the nest. Thus, the hydraulic head measurements in each nest are referenced to the local elevation of the nest. Gauge pressure readings were taken using a portable pressure transducer, commercially referred to as the Tensimeter (Soil Measurement Systems, Tucson, Ariz., 2 Marthaler et al. 1983). Water potential readings were taken at weekly intervals during the winter and monthly intervals late in the summer.

Water balance estimates

Parameters used to evaluate the water balance of a location estimate how much usable energy and water are available (for evaporation and transpiration), how much evaporation demand is met by available water, and how much water is usable excess. In its simplest form, the equation describing annual conservation of water mass for a unit watershed can be written as:

$$P - Q - E = S \quad (1)$$

Where P is the average annual precipitation, Q is the average annual discharge, E is the annual evapotranspiration, and S is the change in the amount of moisture stored. The signs indicate whether water is entering (positive) or leaving (negative) the system.

If an average is taken over many years of record, then the S term can be assumed to equal zero, and Equation [1] becomes (Freeze and Cherry 1979):

$$P = Q + E \quad (2)$$

The terms on the right in Eq. [1] can be modified to various levels of detail, depending on the important characteristics of a region or on the available database.

Fig. 3. Schematic of monitoring station at Site 6: (a) the location of nested tensiometers with respect to the neutron probe access tube and (b) vertical extent of tensiometer and neutron probe measurements.

For example, Eagleson (1978) presented the water-balance equation for a unit watershed as:

$$P_A = Q_{SA} + Q_{GA} + E_{TA} + S_S + S_g \quad (3)$$

Where P_A is the annual (seasonal) precipitation, Q_{SA} is the annual (seasonal) surface runoff, Q_{GA} is the annual (seasonal) sub-surface flow through the watershed, E_{TA} is the annual (seasonal) total evapotranspiration, S_S is the annual (seasonal) change in surface storage, and S_g is the annual (seasonal) change in soil moisture and groundwater storage.

For rangeland catchments in central California, large annual fluctuations in precipitation (Fig. 2a) results in large variability in the amount annual of recharge, which in turn results in large changes in the amount of moisture stored in the soil profile (S_g). In the absence of surface runoff (Q_{SA}) and surface storage (S_S) on catchment slopes, Eq. [3] can be re-written for these rangelands as:

$$P_A = Q_{GA} + E_{TA} + S_g \quad (4)$$

In this study the moisture status for locations within the catchment was determined using a modified version of Eq.[1] where the dynamic water content for a vertical soil profile was evaluated using the equation:

$$P_p = S_E + S_Q \quad (5)$$

Here water infiltrating the surface (P_p) was partitioned as surface evapotranspiration or deep seepage based on the direction flow gradients as indicated by the position of a zero-flux boundary (Fig. 4). (The zero-flux boundary is determined along the vertical profile as the location where hydraulic gradients are directed, in opposite directions, away from the point). All changes in moisture content (S_p) above the zero-flux boundary were assigned to ET (S_E), while all losses below the boundary were assigned to deep seepage (S_Q).

Since soil moisture content was monitored at monthly intervals and hydraulic gradients were measured at weekly intervals, the monthly changes in moisture content were proportioned according to the length of time the gradient direction was observed. For example, if the change in moisture content at a given depth, over a single month, was 10.0 cm and hydraulic gradients were positive for 3 of the 4 weeks, it was assumed that 7.5 cm of the moisture was lost to deep seepage, while 2.5 cm was released as ET to the surface. From data collected on moisture content and associated potentials in the soils the amount of moisture contributing to deep

Fig. 4. Migration of the zero-flux boundary in the soil profile at Sites 9 and 13. Vertical arrows indicate the direction of the hydraulic gradient.

seepage was estimated by assuming that positive flow gradients lying below the zero flux plane directed flow into the deep profile. For example, in Site 9 the zero flux plane migrated to a depth of 5.0 m over a period of 7 months while in Site 13 it was located 3.0 m below the ground surface (Fig. 4).

Observations

The data collected includes measurements of soil matric potential from 13 sites and water content from 12 sites within the slopes, and from 16 locations along the catchment valley. Site 12 was not included in the analysis because of installation errors in the neutron access tube. Monitoring began in April 1993, following a winter during which the recorded rainfall in the region was the highest in at least the past 7 years (324 mm), and continued through September 1994, a year which was much drier (Fig. 2).

Recharge events in the catchment

Effectively saturated conditions close to the surface were evident in the tensiometer measurements when monitoring began in April 1993, and recharge along the vertical profile of the monitored sites was indicated by positive hydraulic gradients (Table 2). Following the rains in early April there was a 2-week precipitation free period when tensiometers close to the surface began to record decreases in hydraulic potentials. At depths below 0.2 m from the surface, potentials also began to decrease slower such that by the second week of April hydraulic gradients in the top 0.5 m

of the profile at all sites were directed towards the surface. A small rainfall event (12 mm) during the third week of April, which was spread over a period of 48 hours, did not change this trend. By the end of April, most of the sites were losing water to the surface from the top 0.5 m, while deeper in the soil, flow was directed into the profile.

During the winter of 1993–94, the first rainfall (12 mm) was recorded in mid-October. This event was not detected as soil moisture changes by any of the tensiometers located in the catchment. The second event (20 mm) occurred approximately 1 month later was insufficient to bring potentials at the near surface within functioning range of the tensiometers. At the end of November, 2 storms of 42 mm total precipitation briefly increased hydraulic potentials, but in the next 10 days these values again decreased below the tensiometer range. Surface water recharge deep enough to penetrate to depths below 0.20 m was observed following 5 rainfall clusters which occurred between December and April. The first recharge event was initiated after 74 mm of precipitation over a period of 6 days in mid-December. The second event occurred almost 45 days later following a 6-day period in late January when 66 mm of rain occurred. A week later, 40 mm of rain, which occurred over 3 days, provided sufficient moisture for the third recharge event. The largest rainfall of the season (90 mm), recorded over a 5 day period in late February resulted in the fourth recharge event. During this period, profiles 1.5 m below the surface were close to

Table 2. Hydraulic gradients measured along the vertical profile of 3 sites. Bold arrows indicate direction of flow. Clear arrow indicate hydrostatic conditions.

Site 6				
Depth (m)	4/1/93	7/21/93	2/25/94	7/18/94
-0.20	0.59 ↓	0.00 ⇄	0.91 ↓	0.00 ⇄
-0.51	0.09 ↓	0.00 ⇄	0.77 ↓	0.00 ⇄
-0.98	1.31 ↓	0.00 ⇄	1.04 ↓	0.00 ⇄
-1.32	1.72 ↓	-4.29 ↑	1.21 ↓	-3.05 ↑
-1.99	0.52 ↓	-1.35 ↑	10.78 ↓	-0.10 ↑
-2.48	1.58 ↓	-7.70 ↑	-1.72 ↑	-1.67 ↑
-2.99	1.34 ↓	0.94 ↓	-2.25 ↑	-3.65 ↑
-3.68	0.20 ↓	0.81 ↓	0.58 ↓	-0.71 ↑
-4.95	1.39 ↓	0.19 ↓	1.03 ↓	2.08 ↓
-5.90				
Site 9				
-0.24	4.42 ↓	6.46 ↓	1.59 ↓	0.00 ⇄
-0.42	1.50 ↓	-2.58 ↑	0.78 ↓	0.00 ⇄
-0.76	0.04 ↓	0.22 ↓	1.90 ↓	0.00 ⇄
-0.99	0.55 ↓	-6.23 ↑	0.94 ↓	-5.73 ↑
-1.54	0.84 ↓	1.57 ↓	12.69 ↓	-2.76 ↑
-2.06	1.21 ↓	1.33 ↓	1.09 ↓	2.68 ↓
-2.55	2.47 ↓	1.26 ↓	-0.28 ↑	2.70 ↓
-2.87	0.35 ↓	0.40 ↓	-2.21 ↑	-3.67 ↑
-3.45	1.72 ↓	2.32 ↓	-0.26 ↑	-2.70 ↑
-3.86	0.87 ↓	-0.06 ↑	-2.49 ↑	-0.06 ↑
-4.84				
Site 13				
-0.22	1.22 ↓	0.00 ⇄	0.94 ↓	0.00 ⇄
-0.51	1.57 ↓	-12.94 ↑	1.76 ↓	0.00 ⇄
-0.79	1.07 ↓	-6.42 ↑	1.07 ↓	-14.87 ↑
-1.03	-1.11 ↑	3.63 ↓	0.85 ↓	1.86 ↓
-1.51	3.24 ↓	-5.56 ↑	2.64 ↓	0.18 ↓
-2.02	0.92 ↓	0.70 ↓	2.93 ↓	0.56 ↓
-2.53	1.04 ↓	0.19 ↓	-1.12 ↑	0.14 ↓
-3.01	0.20 ↓	1.12 ↓	2.79 ↓	-1.12 ↑
-3.53	0.79 ↓	-0.08 ↑	0.52 ↓	-4.33 ↑
-3.87	0.41 ↓	-0.05 ↑	0.09 ↓	-0.73 ↑
-4.64				

saturation, the deepest observed during the entire wet season. The final recharge occurred 2 months later when at the end of April a cluster of rainfall events provided 45 mm of precipitation.

Thus during the wet season which extended over 206 days, there were only 5 significant periods (totaling 21 days, and 71% of the season's precipitation) when moisture deposited at the soil surface migrated below the top 0.50 m of the soil profile. Each of these periods had more than 40 mm of rainfall deposited. In 4 of these events, groundwater recharge (as detected in the magnitude and direction of hydraulic gradients) significantly altered the moisture profile of the top 1.0 m of the soil. During a single cluster of events in late February, 20% of the seasons' rainfall was recorded, near saturated profiles were detected up to 1.5-m depths. However at greater depths the changes in potential values were small during the entire winter season.

Hydrologic Processes on Catchments Slopes.

The vertical soil profiles of the 12 monitored sites showed a sinusoidal pattern of wetting and drying (Fig. 5). Early in May 1993 all the sites recorded high amounts of moisture at all depths (~0.15 to 0.35 cm³ cm⁻³). Over the next month all the shallow profiles recorded losses in moisture content, and in the ensuing months moisture losses from the profiles continued, but at decreasing rates. With the start of the winter rains, the profiles began to moisten with increases in wetness occurring during the first wet month (i.e. December 1993). In the next 2 months, when the bulk of the season's rain fell, small increases in soil moisture were detected in all profiles, but these were much smaller than those observed early in the winter (~0.20 to 0.25 cm³ cm⁻³). Shortly after the wet season ended in early March 1994, the shallow profiles began to record losses in moisture. The largest decreases were observed in April, and smaller reductions occurred in the following precipitation free months. This drying pattern was similar to that of the previous year with the exception that the drying process in 1994 began almost 60 Julian days earlier (Fig. 5).

At each of the monitored sites, the total moisture lost from the near surface profile during the summer of 1993 was replenished during the following winter. Similar amounts of moisture were then lost from the profiles by the end of August 1994. In essence, these profiles reached a fixed

Fig. 5. Changes in volumetric moisture content at various depths along the vertical profiles of (a) Site 6 and (b) Site 8.

upper and lower limit in storing soil moisture towards the end of each season irrespective of the amount of rainfall received the previous wet season. At depths greater than 2.0 m, the amount and depth to which changes in volumetric moisture content occurred varied considerably with each profile showing a distinct response to seasonal changes in precipitation. Large losses in moisture, following a wet winter (1992–93), extended beyond the 2.0-m depth in 4 of the 5 deep sites. The single exception, Site 7, recorded losses in moisture, which were largely restricted to the top 1.9 m of the profile.

There were 2 distinct patterns of drying observed in the 5 deep profiles. At Sites 6, 7, and 8 drying began at the near surface zones early in the summer and migrated downwards as the summer progressed (Fig. 6a). In this downward migration, the near surface zones reached a critical moisture level early in the summer after which drying was observed lower in the profile.

In the subsequent months this pattern was repeated such that the center of the drying zone was located at a depth of 3.3 m in Site 6 and 2.0 m in Site 8. This 'step-wise' drying pattern is significantly different from that observed in Site 9 and 13, where the drying was relatively uniform along the entire profile (Fig. 6b).

During the following winter (1993–1994), the depths to which the deep profiles wetted were less than that observed at the end of the previous winter rains (Fig. 7). Except for Site 13, in which the wetting front migrated to 2.4 m, wetting in the remaining sites was restricted to depths less than 2.0 m. Immediately following the last winter rains in March 1994, all profiles began to lose moisture along the entire wetted length. Unlike the previous summer, where there was 'step-wise' drying in some profiles, moisture losses were recorded at near equal rates at all the wetted lengths. In the deeper sections, which were not wetted by the winter rains, small decreases in moisture content continued to occur during the summer. For the first 6 dry months the loss in moisture in all the sites was much greater than the increases recorded during the wet period.

Comparing the moisture levels of different sampling dates with those observed in early May 1993, provides a measure of the 'relative wetness' within the catchment (Table 3). The relative wetness recorded in the deep profiles during May 1993 was never exceeded and only 1 profile (7N) registered levels similar to those at the start of the recording period. The peak in

Fig. 6. Patterns of drying in 2 deep sites (6 and 9) during the summer of 1993. (a) At Site 6 drying was stepwise while (b) at Site 9 drying was relatively uniform along the entire vertical soil profile.

Table 3. Percentage of moisture present relative to early March 1993 along the vertical profile of monitored sites.

Site	1 May 1993	1 Jul. 1993	1 Sept.	1 Nov. 1993	1 Jan. 1993	1 Mar. 1994	1 May 1994	1 Aug. 1994
	----- (%) -----							
1*	100	82	79	77	95	102	91	82
2*	100	83	74	72	86	98	85	67
3*	100	70	67	64	101	108	80	57
4*	100	67	65	62	86	108	84	61
5*	100	78	74	71	90	100	85	70
10*	100	68	59	55	92	110	67	53
11*	100	75	73	69	86	109	92	65
6	100	85	73	71	77	84	80	69
7	100	88	88	88	97	100	93	83
8	100	92	89	83	88	89	82	77
9	100	91	85	79	81	88	83	75
13	100	88	86	84	86	92	84	75

*Shallow Profiles

moisture levels was in early March 1994, when the soil wetness ranged between 84–100% of the May 1993, values. The moisture content at all sites early in August 1994 had reached levels lower than those recorded prior to the start of the wet season in November 1993 indicating that the catchment was already drier than it had ever been in the previous year.

Spatial variability in total soil water content was detected both among and within all 12 profiles. Of the deep profiles monitored, Site 7 consistently contained the most water per unit volume of soil while Site 8 was always the driest (Fig. 8). Throughout the monitoring period the

difference in wetness between these 2 sites remained fairly constant. In the other 3 deep sites the relative difference in wetness, however, continued to change at different times of year. Among the shallow profiles the pattern of changes in moisture content were similar to that observed for the deeper profiles.

Early in the summer of 1993, when steady vertical flow in the profile (which originated as surface infiltration) ceased, the contribution to deep seepage was through the draining of the soil profile. This draining process began close to the surface and as the summer progressed, migrated deeper into the profile. As the

near-surface profiles began to dry as the summer progressed, a zero-flux boundary migrated into the deeper zones (Fig. 5). The zone above the boundary had a net negative gradient, resulting in moisture moving towards the surface while the profile below the boundary continued to release moisture to deep seepage.

Within and among the 3 zones dominated by transpiration from grasses and surface evaporation, transpiration from shrubs and trees, and deep seepage, respectively, continuous fluctuations occurred in the magnitude and directions of hydraulic gradients, resulting in the continuous redistribution of moisture in

Fig. 7. Extent of migration of the wetting front in 4 sites (6, 7, 9, and 13) following a wet winter in 1993 and a significantly drier winter in 1994.

Fig. 8. Monthly changes in soil moisture content along the vertical profile of Sites 6, 7, 8, 9, and 13.

the soil (Table 2). Early in the summer, large negative gradients close to the surface resulted in the movement of water from below the grass root zone towards the surface. However, as the annual grasses dried and mulch covered the surface, little of the soil moisture was lost to the atmosphere. A significant portion of soil moisture was relocated within the grass root

zones, where the soil was drier from transpiration losses that occurred before the grasses died. As this moisture was being redistributed, the continuous transpiration losses in the shrub/tree root zone allowed moisture from the near-surface profile and the deeper profiles to migrate toward this dry zone. This shifting of energy gradients in the profile resulted in a continuous

movement of soil moisture between the surface and shrub/tree root zone. Within the shallow profile sites (where the bedrock lies between 1.0 and 2.0 m from the surface) there was a different hydrologic dynamic, with moisture migrating to the deeper profile in the winter. As the winter ended, the soil began to dry from gravitation drainage and from losses to ET. Once the grasses died, moisture losses were reduced, and the subsurface profile approaches a near-hydrostatic condition. Toward the end of the summer, most movement of soil water in the slopes was restricted to the deep profiles. In the shallower sections of the deep profile, the roots of transpiring trees and shrubs drew water from the soil. In the deeper profile moisture, continued to be lost to deep seepage.

Results

Parameters used in determining the site-specific water balance for Site 9 are summarized in Figure 9. Similar parameters were used in the other sites for which the dynamic moisture content was evaluated. In all 6 sites, for a brief period between January and February 1994, the amount of precipitation recorded was greater than the calculated ET and seepage losses during

Table 4. Changes in moisture content at 6 locations resulting from precipitation, ET and deep seepage.

	May-July '93	Aug-Oct '93	Nov '93-Jan '94	Feb-Apr '94	May-July '94	Cummulative
<i>Site 2N</i>	(cm)					
Rainfall	0	1	21	25	3	50
Change water content	-13	-2	9	-3	-9	-17
ET loss	-13	-2	0	-7	-9	-31
Deep seepage loss	0	-1	-12	-21	-3	-37
<i>Site 6N</i>						
Rainfall	0	1	21	25	3	50
Change water content	-33	-12	12	1	-17	-50
ET loss	-22	-10	0	-4	-20	-55
Deep seepage loss	-12	-4	-9	-20	-1	-45
<i>Site 7N</i>						
Rainfall	0	1	21	25	3	50
Change water content	-17	-1	0	-11	-14	-43
ET loss	-10	-1	0	-6	-15	-32
Deep seepage loss	-7	-1	-21	-30	-3	-62
<i>Site 8N</i>						
Rainfall	0	1	21	25	3	50
Change water content	-6	-8	4	-5	-4	-20
ET loss	-5	-3	0	-6	-4	-18
Deep seepage loss	-2	-6	-16	-24	-3	-51
<i>Site 9N</i>						
Rainfall	0	1	21	25	3	50
Change water content	-16	-15	5	1	-12	-37
ET loss	-3	-1	0	-1	-3	-8
Deep seepage loss	-13	-15	-15	-23	-13	-79
<i>Site 13N</i>						
Rainfall	0	1	21	25	3	50
Change water content	-15	-3	4	-5	-10	-28
ET loss	-8	-2	-1	-7	-10	-28
Deep seepage loss	-8	-2	-15	-23	-3	-51

Fig. 9. Example of parameters used to calculate the (a) water balance at and (b) cumulative water losses and gains (for Site 9).

Fig. 10. a. Cumulative moisture losses to ET at Sites 2, 6, 7, 8, 9, and 13. b. Cumulative moisture losses to seepage at Sites 2, 6, 7, 8, 9, and 13.

the same period. For the remaining 14-month period, the monthly net moisture losses were much greater than net gains in all the sites. However, among sites where the monthly precipitation was assumed to be the same (since they were located in the same catchment), the monthly losses to ET and seepage varied significantly (Table 4).

At Site 2, ET losses were large (13 cm) early in the summer of 1993, and then gradually ceased over the next 6 months before increasing again in February 1994 until the end of the monitoring period (Fig. 10a). Deep seepage was detected with the start of the winter rains in 1994, and observed to continue until the end of April 1994 (Fig. 10b), during which time 33 cm of water was lost from this vertical profile. By late July 1994, there was a cumulative loss of 68 cm of water to ET and deep seepage at this location.

In the remaining 5 sites, deep seepage losses were observed throughout the monitoring period. In 4 of these sites (6, 7, 8, and 13) the seepage losses were also largest (between 20–30 cm) immediately after the wet season in 1994. At Site 9, except for a brief period in November

1993, deep seepage continued at a steady rate throughout the monitoring period. By the end July 1994, the largest amount of moisture lost to deep seepage was at Site 9 (79 cm) and the least was at Site 2 (37 cm). The pattern of ET losses from these 5 sites was similar to that observed at Site 2. The largest ET losses were recorded in Site 2 (65 cm) and the least were at Site 9 (<10 cm), with the remaining sites showing losses ranging between 30 and 50 cm.

Conclusions

Solutions to a simple water-balance equation, comprising of precipitation, evapotranspiration, runoff, and storage as the key parameters, suggest that there was significant variability both spatial and temporal in the amount of soil moisture lost to evapotranspiration and deep seepage. During the 16-month monitoring period there was a total of 50 cm of rainfall that fell in the catchment. Measurements of water potential and soil moisture content at various locations within the catchment suggest that during this time losses to evaporation ranged from 9 to 55 cm while those to deep seepage ranged between 37 and 79 cm. A simple deduc-

tion of the losses (evaporation and deep seepage) from the input (rainfall) shows that all monitored locations had a substantial decrease in the amount of water that was stored in the soil profile.

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Comparison of 3 techniques for monitoring use of western wheatgrass

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Abstract

Forage use data can help rangeland and wildlife managers make informed decisions. However, managers need to know if forage use techniques that are commonly used to estimate ungulate herbivory under field conditions produce comparable results. The objective of this 2-year study was to directly compare forage use measurements obtained via the paired-plot method and 2 height-weight methods (using on-site height-weight curves and the pre-established United States Forest Service height-weight gauge). In June, July, and October of 1997 and 1998, we measured forage use of western wheatgrass (*Pascopyrum smithii* Rydb.) by cattle (*Bos taurus* L.) and wild ungulates, mainly elk (*Cervus elaphus* L.). On-site height-weight curves and the USFS gauge consistently produced lower estimates (overall means = 8 and 7%, respectively) than the paired-plot method (overall mean = 31%). Height-weight estimates did not differ ($P > 0.05$) when calculated with either on-site curves or the USFS gauge. Within sampling areas, paired-plot estimates were relatively more precise (mean CV = 63%) than on-site curves (mean CV = 238%) or the USFS gauge (mean CV = 271%). Selective grazing likely contributed to higher CVs for height-weight techniques. Our findings are important for rangeland and wildlife managers because the forage monitoring technique they use may influence the results obtained and, consequently, grazing management and wildlife harvest decisions. Managers should ensure that chosen monitoring techniques provide an appropriate evaluation of management goals and objectives.

Key Words: Arizona, height-weight, herbivory, paired-plot, stubble height

As demands upon rangeland resources increase, managers must monitor rangeland uses and resource responses to satisfy a growing number and variety of stakeholders. Methods such as the paired-plot and height-weight techniques are commonly used for monitoring forage use on rangelands (Stoddart et al. 1975, Bonham 1989). Forage use estimates provide neither complete nor infallible information on herbivore activities or resource impacts (Cook 1962, Sharp et al. 1994, Laycock 1998,

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Resumen

Los datos acerca de la utilización del forraje pueden ayudar a los manejadores de pastizales y de fauna silvestre a tomar decisiones bien fundamentadas. Sin embargo, los manejadores necesitan saber si las técnicas que comúnmente se utilizan en campo para estimar el uso de forraje de los ungulados producen resultados comparables. El objetivo de este estudio de 2 años fue comparar directamente las medidas de uso de forraje obtenidas mediante el método de parcelas apareadas y 2 métodos de altura-peso (usando curvas de altura-peso y el medidor altura peso preestablecido por el Servicio Forestal de Estados Unidos (USFS)). En Junio, Julio y Octubre de 1997 y 1998 medimos el uso del forraje del "Western wheatgrass" (*Pascopyrum smithii* Rydb.) por el ganado (*Bos taurus* L.) y por ungulados silvestres, principalmente alce, (*Cervus elaphus* L.). Las curvas de altura-peso obtenidas en el sitio y el medidor de altura-peso del USFS produjeron estimaciones consistentemente mas bajas (media general = 8 y 7% respectivamente) que el método de parcelas apareadas (media general = 31%). Las estimaciones de altura-peso no difirieron ($P > 0.05$) cuando se calcularon por las curvas de altura-peso en el sitio o por el medidor del USFS. Dentro de las áreas de muestreo, las estimaciones del método de parcelas apareadas fueron relativamente mas precisas (CV de la media = 63%) que las de las curvas en el sitio (CV de la media = 238%) o que las del medidor del USFS (CV de la media = 271%). El apacentamiento selectivo probablemente contribuyó para obtener CV altos en los métodos de altura-peso. Nuestros hallazgos son importantes para los manejadores de pastizales y fauna silvestre porque la técnica de monitoreo de utilización de forraje que ellos usan puede influir en los resultados obtenidos y, consecuentemente, el manejo del apacentamiento y de las decisiones de cosecha de la fauna silvestre. Los manejadores deben asegurarse de escoger la técnica de monitoreo que provee una evaluación apropiada para las metas y objetivos de manejo.

Rasmussen 1998). Forage palatability, relative abundance of forage species, plant growth and morphology, and interspecific differences in foraging behavior may confound forage use estimates obtained by different monitoring techniques (Rechenthin 1956, Cook 1962, Hanley 1982, Zhang and Romo 1995). With so many variables influencing the efficacy of forage monitoring, managers need to know if techniques commonly used to estimate ungulate herbivory under field conditions produce comparable results (Smith and Ruyle 1997).

The paired-plot technique uses protected plots (small grazing exclosures), each paired with a similar unprotected (grazed) plot

via ocular estimate. The ratios of unprotected and protected clipped dry forage weights are used to calculate percent forage use (Bonham 1989, Interagency Technical Reference 1996). The height-weight technique involves measuring grazed and ungrazed plant heights along a transect and calculating forage use based on height-weight relationships (Interagency Technical Reference 1996). These relationships are established by either clipping ungrazed plants and developing height-weight regression equations for a particular range site and season or by using pre-established USFS height-weight gauges (Interagency Technical Reference 1996). The paired-plot method is considered objective and quantitative but requires considerable time and expense (Klingman et al. 1943). The height-weight technique requires less equipment, and if pre-established height-weight gauges are used, much less time than the paired-plot technique (Interagency Technical Reference 1996). However, the height-weight technique is considered more subjective and qualitative than the paired-plot method (Lomasson and Jensen 1943, Mitchell et al. 1993). Furthermore, some question whether the USFS gauge is appropriate to use across seasons and sites (Mitchell et al. 1993).

Although the pros and cons of the paired-plot and height-weight techniques have been debated, there have been no field experiments that have directly compared whether these techniques provide similar forage use estimates for free-ranging wild and domestic ungulates. The objective of this 2-year study was to compare western wheatgrass (*Pascopyrum smithii* Rydb.) forage use estimates collected with the paired-plot and 2 height-weight methods (i.e., using on-site height-weight regression curves and the pre-established USFS height-weight gauge) under field conditions.

Materials and Methods

Study Area

This study was conducted from March 1997 to October 1998 on the Walker Basin Livestock Grazing Allotment, Coconino National Forest in central Arizona. The Walker Basin Allotment is comprised of about 31,000 ha of private and USFS rangeland. Annual precipitation averages 33 cm and typically occurs in a bimodal pattern from December to February and July to September (National Oceanographic and Atmospheric Administration 1997). Winter

<p>Pasture 1</p> <p>Grazed by cattle 1998</p> <p>(2100 ha)</p>	<p>Pasture 2</p> <p>Grazed by cattle 1998</p> <p>(1900 ha)</p>
<p>Pasture 3</p> <p>Grazed by cattle 1997</p> <p>(850 ha)</p>	<p>Pasture 4</p> <p>Grazed by cattle 1997</p> <p>(1900 ha)</p>

Fig. 1. Pasture layout for the study site on the Walker Basin Allotment, central Arizona, 1997/1998. Cattle grazed southern pastures (3 and 4) in 1997 and northern pastures (1 and 2) in 1998. Elk had access to study pastures year-round.

precipitation is mainly in the form of snow. Our study area (about 6,750 ha) was a pinon-juniper (*Pinus edulis* Engelm.—*Juniperus osteosperma* Torr.) savanna with a herbaceous understory dominated by western wheatgrass, the key forage species. The study area consisted of 4 pastures ranging from 850–2,100 ha in size (Fig. 1). Each year, 2 pastures (hereafter called grazed pastures) were grazed during summer and fall by cattle (*Bos taurus* L.) and 2 pastures (hereafter called rested pastures) were rested from cattle grazing. Grazed pastures were occupied by 400–450 mature, cross-bred Hereford cows with calves for about 14 days during the growing season. All pastures were subject to year-round grazing by wild ungulates, mainly elk (*Cervus elaphus* L.).

General Sampling Procedure

We used the paired-plot and 2 height-weight techniques (Interagency Technical Reference 1996) to evaluate forage use in all pastures 3 times each year: 1) in early/mid-June, immediately-before-cattle entered grazed pastures, 2) in mid-June/early July, immediately-after-cattle exited grazed pastures, and 3) in mid-October, at the end of the growing season, about 3 months-after-cattle had left the study area. The grazing schedule allowed us to monitor various levels (13–61%) of relative (immediately-before and immediately-after-cattle) and total forage use (months-after-cattle) by domestic and wild ungulates. Relative use describes the amount of forage consumed or destroyed up to a certain time during the growing season but prior to peak standing crop (e.g., June or July) (Frost et al. 1994). Total forage use, or simply forage use, is the “proportion of current-year’s forage consumed or destroyed by grazing ani-

mals,” measured at the end of the growing season (Glossary Revision Special Committee 1989).

Year 1 (1997)

We randomly located 3 sampling areas (about 50 x 600 m) in each pasture with the restriction that they were 0.4 km from well-traveled roads, fences and water and 0.3 km from each other. Six paired-plot units (protected and unprotected macroplots, 1.7 m² ea) and 1 height-weight line transect were placed within each sampling area (Fig. 2), for a total of 72 paired-plot units in the entire study area. Seventy-two paired-plot units within the 6,750-ha study area were considered to be the optimum trade-off between the number necessary to provide a quantitative seasonal comparison between the paired-plot and height-weight techniques, and the number of plots that a resource manager could realistically sample within a year. Height-weight transects were about 400 m long, located between protected and unprotected macroplots and 10 m from protected macroplots.

To avoid attracting animals to sampling areas, each protected macroplot was 100 m from the others. Protected and unprotected macroplots were 50 m apart and unprotected plots within a paired-plot unit were 10 m apart. Two unprotected macroplots, rather than the traditional 1, were ocularly matched with each protected macroplot to account for possible patch grazing by cattle and elk (Klingman et al. 1943, Grelen 1967). Each unprotected macroplot was marked with 1 wooden stake that protruded about 24 cm above ground level. To minimize bias due to enhanced growth within protected macroplots (Owensby 1969), 72 new

Fig. 2. Typical sampling area layout used to estimate forage use with the paired-plot and height-weight techniques, 1997/1998. Each sampling area contained 6 paired-plot units (1 protected and 2 unprotected 1.7-m² macroplots (Klingman et al. 1943)).

paired-plot units were established in March of both years.

Before initially establishing paired-plot units, the precision of ocular pairings was tested by clipping and weighing western wheatgrass from 29 pairs of 0.25-m² circular subplots that were later used to collect forage data (described below). A paired t-test revealed no difference among subplot pairings ($P = 0.2$). The same observer always selected paired-plot units.

Forage use via the paired-plot technique

During each sampling period, we clipped western wheatgrass from 2 randomly selected paired-plot units in each sampling area (i.e., 6 paired-plot units/pasture/sampling period). A 0.25-m² circular plot frame was used to delineate the 4 subplots to be clipped within each 1.7-m² macroplot. We averaged the 4 subplot dry weights to obtain 1 mean protected weight for each protected macroplot. For the 2 corresponding unprotected macroplots, we averaged the 8 subplot weights (4 subplots $\times$ 2 macroplots) to obtain 1 mean unprotected weight. Percent use for a paired-plot unit was calculated as the ratio of mean unprotected and protected dry weights. Negative utilization values from subplots were zeroed (Werner and Urness 1998). Mean percent use for a sampling area was calculated from the 2 randomly selected paired-plot units. Mean percent use for a pasture was calculated from the 3 sampling areas in that pasture.

Forage use via the height-weight techniques

Height-weight sampling occurred concurrently with paired-plot sampling and followed guidelines as outlined in the Interagency Technical Reference (1996).

During each sampling period, we measured average heights of 60 western wheatgrass plants along a 400-m transect (1 transect/sampling area = 3/pasture). About every 3 m, the grazed or ungrazed western wheatgrass plant nearest the observer's toe was measured. A plant was defined as the vegetation occupying a circle of turf at least 2 inches in diameter. Each sampling period, 10 ungrazed western wheatgrass plants per sampling area were clipped to develop 36 on-site height-weight curves. We used these height-weight curves to estimate forage use for each transect. Forage use was also estimated along each transect with the pre-established USFS culmless western wheatgrass height-weight gauge. Mean use for a pasture was calculated from the 3 sampling areas with both techniques. Finally, each year's immediately-before-cattle, immediately-after-cattle, and months-after-cattle on-site height-weight curves from each sampling area were combined and compared to the pre-established USFS height-weight gauge curve (Fig. 4).

Year 2 (1998)

Forage use via the paired-plot technique

In 1998, the paired-plot sampling procedure was altered slightly to address high standard errors (range = 0–35%) for 1997 subplot use estimates within sampling areas. Three subsamples were taken in each paired-plot unit by ocularly matching 0.25-m² subplots. We ocularly matched three, 0.25-m² subplots within a protected macroplot to three, 0.25-m² subplots within each of the 2 unprotected macroplots. Percent use for a subsample was the ratio of dry weights clipped from the 2 unprotected 0.25-m² subplots (averaged) and the corresponding 0.25-m² protected subplot. Percent use for a paired-plot unit was the

mean of the 3 matched subsample use estimates. Means for sampling areas and pastures were calculated as described in 1997.

Forage use via the height-weight techniques

Methodology used for the height-weight transect was the same as in 1997. However, 1997 paired-plot use estimates were consistently higher ($P < 0.0001$, $n = 36$) than height-weight use estimates (Halstead et al. 1998). This discrepancy may have been due to herbivores being attracted to the wooden stakes used to delineate unprotected macroplots. If animals were attracted to stakes, this could have led to higher use within unprotected macroplots than along height-weight transects and help explain the difference between paired-plot and height-weight forage use estimates. We tested this hypothesis by applying the height-weight method (with on-site curves) to 60-point transects within unprotected macroplots. Each sampling period, the heights of 30 western wheatgrass plants were measured within each of the 4 unprotected macroplots scheduled to be clipped within a sampling area (two, 60-point macroplot transects/sampling area). Heights of grazed or ungrazed plants were systematically measured at 15-cm intervals within the 4 macroplots. In each sampling area, we compared mean use from the 2 macroplot height-weight transects to the mean use calculated from the 400-m height-weight line transect.

Statistical Analysis

We used a 3 $\times$ 3 $\times$ 4 factorial analysis of variance (ANOVA) to examine differences across forage use techniques (paired-plot, on-site height-weight, and USFS height-weight), sampling periods, and pastures. Variances were unequal for the height-weight and paired-plot forage use estimates. Therefore, the arc-sine transformation was applied to forage use data prior to analysis as recommended by Steel and Torrie (1980) for percentage data. A 2 $\times$ 4 ANOVA was used to detect differences among use estimates from line and macroplot height-weight transects between locations (line vs macroplot transects) and among pastures. When F-tests were significant ($P < 0.05$), LSD tests were used to detect differences among means ($P < 0.05$). Coefficients of variation were calculated for each technique within sampling areas as an indicator of technique precision.

Results

Paired-Plot vs Height-Weight Techniques

The paired-plot technique produced significantly higher ($P < 0.05$) use estimates than either of the 2 height-weight techniques across all pastures (Fig. 3). Compared across pastures and sampling periods, paired-plot estimates were about 23 percentage points (or about 4 times) higher than height-weight estimates using on-site curves and the USFS gauge (Fig. 3).

Matching individual subplots within macroplots in 1998 did not reduce standard errors of paired-plot estimates within sampling areas (SE range = 0–35% and 0–36% in 1997 and 1998, respectively). Standard errors within sampling areas for height-weight techniques were relatively lower than paired-plot estimates both years (SE range = 0–3% and 0–6% in 1997 and 1998, respectively). However, lower standard errors for the height-weight techniques were a function of their lower means relative to the paired-plot technique. Mean coefficients of variation within sampling areas were higher for on-site height-weight curves (CV = 238%) and the USFS gauge (CV = 271%) than for the paired-plot technique (CV = 63%). Selective grazing, a common occurrence on light- to moderately-stocked ranges, evidently contributed to higher CVs for the height-weight techniques. For example, a few individual plants measured along height-weight transects were typically heavily-grazed (up to 82% use), however, the majority of plants were either ungrazed or lightly-grazed.

The effect of sampling period on forage use estimates was significant ($P < 0.001$). Immediately-after-cattle use estimates were generally higher (mean = 21 ± 3 (SEM) percentage points) than immediately-before-cattle (mean = 9 ± 3 (SEM) percentage points) and months-after-cattle (mean = 16 ± 3 (SEM) percentage points) use estimates with all techniques ($P < 0.05$). This difference was expected because immediately-after-cattle use estimates were made 1–2 days after cattle had exited grazed pastures and around the mid-point of the growing season (i.e., before any regrowth had occurred and before total forage production had been achieved).

Bork and Werner (1999) suggested that zeroing “negative” paired-plot data between protected and unprotected plots as done in our study inflates forage use estimates on spatially heterogeneous ranges. Zeroed paired-plot data in our

Fig. 3. Western wheatgrass use (%) in 4 pastures measured using on-site height-weight (HW) curves, the USFS height-weight gauge, and the paired-plot technique, averaged over 1997 and 1998. Pasture means with the same upper case letters are not significant at $P \leq 0.05$. Technique means across pastures with the same lowercase letters are not significant at $P \leq 0.05$. Analysis of variance was performed on arc-sine transformed data, however, actual percent forage use data are presented for ease of interpretation.

study were about 9 percentage points higher than non-zeroed paired-plot data ($P < 0.0001$, $n = 72$; Wilcoxon signed rank test). However, non-zeroed paired-plot estimates were still about 12 percentage points higher than use estimates obtained with either of the 2 height-weight techniques ($P < 0.0001$).

On-Site Height-Weight Curves vs the USFS Gauge

On-site height-weight curves fluctuated with plant phenological development: months-after-cattle curves showed proportionately more weight in the lower half of plants than immediately-before-cattle or immediately-after-cattle curves (Fig. 4,

Table 1). The USFS gauge curve generally showed a more linear relationship than on-site curves (Fig. 4, Table 1). However, mean use calculated with the USFS gauge did not differ ($P > 0.05$) from forage use calculated with on-site curves in any pasture (Fig. 3) or during any sampling period.

Line vs Macroplot Height-Weight Transects

There was no significant difference between line and macroplot height-weight transect estimates ($P = 0.23$), indicating herbivores were not attracted to the unprotected macroplots marked by wooden stakes.

Table 1. Third-order polynomial regression equations and r^2 -values for 6 on-site height-weight curves, and the USFS height-weight gauge curve for culmless western wheatgrass. On-site curves were developed for 3 sampling periods (immediately-before-cattle or IBC, immediately-after-cattle or IAC, and months-after-cattle or MAC) in 1997 and 1998 in central Arizona. Sampling periods were early/mid-Jun. (IBC), mid-Jun./early Jul. (IAC), and mid-Oct. (MAC). See Figure 4 for height-weight graphs.

Curve, Year	Regression equation	r^2
IBC, 1997	$y = 0.0997x^3 - 0.9213x^2 + 9.1949x + 0.875$	0.9999
IAC, 1997	$y = 0.0528x^3 - 0.2861x^2 + 7.4149x + 2.2889$	0.9996
MAC, 1997	$y = 0.1621x^3 - 1.253x^2 + 6.3614x - 0.0194$	0.9999
IBC, 1998	$y = 0.0996x^3 - 0.7972x^2 + 8.1091x - 0.3697$	0.9997
IAC, 1998	$y = 0.1209x^3 - 1.1111x^2 + 8.6832x + 4.2499$	0.9994
MAC, 1998	$y = 0.1709x^3 - 1.5511x^2 + 8.496x - 0.6955$	0.9997
USFS	$y = -0.1329x^3 + 3.037x^2 - 8.1332x + 10.55$	0.9987

Fig. 4. On-site height-weight curves vs the USFS height-weight gauge curve for culmless western wheatgrass for 3 sampling periods (immediately-before-cattle or IBC, immediately-after-cattle or IAC, and months-after-cattle or MAC) in 1997 (a) and 1998 (b) in central Arizona. Sampling periods were early/mid-Jun. (IBC), mid-Jun./early Jul. (IAC), and mid-Oct. (MAC). See Table 1 for regression equations and r^2 -values.

Discussion

Paired-Plot vs Height-Weight Techniques

Differences in forage use estimates obtained with the paired-plot and the 2 height-weight methods were substantial. The paired-plot technique consistently produced higher use estimates than either of the 2 height-weight techniques across

all pastures and sampling periods. This finding is important information for rangeland and wildlife managers because the forage use monitoring technique they choose may influence the results obtained and, consequently, grazing management and wildlife harvest decisions.

We propose several hypotheses to help explain the disparity between paired-plot and height-weight forage use estimates. Part of the problem lies, as it usually does

with allometric utilization monitoring techniques, in accurately converting height remaining to weight removed (Bonham 1989, Mitchell et al. 1993, Laycock 1998). The height-weight technique does not account for the selective way that most ungulates graze individual plants (McKinney 1997). Ungulates typically remove only some of a plant's leaves or tillers which results in a single plant of varying heights (McKinney 1997). However, the height-weight model assumes that herbivores "clip" all parts of a single plant to the same height (Reid and Pickford 1941). To illustrate, assume half of a plant has been grazed to the ground while the other half is left ungrazed. Following the height-weight methodology (Interagency Technical Reference 1996), the plant would be recorded as having 50% of its height removed, as if the entire plant had been grazed to half its height. Based on western wheatgrass height-weight curves, 50% height removed is equivalent to about 35% utilization (Fig. 4). However, because proportionally more weight is in the lower portion of the plant (and was removed on the grazed half), the hypothetical plant has actually had about 50% of its weight removed (50% utilization). This bias would ostensibly occur more on lightly to moderately-stocked ranges (as in our study; Fig. 3) than on heavily-stocked ranges because animals tend to be less selective (i.e., graze more uniformly) on heavily-stocked ranges (Holechek et al. 1998). Three-dimensional height-volume relationships more accurately predict forage production than 2-dimensional height-weight regression equations (Johnson et al. 1988) and may also more accurately assess forage removed. However, quantifying the volume of the specific sections removed from individual plants (e.g., lighter upper sections vs heavier lower sections) would be prohibitively cumbersome for management purposes.

The paired-plot method may overestimate forage use if cages create microclimates that enhance forage growth (Owensby 1969, Sharrow and Motazedian 1983). Microclimates may arise when perching birds "fertilize" exclosures, in years with above average precipitation, or when exclosures are not moved each year, allowing more than 1-year's production to accumulate (Grelen 1967, Owensby 1969, Sharrow and Motazedian 1983). We addressed the latter concern by moving cages at the beginning of each growing season so that they protected forage for 7 months. However, this effort did not pre-

clude the possibility of enhanced growth within protected plots, especially in 1998, when precipitation was higher as evidenced by greater western wheatgrass standing crop and stubble heights (Halstead 1998). For example, during 1998, western wheatgrass standing crop averaged about $131 \text{ kg ha}^{-1} \pm 18$ (SEM) higher and stubble heights averaged about $3 \text{ cm} \pm 1$ (SEM) higher than in 1997 (Halstead 1998).

On-Site Height-Weight Curves vs the USFS Gauge

Forage use estimates made with on-site height-weight curves and the pre-established USFS height-weight gauge were remarkably similar across pastures (Fig. 3) and sampling periods. Mitchell et al. (1993) concluded that height-weight curves changed statistically with phenological development and location. However, their analysis was conducted on height-weight regressions and not on use estimates derived from those equations. On-site height-weight curves in this study changed across time (Fig. 4), but not enough to produce use estimates different from those calculated with the pre-established USFS gauge. Time required to develop height-weight curves made forage use calculation with on-site curves slower than with the USFS gauge. However, data from this study suggest developing western wheatgrass height-weight curves for a particular site or season may be unnecessary. Other researchers have indicated that height-weight relationships for other forage species on the same range site are fairly consistent across years (Heady 1950, McDougald and Platt 1976). Nevertheless, those monitoring other forage species or dissimilar sites should field check on-site height-weight curves against the USFS gauge before using pre-established gauges to calculate forage use.

Conclusions and Management Implications

The primary goal of this study was to directly compare 3 forage use techniques under field conditions commonly encountered by land managers on arid and semi-arid rangelands (i.e., seasonal, irregular grazing by more than one large ungulate species in a heterogeneous, patchy environment). Technique accuracy was not addressed because such studies typically involve an artificial population and simulated herbivory (e.g., mowing or clipping) which would have negated our ability to

quantify the selective way that free-ranging ungulates graze under field conditions.

The paired-plot technique consistently produced higher forage use estimates than both height-weight techniques across all pastures and sampling periods during both years of the study. On the other hand, on-site and pre-established USFS western wheatgrass curves consistently produced similar forage use estimates. We believe the differences among the paired-plot and height-weight techniques, and the similarities between the height-weight techniques are real for western wheatgrass in central Arizona because of the consistency of results.

As this study showed, popular forage use monitoring techniques can produce different results on the same range site. Managers should consider that different forage use techniques might produce different estimates, and if used alone, will result in different grazing and wildlife management decisions. The monitoring technique(s) chosen must address the resource objectives that are formulated in management plans. If it is important to know the relative or total percentage of current-year's growth removed by herbivores on a management unit for a particular season or year, forage use techniques might be used with the caveat that the paired-plot technique may result in higher use estimates than height-weight techniques.

Effective rangeland management does not always require, or does not only require, measurements of forage use. In some situations, residual vegetation data (e.g., stubble height) may provide more useful information than forage use data (Smith 1998, Scarnecchia 1999) because it is correlated with erosion protection, soil moisture retention, forage regrowth potential, and small animal and insect habitat (Papanastasis 1985, Hall and Lindenmuth 1998, Holechek et al. 1998). Stubble height data can be collected simultaneously with height-weight data and has the advantage of directly and quantitatively assessing plant material left after grazing (Hall and Lindenmuth 1998). Use pattern maps (e.g., stubble height and/or height-weight data) coupled with relevant trend data (e.g., plant species composition, herbaceous and shrub cover, vegetation structure) can help managers to more comprehensively evaluate management strategies. More complex resource issues (e.g., management of threatened or endangered species) may require more intensive monitoring programs.

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A method for estimating cattle fecal loading on rangeland watersheds

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Abstract

Water quality contamination by pathogens and nutrients from cattle fecal deposits is a concern on rangeland watersheds. The temporal and spatial deposition of fecal material relative to storm events and water-bodies determines much of the risk a grazing scheme presents to water quality. The objective of this study was to develop and evaluate a comparative technique to estimate cattle fecal loading across a watershed through time. Once the method was developed, dry and wet season trials were conducted on a 138 ha experimental rangeland watershed at the San Joaquin Experimental Range in 1996–97. Fifty-four permanent 40 m² belt transects were established across the watershed. Observers ocularly assigned a rank of 1 (smallest diameter) to 5 (largest diameter) to each fecal deposit within a transect. A regression relationship was developed to predict fecal deposit dry weight by rank. Load per transect was calculated as the total weight of all fecal deposits in a transect. All fecal deposits in transects were collected and actual fecal load determined. The comparative yield methodology was successfully adapted to estimate rangeland fecal loading. Regression relationships predicting fecal deposit dry weight by ranks were highly significant for all observers ($p < 0.001$). The R^2 values ranged from 0.97 to 0.99 in the dry season and 0.89 to 0.94 in the wet season. There was no significant difference between the weighed fecal load estimate and the estimates of observers using the comparative method ($p < 0.05$). This method provides a rapid, simple method for estimating spatial and temporal livestock fecal loading on rangeland watersheds.

Key Words: water quality, pathogens, nutrients, grazing

Water quality contamination by pathogens and nutrients in livestock fecal deposits is a subject of concern on rangeland watersheds (Atwill 1996, Nader et al. 1998). Recent events in California illustrate the need for land managers to evaluate the risk of pathogen and nutrient loading that their grazing animals present to water quality on priority watersheds that supply municipal drinking water (Barry et al. 1998). Managers need methods that provide site specific data to confirm or negate the risk of contamination. In situations where the risk is unacceptable, managers must be able to propose and defend viable grazing manage-

Resumen

La contaminación del agua por patógenos y nutrientes provenientes de heces fecales del ganado es motivo de preocupación en las cuencas hidrológicas de pastizal. La deposición espacial y temporal del material fecal en relación a los eventos de tormentas y cuerpos de agua determina mucho del riesgo que un esquema de apacentamiento presenta para la calidad del agua. El objetivo de este estudio fue desarrollar y evaluar una técnica comparativa para estimar la carga de material fecal a lo largo de una cuenca hidrológica a través del tiempo. Una vez que el método se desarrolló, se condujeron ensayos en las épocas seca y de lluvia de 1996 y 1997, los ensayos se llevaron a cabo en una cuenca hidrológica de pastizal de 138 ha situada en "San Joaquín Experimental Range". A lo largo de la cuenca se establecieron 54 transectos permanentes de 40 m². Los observadores asignaron en forma ocular una clasificación del 1 (diámetro mas pequeño) al 5 (diámetro mas grande) a cada uno de los depósitos fecales encontrados dentro del transecto. Se desarrolló una relación de regresión para predecir el peso seco del depósito fecal por categoría. La carga por transecto se calculó como el peso total de los depósitos fecales dentro del transecto. Todos los depósitos fecales del transecto se colectaron y se determinó la carga fecal actual. La metodología comparativa se adaptó exitosamente para estimar la carga fecal del pastizal. Las relaciones de regresión para predecir el peso seco de los depósitos fecales por categoría fueron altamente significativos para todos los observadores ($P < 0.001$). Los valores de r^2 variaron de 0.97 a 0.99 en la época seca y de 0.89 a 0.94 en la época de lluvia. No hubo una diferencia significativa entre la estimación de la carga fecal obtenida mediante pesaje y la estimada por los observadores utilizando el método comparativo ($P < 0.05$). Este método provee un método rápido y simple para estimar la carga espacial y temporal de depósitos fecales de ganado dentro de las cuencas hidrológicas de pastizal.

ment alternatives. If managers do not take this initiative, regulatory control of grazing on priority watersheds is likely.

Estimating the spatial and temporal loading of livestock fecal material, thus nutrients and pathogens, on a watershed is a critical step in determining the risk to water quality presented by grazing management schemes. The *timing* of fecal loading relative to runoff as well as its *location* relative to riparian areas and water-bodies determines much of the potential for contaminants in livestock fecal deposits to reach source water.

Hand collection of fecal deposits from plots across a landscape is one method of estimating fecal loading. The process is time

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and labor intensive and limits sample size. A rapid, simple method is needed to estimate fecal loading. Observational methods based upon ranking systems have been successfully used to facilitate herbage yield estimation (Mannetje and Haydock 1963, Haydock and Shaw 1975, Reese et al. 1980, Gillen and Smith 1986, Frost et al. 1990, USDI-BLM 1996). These methods have lower costs per plot which allows for increased sample size and improved estimates of population parameters at the landscape scale. Decreases in precision occur at the plot scale. Many accept this as a worth-while trade-off (Haydock and Shaw 1975, Reese et al. 1980).

The first objective of this study was to adapt the comparative herbage yield methodology to a method for estimating cattle fecal loading on rangelands. The second objective was to test the newly developed comparative fecal load method by comparing watershed scale loading estimates by several observers to estimates from hand collection and weighing of fecal deposits during wet and dry seasons. Our null hypothesis was that this method would not accurately estimate watershed fecal loading across seasons or observers.

Methods

Study Site

The study was conducted on a 138 ha experimental rangeland watershed at the San Joaquin Experimental Range in Madera County, Calif. Vegetation is oak savanna with annual grassland understory. Climate is Mediterranean with mean annual precipitation of 485 mm. Precipitation falls almost entirely as rainfall from November through May (wet season) with almost no precipitation falling from June through October (dry season). In November 1995, 54 permanent 40 m² belt transects were established across the watershed. An individual transect served as the experimental unit in this study. Transects were 30.5 m long by 1.3 m wide and staked at both ends. Following a stratified-random design, the transects were distributed proportionally across the watershed to encompass slope classes of 0–10, 11–20, 21–30, >30%, with additional transects placed in the riparian zone and around livestock concentration areas. Transect numbers per stratification were 14, 15, 5, 5, 10, and 5, respectively. The stratified sampling design was used to insure that important topographic and managerial areas representing the range of fecal loading on the watershed were

included. Transect starting points were randomly positioned within each stratification via random selection from a grid. Orientation of the transects was determined via random compass bearing. The watershed was grazed continuously with a 30 unit commercial, cow-calf herd from 1 January 1996 through 31 May 1997.

Comparative Fecal Load Method

The comparative fecal load method described in this section closely follows the comparative herbage yield procedures outlined by Haydock and Shaw (1975) and addresses the first objective of our study. The comparative herbage yield method uses the quadrat as both the basic unit for ranking and as a sample unit. Our comparative fecal load method used the individual fecal deposit as the basic unit for ranking and the 40 m² transect as the experimental unit. A transect could contain 0, 1, or numerous fecal deposits of various sizes. The transect fecal load (kg) was the sum of the weight of the fecal deposits in the transect. The comparative yield method bases rank (1, 2, 3, etc.) on estimated herbage dry weight (g). Our comparative fecal load method used fecal deposit diameter (cm) to establish rank (1, 2, 3, etc.).

The *first step* was to select 5 reference fecal deposits to set the ranking scale for the sample period. Rank 1 (smallest) and 5 (largest) were established by surveying the general sampling area and selecting fecal deposits encompassing the range of sizes within the area. Once reference fecal deposits 1 and 5 were established, reference fecal deposit 3 was defined to have a diameter half-way between 1 and 5. Reference fecal deposits 2 and 4 were then selected to have diameters half-way between 1 and 3 and 3 and 5, respectively. Following establishment of the reference fecal deposit dimensions, each observer spent 15 to 30 minutes calibrating their mind and eye to the reference set and the ranking scale it established for that specific sample period and location.

The *second step* was to record the rank of each fecal deposit in a transect based upon the 5 references established in step 1. Half scores were also utilized (1.5, 2.5, etc.). Data was recorded using the sheet developed by Frost et al. (1990) for comparative herbage yield.

The *third step* was to rank and collect a set of fecal deposits for development of the calibration curve to calculate fecal deposit dry weight (g) from individual fecal deposit ranks. The calibration curve was derived by regression analysis where

fecal deposit dry weight was the dependent variable and fecal deposit rank the independent variable. Calibration was accomplished using the Type 3 method described by Haydock and Shaw (1975). Approximately half way through sampling, observers collectively selected a minimum of 15 fecal deposits that covered the range of ranks from 1 to 5. These calibration fecal deposits were ranked by each observer and subsequently collected for dry weight determination.

The *fourth step* was to develop a calibration curve for each observer using regression procedures. Steps 3 and 4 were extremely critical because they quantified the individual biases of each observer.

The *final step* was to use the calibration curve to estimate dry weight (g) of each fecal deposit in a transect. Total fecal load (kg) for the transect was the sum of all individual fecal deposit weights. Fecal loading per unit area was calculated from the known area of the transect. Fecal loading parameters (mean, standard deviation, range, etc.) for this area were then estimated from the entire set of transects dispersed across the watershed.

Testing the Method

A dry and wet season trial were conducted to address our second objective of evaluating the method. The dry season trial began on 31 May 1996 when all fecal deposits were cleared from each transect. The dry season trial ended and the wet season trial began when all transects were sampled and subsequently cleared on 1 November 1996. The wet season trial, and the study, ended 31 May 1997 when all transects were re-visited and sampled. All transects were sampled once at the end of each trial. Each observer worked independently. Following ranking of all fecal deposits in a transect, all fecal material was collected, dried at 60° C for 96 hours, and weighed to determine total dry weight fecal load. There were 4 observers in the dry season and 3 observers in the wet season trial. Observers A and B participated in both trials. Observers C and D only participated in the dry season trial and Observer E participated only in the wet season trial. Calibration curves predicting fecal deposit dry weight from ranks were developed for each observer and the relationship used to calculate individual watershed fecal load estimates.

Calibration curves for each observer in each season were developed using regression, with adjusted multiple coefficients of determination (R^2) and analysis of variance for the regression coefficients used to

characterize the significance of each observer's ability to predict fecal deposit weight as a function of rank. Both linear and quadratic regression models were tested. Regression models were forced through the origin because a zero rank must equal a zero fecal deposit dry weight. To determine the need to develop separate calibration curves for each observer within a season, the equality of curves developed for Observers A, B, C, and D for the dry season and Observers A, B, and E for the wet season was tested. To determine the need to develop separate calibration curves for the dry and wet season, the equality of dry and wet season calibration curves for Observers A and B was tested. Given that the intercept of all calibration curves was forced through 0, only the equality of slopes could be tested. The equality of the regression lines was tested by conducting pairwise F-tests following Dixon (1992) with the F-test calculated as,

$$F = \frac{(\text{Regression SS across groups})/(\sum p_i + g - p - 1)}{(\text{Residual SS within groups})/(N - g - \sum p_i)}$$

where *Residual Sums of Squares (SS) within groups* = Residual SS of group *i*, *Total SS* = Residual SS of the data prior to grouping, *Regression SS across groups* = (*Total SS* - *Residual SS within groups*), *p* = number of independent variables in the regression equation for all groups taken together, *p_i* = number of independent variables in the equation for the *i*th group, *g* = number of groups, and *N* = number of cases in all the groups combined.

Analysis of variance was used to test for differences between mean watershed fecal load estimates from hand collected samples and comparative load based estimates from ranks for each observer. Differences between mean watershed fecal load estimates among observers was tested in the same model. Each trial (season) was subjected to an individual ANOVA.

Results and Discussion

Calibration Curves

Calibration curves for each observer in each season are presented in Table 1. The *R*² values for linear calibration curves across observers ranged from 0.84 to 0.94 and from 0.75 to 0.90 for the dry and wet season trials, respectively. Based upon a 5 percentage point or greater improvement in *R*² values, the quadratic equation with observer rank and the square of the observer rank best fit the data (Table 1).

While there is no rule in comparative yield, Haydock and Shaw (1975) found

Fig. 1. Theoretical calibration curve for fecal deposit dry weight predicted by rank when reference fecal deposit ranks are established from fecal deposit diameter.

that the relationship between quadrat herbage dry weight and rank was explained by simple linear regression. This is logical given that they selected their reference quadrats to insure a linear relationship between rank and quadrat dry weight. In developing their reference set, Haydock and Shaw (1975) specifically state that reference quadrat 5 be selected to have 5 times the dry weight as the quadrat for reference rank 1, and that reference quadrat 3 be selected to have dry weight half-way between ranks 1 and 5. This leads to the linear relationship for calibration curves that they were seeking for their method.

In our adaptation of the comparative yield method, the first step is to select reference fecal deposits 1–5 based upon diameter. Considering that the shape of a fecal deposit can be approximated as a short cylinder, it becomes clear that the relationship between fecal deposit diame-

ter (2*r*) and fecal deposit dry weight (*h* × *r*² × fecal deposit dry weight specific gravity) is not linear. Figure 1 illustrates the theoretical relationship between fecal deposit rank and fecal deposit dry weight at a constant fecal deposit depth of 2 cm, a specific gravity of 0.2, and with diameters for reference fecal deposit ranks 1, 3, and 5 equal to 2, 6, and 10 cm, respectively.

During the dry season, we found that 3 of the 6 pair-wise comparisons of calibration curves among the 4 observers were significantly different (Table 1, Fig. 2). For example, the calibration curve for Observer A compared to Observer B was significantly different based upon the pair-wise F-test for the equality of regression lines (*P* = 0.013). The predicted dry weight for a fecal deposit of rank 2 was 96 g compared to 99 g, or 394 g compared to 330 g for a fecal deposit of rank 4 for Observer A and B, respectfully. This result indicated that it was important to

Table 1. Comparative fecal load calibration curves developed for each observer for the dry and wet season trials that were used to predict fecal deposit dry weight from observer rank, *n* = 15 for each observer. Samples were taken on a 138 ha watershed at the San Joaquin Experimental Range in 1996–97.

Season	Observer*	Regression Equation	<i>R</i> ²
Dry	A ^{a,1}	-2.95(rank) + 25.36(rank ²)	0.97
	B ^{b,c,1}	16.59(rank) + 16.50(rank ²)	0.99
	C ^b	-3.62(rank) + 19.07(rank ²)	0.98
	D ^{a,c}	20.35(rank) + 16.16(rank ²)	0.97
Wet	A ^{a,2}	71.45(rank) + 16.78(rank ²)	0.94
	B ^{a,2}	19.01(rank) + 24.52(rank ²)	0.93
	Ea	35.10(rank) + 23.40(rank ²)	0.89

*Within each season, calibration curves for observers with the same letter were not significantly different (*P* < 0.05). For Observers A and B across seasons, calibration curves with the same number were not significantly different (*P* < 0.05).

Fig. 2. Calibration curves used to predict fecal deposit dry weight from ranks for Observers A, B, C, and D for the dry season trial conducted on a 138 ha watershed at the San Joaquin Experimental Range on 1 November 1996.

develop separate calibration curves for each observer during the dry season. There were no significant differences among calibration curves for Observers A, B, and E during the wet season (Table 1, Fig. 3), which indicated it was not as important to develop separate calibration curves for each observer during this season. In this season, a composite calibration curve could have been developed and used for all observers.

Calibration curves for the dry and wet season were significantly different for both Observer A ($P = 0.0004$) and B ($P = 0.001$), which indicated it was important to develop separate calibration curves for each observer for each season. Fecal deposit dry weight for a given rank was consistently heavier during the wet season trial for both observers. This could be due to higher fecal deposit density under green versus dry feed conditions.

Fig. 3. Calibration curves used to predict fecal deposit dry weight from ranks for Observers A, B, and E for the wet season trial conducted on a 138 ha watershed at the San Joaquin Experimental Range on 31 May 1997.

Given the differences in calibration curves for observers in the dry season and for Observers A and B across seasons, we recommend that individual calibration curves be developed for each observer in each season. We recommend that fecal deposit diameter be used as the principle variable in determining fecal deposit size and that the quadratic form be investigated when developing the best fit regression-based calibration curve. Reference fecal deposits should be reexamined each day of consecutive sampling. A new reference set should be developed when sampling is spread discontinuously over several days or when a change in fecal deposit appearance occurs. Changes in sample site, season, cattle class or age, feed type or moisture, or a rainfall event can all alter the relationship between appearance and dry weight of fecal deposits and new calibration curves should be developed.

Table 2. Watershed fecal loads estimated by each observer using the comparative fecal load method and by hand collection for both dry and wet season trials, $n = 54$ for each estimate. Samples were taken on a 138 ha watershed at the San Joaquin Experimental Range in 1996–97.

Season	Estimate	Mean*	SE
		(kg ha ⁻¹)	
Dry	Hand Collected	37.2	8.2
	Observer A	53.9	10.9
	Observer B	50.1	10.6
	Observer C	43.4	10.0
	Observer D	48.8	10.1
Wet	Hand Collected	27.6	7.3
	Observer A	34.8	6.8
	Observer B	23.3	5.0
	Observer E	31.7	7.1

*There were no significant differences ($P < 0.05$) between methods nor among observers within each season of sampling.

Watershed Fecal Load Estimation

There were no significant differences in watershed fecal load estimated by each observer using the comparative fecal load method and by hand collection for either the dry ($P = 0.70$) or the wet ($P = 0.49$) season trial (Table 2). Our null hypothesis that the comparative fecal load method developed in this study would not accurately estimate average fecal loading on the watershed across seasons or observers was rejected.

Regardless of method, there was high variability associated with watershed fecal load estimates. The observed variability verifies the need for a rapid, simple sampling method that allows increased sample size. Fifty-four transects represented the largest number that a 2 person team could

physically harvest in a single day from the 138 ha watershed evaluated in this study. Mean time to collect all fecal material from each transect was approximately 5 minutes. Mean time for a person to conduct the comparative fecal load method per transect was approximately 2 minutes. At 54 plots, that was 4.50 and 2.25 hours of transect sampling time for the hand collection and comparative methods, respectively. Regardless of the number of transects, the comparative fecal load method required an hour to select a reference fecal deposit set and sample the calibration fecal deposit set. Travel time between transects was faster for the comparative fecal load method because technicians were not carrying sacks of fecal material. Travel time among transects accounted for about half of the time spent in the field each day. By employing the comparative fecal load method, sample size was increased 45%, from 54 to 78 transects per day. Also, only 1 observer rather than the team of 2 employed in the hand collection method was required.

If transects are permanently established for estimation of loading over time, all fecal deposits should be cleared from the transect following ranking. This is not necessary for temporary transects where repeated sampling is not an objective. Loading estimates for specific areas (flood-plain, uplands, etc.) of the watershed can be developed if transect locations are stratified or targeted to adequately represent the area of interest. If multiple

observers are used, load can be averaged across observers. It is recommended that when comparisons are to be made, a single observer or consistent set of observers be utilized to reduce potential bias from observer differences.

Conclusion

Estimating livestock fecal loading on rangelands via hand collection of fecal material from plots is cost prohibitive and limits sample size in a system where large numbers of samples are preferable. We were able to successfully adapt the comparative herbage yield methodology to estimate livestock fecal loading on rangelands. This method provided a rapid, simple method for collecting plot-based, site-specific estimates of spatial and temporal livestock fecal loading on rangelands. When used in conjunction with a systematic sampling scheme of plots across a pasture or watershed, fecal loading through time can be estimated at the riparian, upland, pasture, or watershed scale. Quantification of fecal loading through space and time is a critical first step in evaluating the risk to water quality under various grazing management scenarios.

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Early establishment of Douglas-fir and ponderosa pine in grassland seedbeds

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Abstract

Grasslands of interior British Columbia are being encroached upon by Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) and ponderosa pine (*Pinus ponderosa* Dougl.). A pot experiment placed in the field was conducted to determine the effect of forest and grassland seedbeds on seedling emergence and early establishment of the 2 species with 2 seed collections each. For these seedbeds, structural characteristics were evaluated and the effect of seedbeds water extracts on seed germination was determined. Seedling emergence of both species was significantly reduced by Douglas-fir needles and enhanced by fescue litter and cattle manure compared to mineral soil. The rate of emergence was reduced by Douglas-fir needles and sagebrush litter, and for some collections, by ponderosa pine needles, but was always enhanced by manure compared to mineral soil. Seedling survival was generally not affected by seedbeds. Douglas-fir seedlings emerging earlier in the season survived better, and both Douglas-fir and ponderosa pine seedlings emerging earlier lived longer than those emerging later. Seed germination of ponderosa pine was not affected by the water extract while that of Douglas-fir was reduced by the water extract from sagebrush litter. Therefore, differences in seedling emergence of the 2 species among seedbeds were related more to structural than to chemical characteristics of seedbeds. Successful establishment of the 2 species in grasslands within this region likely relies on the ability of seeds to germinate early in the growing season on seedbeds in which soil moisture is conserved, as summer droughts are severe.

Key Word: allelopathy, litter structure, seedbed ecology, *Pinus ponderosa* Dougl., *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco

The encroachment of woody plants is a major threat to range resources at a global scale, reducing grassland area and carrying capacity, and inhibiting livestock movement (Burkhardt and Tisdale 1976, Strang and Parminter 1980, Gruell 1983, MacDonald and Wissel 1991, Richardson and Bond 1991). Fire

Resumen

Los pastizales del interior de Columbia Británica están siendo invadidos por "Douglas-fir" (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) y "Ponderosa Pine" (*Pinus ponderosa* Dougl.). Se realizó un experimento en macetas, ubicado en el campo, con el objetivo de determinar el efecto de la cama de siembra (bosque y pastizal) y el origen de la semilla (dos colecciones) en la emergencia y establecimiento de plántulas de estas especies arbóreas. Se evaluaron las características estructurales de la cama de siembra y extractos de agua de ellas en la germinación de la semilla. Las hojas de "Douglas-fir" redujeron significativamente la emergencia de plántulas de ambas especies, en cambio en el mantillo de "fescue" y el estiércol de ganado la aumentaron, esto en comparación con el suelo mineral. La tasa de emergencia se redujo por las hojas de "Douglas-fir" y el mantillo de "Sagebrush"; en algunas colecciones de semilla las hojas de "Ponderosa pine" también redujeron la tasa de emergencia, sin embargo, la tasa de emergencia siempre mejoró con el estiércol comparado con el suelo mineral. En general, las camas de siembra no afectaron la sobrevivencia de las plántulas. Las plántulas de "Douglas-fir" emergieron más temprano y sobrevivieron mejor, las plántulas que emergieron primero, tanto de "Douglas-fir" como de "Ponderosa pine", vivieron más tiempo que las que nacieron al último. La germinación de semillas de "Ponderosa pine" no fue afectada por el extracto de agua mientras que la de semillas "Douglas-fir" sí se redujo con el extracto de agua de mantillo de "Sagebrush". Por lo tanto, la diferencia en germinación de plántulas de las dos especies se relaciona más a las características estructurales que a las características químicas de la cama de siembra. El establecimiento exitoso de las dos especies en los pastizales de esta región, se basa, probablemente, en la capacidad de las semillas para germinar a inicios de la estación de crecimiento en camas de siembra en las que la humedad del suelo se conserva en el verano cuando la sequía es severa.

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suppression, disturbance, climatic variation, and interactions of these factors in the last 100 to 150 years are thought to be responsible for tree encroachment (Tisdale 1950, Parminter 1978, Strang and Parminter 1980, Arno and Gruell 1986, Mast et al. 1998). In the southern interior of British Columbia, conifer forests are the dominant vegetation; natural grasslands are limited resources and are susceptible to tree encroachment. Tree encroachment was first reported about 80 years ago (Whitford and Craig 1918) and the loss of grasslands to encroachment in recent years was more than 30% over a 30-year period in certain areas (Ross 1997).

The dominant conifer species in the grassland/forest ecotone, interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) and ponderosa pine (*Pinus ponderosa* Dougl.), regenerate from seeds. The invasion by trees requires a sequence of favorable events from seed production and dispersal to seedling emergence and survival (Hill et al. 1995). Therefore, understanding the eco-physiological aspects of seed germination, seedling emergence, and seedling establishment of these tree species under grassland conditions is critical in explaining this phenomenon, and in providing a baseline for management strategies aimed at controlling tree encroachment. Numerous researchers have studied the effects of forest floors on seedling emergence and establishment of conifers (Bramble and Goddard 1942, Chrosiewicz 1974, Williams et al. 1990, McLaren and Janke 1996). Douglas-fir litter inhibited seedling emergence of itself in a monocultural plantation by reducing water availability and by acting as a mechanical barrier (Caccia and Ballaré 1998). Seedling emergence of ponderosa pine was generally enhanced by mineral or ash covered soils compared to undisturbed soils covered with plant litter (Roe and Squillance 1950, Foiles and Curtis 1965). No study has compared seedling establishment of conifers, particularly Douglas-fir and ponderosa in forest and grassland seedbeds. Objectives of this study were to determine: (1) effects of mineral soil, litter of grass and big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young), needles of Douglas-fir and ponderosa pine, and cattle manure on seedling emergence and establishment of Douglas-fir and ponderosa pine, and (2) if significant differences were found in seedling emergence and establishment among seedbeds, whether they were attributed to structural or chemical characteristics of these materials.

Materials and Methods

Seed collection and treatment

Two collections of Douglas-fir and 2 collections of ponderosa pine seeds were obtained from British Columbia Ministry of Forests Tree Seed Centre and were stored at -18°C before use (Table 1). These seeds were collected from low elevation sites ($<1,000$ m above sea level) in the grassland/forest ecotone, within 50 km from Kamloops.

In the seedbed experiment, seeds were

Table 1. Descriptions of Douglas-fir and ponderosa pine seed collections from the Interior of British Columbia.

Species/collection	Location	Elevation (m)	Date	Seed (No.g ⁻¹)
Douglas-fir 1	Nesbitt Lake, 50°44'N 121°06'W	900	Sep. 93	75
Douglas-fir 2	Pher Lane, 50°43'N 120°52'W	750	Aug. 93	80
Ponderosa pine 1	Sugarloaf Hill, 50°38'N 120°27'W	875	Aug. 94	19
Ponderosa pine 2	Indian Gardens, 50°44'N 120°49'W	725	Aug. 95	21

subjected to field stratification. Seeds were soaked in pre-cooled distilled water at 4°C for 2 hours and then placed in the field in early December 1997. The field site was located within a long-term enclosure dominated by rough fescue (*Festuca campestris* Rydb.) within the Lac du Bois Grasslands near Kamloops at an elevation of 900 m. Approximately 60 seeds were placed in each custom made, metal screen envelope (6 x 8 cm). These envelopes were randomly placed at the bottom of each of the 4 metal screen boxes (60 x 60 x 5 cm). These boxes were fixed to the ground with their bottoms 1 cm below the soil surface and covered with grass litter. The lids of boxes were then sealed with metal wire to minimize seed predation and covered with grass litter. Seeds were retrieved from the field on 1 May 1998. Seeds used in the water extract experiment were not stratified.

Seedbed experiment

Seedbed experiment was conducted in a randomized complete block design with 6 treatments, including mineral soil, Douglas-fir needle, ponderosa pine needle, sagebrush litter, fescue litter and cattle manure. This was a pot experiment placed in the field with 4 replicates and the experiment was repeated. Mineral soil from the top 15 cm of the soil profile was collected along a roadside in the Lac du Bois Grasslands. The soil was then sifted through a 1.0 cm sieve and heated at 80°C for 48 hours to eliminate viable seeds. Other litter materials, including needles of Douglas-fir and ponderosa pine from ground, dry leaves of big sagebrush from standing plants, standing dead leaves of rough fescue, and dry cattle manure more than 1-year old, were collected from the Lac du Bois Grasslands. Douglas-fir needles were separated from twigs, cones, and rocks with a 3.5 mm sieve and then sorted on a 2.0 mm sieve to remove seeds and other small objects. Ponderosa pine needles and the rough fescue litter were hand sorted and cut to fit into pots. Cattle manure was broken into fragments of about 1 cm in diameter.

Pots measuring 12 x 12 x 12 cm were filled with 8 cm of mineral soil and covered with seedbed materials. The litter depths selected were similar to those observed in the field, 1 cm depth for big sagebrush litter and 3 cm for Douglas-fir and ponderosa pine needles, fescue litter and cattle manure. Mineral soil treatment was not covered by any litter. Forty seeds were placed on the litter surface in each pot and shaken by hand. Seeds in the mineral soil treatment remained visible on the surface; those in fescue litter and ponderosa pine needle treatments fell to the bottom of the seedbed materials within 1 cm from mineral soils. Seeds in the Douglas-fir needle, sagebrush litter and cattle manure treatments remained at the top 0.5 cm of the seedbed materials but invisible from the surface. Pots were then placed outside under tree canopies and covered with mesh metal screens to minimize seed predation by birds and other animals. The first trial was initiated on 12 May 1998 and the second trial 2 weeks later. The duration of each trial was 90 days. Air temperatures during the experimental period were obtained from the weather station at Kamloops Airport, which is located about 1 km south of the experimental site.

Four hundred ml of distilled water were applied to each pot at the beginning of the experiment to ensure that the soil reached field capacity. Four additional pots filled with mineral soil were used as controls to monitor soil water change and to ensure no seeds survived the oven-drying process. Control pots were weighed every 2 days before watering for soil water content determination. One hundred ml of distilled water were added to each pot of the experiment on each of the first 3 checking dates. Fifty ml of distilled water were added each time when the soil moisture content in the control pots was below 35% d.w., a pre-determined level about 80% of the soil field capacity. Seedling emergence was checked every 2 days. Seedlings that reached at least 1 cm above the soil surface (mineral soil treatment) or 3 mm above litter materials (all other treatments) were considered emerged. Day of emer-

gence for each seedling was recorded and seedlings were marked with colored paper clips. Dead seedlings, determined by visual inspection, were recorded and removed. The total length of each surviving seedling was measured at the end of the experiment; seedlings were washed, oven-dried at 80°C for 48 hours, and weighed.

Bulk density of mineral soil and other seedbed materials was determined as dry weight per gross volume after oven drying at 80°C for 48 hours. Net volume was estimated by placing materials into beakers filled with a pre-determined amount of distilled water. The increase in the volume of distilled water after adding these materials was determined after 10 seconds. The relative volume of seedbed materials was calculated as the percentage of net volume in gross volume. There were 8 replicates for each seedbed type using different samples from the above seedbed experiment.

Water extract experiment

The 6 types of seedbed materials used in the above experiment as well as soils from beneath Douglas-fir needle, ponderosa pine needle, big sagebrush litter, fescue litter and cattle manure were used in the water extract experiment. With distilled water being the control, this experiment had 12 treatments arranged in a completely randomized design with 4 replicates and was repeated once. The amount of materials used for water extract was determined on a volume base: 1 x 12 x 12 cm for big sagebrush litter, mineral soil and soils (top 15 cm) from beneath Douglas-fir needle, ponderosa pine needle, big sagebrush litter, fescue litter and cattle manure; 3 x 12 x 12 cm for Douglas-fir needle, ponderosa pine needle, fescue litter and cattle manure. These materials were soaked in 400 ml of distilled water, shaken for 30 min, and allowed to sit for 24 hours at room temperature ($22 \pm 1^\circ\text{C}$). The water extract was obtained by filtering the solution through 1 layer of Whatman No. 1 filter paper then 1 layer of Whatman 0.2 μm membrane filter paper. Seeds of 1 Douglas-fir collection and 1 ponderosa pine collection were used in germination tests with 50 seeds in each petri dish (9.5 cm in diameter). Five ml of water extract were added to seeds on top of 2 layers of Whatman No. 1 filter paper and covered with 1 layer of filter paper to ensure full contact between seeds and water extract. Petri dishes were placed in clear plastic bags and incubated in a germinator at 30/20°C for 4 weeks, with 16-hour light/8-hour darkness. The top filter paper was removed after 2 days of incubation. A

seed was considered germinated when the radicle was 2 mm and germination was checked every 2 days. Small amounts of distilled water were added to the filter paper when needed.

Data analysis

Data for each seed collection were analyzed separately. Seedling emergence rate index (ERI)/seed germination rate index (GRI) were calculated as the summation of percent seedling emergence/seed germination on each checking date divided by days, then multiplied by 100 (Evetts and Burnside 1972). Total seedling mortality was the percentage of dead seedlings over total emerging seedlings. Data of total emergence, mortality, and germination percentage were transformed with arcsine before being subjected to Analysis of Variance (Snedecor and Cochran 1980). A 3-Way Analysis of Variance was used to analyze data of the seedbed experiment (treatment, block and trial) and a 2-Way Analysis of Variance was used for the water extract experiment (treatment and trial). When interactions between treatment and trial were significant ($P \leq 0.05$), data were further analyzed within each trial. Means were separated with LSD test. Seedling emergence data were pooled according to species and collections and regression analysis was used to determine relationships between seedling mortality and day of emergence, and between longevity (difference between day of emergence and day of death) and day of emergence. Days in which less than 4 seedlings emerged were excluded from regression analysis for mortality; best-fit equations were selected. Statistical significance for all tests was assumed at $P \leq 0.05$.

Results

Effect of seedbed types on seedling emergence

Percent emergence and seedling emergence rate index (ERI) were significantly affected by seedbed types in both species, ranging from 2.5 to 84.6%, and from 0.06 to 5.15% day^{-1} , respectively (Table 2). Compared to mineral soil treatment, emergence from fescue litter and manure was higher, and that from Douglas-fir needle and big sagebrush litter was mostly lower. Percent seedling emergence in the ponderosa pine needle treatment was not significantly different from that in the mineral soil treatment for both species. Mineral soil treatment had lower seedling emergence in trial 2 than trial 1 for ponderosa

pine 2 (data not shown), which resulted in a significant interaction between treatment and trial. The mean daily temperature in the first 4 weeks was 1.5°C higher for trial 2 than 1, and the soil water content in the control pots was 2.4% lower between weeks 2 and 4 for trial 2 than 1 (data not shown).

Seedling emergence rate, measured by ERI, was significantly higher in manure treatment and lower in Douglas-fir needle and big sagebrush litter treatments than in the mineral soil treatment (Table 2). The emergence rate index (ERI) did not significantly differ between mineral soil and fescue litter treatments, but was similar or lower in ponderosa pine needle compared to mineral soil treatment. The interaction between treatment and trial was significant for Douglas-fir 1 and ponderosa pine 2, apparently caused by the lower ERI for the mineral soil treatment in trial 2.

Seedling mortality and longevity as affected by seedbed type

Total seedling mortality over the experimental period ranged from 30 to 88% of total emerging seedlings, but was generally not affected by seedbed type (Table 2). Only in Douglas-fir 2 was seedling mortality significantly higher in the Douglas-fir needle treatment than others. Longevity of seedlings which did not survive to the end of the experiment was highest in mineral soil, manure and fescue litter, lowest in Douglas-fir needle, and intermediate in ponderosa pine needle and sagebrush litter in 3 of the 4 collections. Seedling longevity of ponderosa pine 2 was not affected by seedbed type.

Seedling length and weight as affected by seedbed type

The length of seedlings that survived to the end of experiments was significantly affected by seedbed type for Douglas-fir, but not ponderosa pine (Table 2). Seedlings were longest in mineral soil and manure, shortest in sagebrush litter, and intermediate in Douglas-fir needle, ponderosa pine needle, and fescue litter. Seedling dry weight was greatest in mineral soil and manure, lowest in Douglas-fir needle, and intermediate in others in all seed collections except for ponderosa pine 1, in which seedling weight was not affected by seedbed type.

Relation between seedling mortality, longevity, and day of emergence

Pooling seedling mortality data according to day of emergence showed that

Table 2. Percent of seedling emergence, emergence rate index (ERI), mortality, longevity, and the length and weight of Douglas-fir and ponderosa pine seedlings as affected by seedbed type.

Species/Seedbed collection	Emergence (%)	ERI (% day ⁻¹)	Mortality (%)	Longevity (day)	Length (cm)	Weight (mg seedling ⁻¹)
Douglas-fir 1						
Mineral soil	48.4 ± 7.6 bc ¹	3.23 ± 0.47 b	49.5 ± 5.8 a	31.5 ± 1.7 ab	12.5 ± 1.2 a	19.5 ± 2.5 a
Douglas-fir	12.5 ± 2.8 d	0.29 ± 0.07 e	61.9 ± 13.2 a	15.9 ± 4.0 c	10.5 ± 1.0 b	13.7 ± 2.6 b
Ponderosa pine	55.6 ± 2.6 b	2.28 ± 0.29 c	58.5 ± 10.6 a	26.8 ± 2.7 b	10.3 ± 0.9 b	17.1 ± 1.0 ab
Sagebrush	41.3 ± 5.9 c	1.31 ± 0.22 d	37.3 ± 4.7 a	11.9 ± 2.0 c	8.2 ± 0.6 c	17.1 ± 1.5 ab
Fescue	75.9 ± 4.3 a	3.19 ± 0.22 b	43.1 ± 7.2 a	26.8 ± 2.1 b	10.5 ± 0.4 b	17.5 ± 1.8 ab
Manure	82.2 ± 2.3 a	4.62 ± 0.23 a	29.3 ± 4.7 a	35.6 ± 5.2 a	12.4 ± 0.3 a	20.0 ± 0.7 a
Douglas-fir 2						
Mineral soil	47.8 ± 4.1 b	3.12 ± 0.29 bc	50.1 ± 5.6 b	29.4 ± 3.0 ab	12.4 ± 0.8 a	19.0 ± 1.3 a
Douglas-fir	6.6 ± 2.1 d	0.14 ± 0.04 e	87.5 ± 6.6 a	14.0 ± 3.3 c	8.6 ± 0.4 cd	12.7 ± 3.0 cd
Ponderosa pine	59.1 ± 2.6 b	2.42 ± 0.15 c	60.0 ± 5.6 b	24.7 ± 2.2 b	10.1 ± 0.7 bc	15.8 ± 0.8 bc
Sagebrush	31.6 ± 7.0 c	1.04 ± 0.21 d	57.8 ± 10.2 b	16.5 ± 2.0 c	7.9 ± 0.9 d	11.4 ± 2.1 d
Fescue	77.2 ± 2.1 a	3.50 ± 0.16 b	47.6 ± 3.8 b	27.2 ± 2.3 b	9.7 ± 0.4 cd	15.9 ± 0.7 abc
Manure	84.6 ± 2.4 a	5.15 ± 0.17 a	34.7 ± 5.8 b	32.6 ± 2.0 a	11.8 ± 0.6 ab	18.8 ± 0.4 ab
Ponderosa pine 1						
Mineral soil	36.0 ± 9.0 b	2.00 ± 0.50 bc	50.6 ± 9.4 a	31.6 ± 3.3 a	19.1 ± 2.2 a	51.0 ± 8.1 a
Douglas-fir	2.5 ± 1.3 c	0.06 ± 0.03 e	50.0 ± 0.0 a	2.0 ± 0.0 c	10.6 ± 1.2 a	37.0 ± 5.5 a
Ponderosa pine	42.2 ± 4.8 b	1.34 ± 0.16 cd	37.7 ± 7.1 a	20.0 ± 3.0 b	16.2 ± 0.6 a	41.6 ± 1.9 a
Sagebrush	23.6 ± 6.6 b	0.76 ± 0.22 d	60.0 ± 6.1 a	26.3 ± 6.6 ab	12.7 ± 1.5 a	40.0 ± 2.7 a
Fescue	67.8 ± 5.0 a	2.22 ± 0.16 ab	61.5 ± 9.9 a	24.9 ± 1.6 ab	14.0 ± 1.5 a	42.1 ± 4.2 a
Manure	67.2 ± 9.5 a	3.00 ± 0.42 a	57.0 ± 9.4 a	27.9 ± 2.9 ab	14.5 ± 1.3 a	47.8 ± 2.1 a
Ponderosa pine 2						
Mineral soil	41.1 ± 10.0 cd	2.30 ± 0.42 b	55.0 ± 4.6 a	32.3 ± 5.5 a	16.3 ± 2.0 a	44.9 ± 4.2 a
Douglas-fir	3.1 ± 0.6 e	0.08 ± 0.02 e	42.9 ± 17.0 a	15.7 ± 1.7 a	12.6 ± 2.1 a	21.2 ± 2.7 c
Ponderosa pine	49.7 ± 3.4 bc	1.48 ± 0.14 c	30.2 ± 5.9 a	18.2 ± 3.4 a	13.7 ± 1.1 a	34.9 ± 3.0 b
Sagebrush	27.8 ± 5.1 d	0.91 ± 0.18 d	41.4 ± 8.7 a	18.2 ± 3.9 a	12.6 ± 1.2 a	36.1 ± 2.0 b
Fescue	61.6 ± 3.5 b	2.16 ± 0.14 b	42.9 ± 7.8 a	21.7 ± 1.9 a	14.6 ± 1.1 a	38.8 ± 4.2 ab
Manure	82.5 ± 4.3 a	3.48 ± 0.32 a	53.5 ± 9.2 a	25.7 ± 1.9 a	13.6 ± 0.7 a	38.0 ± 2.5 ab

¹Values are mean ± SE of 8 replicates and data from 2 trials were pooled. Means with the same letter within a collection and a parameter are not significantly different at P = 0.05.

seedling mortality increased by nearly 1% day⁻¹ with time of emergence in Douglas-fir, indicating that seedlings emerging early in the season survived better than those emerging later (Fig. 1). Time of emergence had no significant effect on seedling mortality in ponderosa pine as indicated by the low r² value (although for ponderosa pine 2, P was less than 0.05). Longevity of those seedlings decreased with time of emergence at a rate of approximately 0.5 day⁻¹ for both species, indicating that seedlings emerging early in the season lived longer than those emerging later (Fig. 2).

Structural characteristics of seedbed

Both bulk density and relative volume varied significantly among the 6 seedbed types (Fig. 3). Bulk density decreased in the order from mineral soil, cattle manure, Douglas-fir needle, big sagebrush litter, ponderosa pine needle, to fescue litter. Relative volume decreased in the order of mineral soil, cattle manure, big sagebrush litter, Douglas-fir needle, ponderosa pine needle, and fescue litter, but there was no significant difference between the latter 2 types.

Effect of water extract on seed germination

Germination percentage and germination rate index (GRI) of ponderosa pine seeds were not affected by the 12 water extract treatments, averaging 89.8 ± 0.4% and 7.70 ± 0.17 % day⁻¹, respectively (data not shown). The treatment effect was significant for Douglas-fir (Table 3). Compared to distilled water and water extract from mineral soil, water extract

from soil beneath ponderosa pine needle enhanced germination by approximately 5%, and that from big sagebrush litter reduced germination by over 20%. Seed germination in all other water extracts was not significantly different from that in distilled water and water extract from mineral soil. The rate of germination, as measured by GRI, was lower in water extract from big sagebrush litter and higher in water extract of manure and mineral soil than in distilled water.

Table 3. Seed germination percentage and germination rate index (GRI) of Douglas-fir as affected by water extract of seedbed materials and of soil beneath them.

Water extract	Germination (%)	GRI (% day ⁻¹)
Distilled water	90.7 ± 1.7 b ¹	9.69 ± 0.20 cd
Douglas-fir	93.3 ± 1.1 ab	9.84 ± 0.22 c
Ponderosa pine	90.5 ± 1.7 b	9.13 ± 0.33 d
Sagebrush	69.4 ± 3.5 c	7.13 ± 0.21 e
Fescue	90.3 ± 1.8 b	10.15 ± 0.27 bc
Manure	93.2 ± 1.1 ab	10.74 ± 0.22 ab
Mineral soil	90.7 ± 1.8 b	11.04 ± 0.18 a
Soil beneath Douglas-fir	91.8 ± 1.0 b	9.98 ± 0.28 c
Soil beneath ponderosa pine	95.5 ± 1.1 a	10.31 ± 0.21 bc
Soil beneath sagebrush	89.0 ± 1.6 b	10.35 ± 0.19 abc
Soil beneath fescue	91.3 ± 1.6 b	9.85 ± 0.32 c
Soil beneath manure	91.2 ± 0.9 b	10.14 ± 0.22 bc

¹Values are mean ± SE of 8 replicates. Means with the same letter within a collection and a parameter are not significantly different at P = 0.05.

Fig. 1. Seedling mortality of Douglas-fir and ponderosa pine as a function of day of emergence. Data for all treatments were pooled according to species and collection.

Fig. 2. Seedling longevity of Douglas-fir and ponderosa pine in relation to day of emergence. Data for all treatments were pooled according to species and collection.

Fig. 3. Structural characteristics of the 6 seedbeds. Data are mean $\pm$ SE of 8 replicates. MS: mineral soil, DF: Douglas-fir needle, PP: ponderosa pine needle, SB: big sagebrush litter, F: rough fescue litter, M: cattle manure.

Discussion

Substrate condition or seedbed is a major determinant in the regeneration niche for seedlings (Grubb 1977). The 6 seedbed types tested in the present study, including Douglas-fir and ponderosa pine needles, are representative of the forest-grassland ecotone in British Columbia, because conifer trees are common in the grasslands as a result of encroachment. Bare soil surface is generally favorable for conifer seedling emergence because litter accumulations on forest floors restrict seed germination and seedling establishment of conifer trees (Bramble and Goddard 1942, Chrosiewicz 1974, Van Wagner 1983), including Douglas-fir (Caccia and Ballaré 1998) and ponderosa pine (Roe and Squillance 1950, Foiles and Curtis 1965). In the present study, both Douglas-fir needle and big sagebrush litter restricted seedling emergence of Douglas-fir and ponderosa pine compared to mineral soil, but fescue litter and dry cattle manure fragment actually enhanced the emergence of the 2 species. Interestingly, ponderosa pine needles did not restrict seedling emergence of its own or Douglas-fir, possibly because the water availability in our experiment was less limited than in other field studies (Roe and Squillance 1950, Foiles and Curtis 1965).

The effect of litter on seed germination and seedling emergence depends on litter type and species studied; both the physical structure and chemical composition of litter may contribute to differences in

seedling emergence observed in the field. Allelopathy has been reported in a wide range of species and the effect was species specific (Grant 1964, Ballester et al. 1979, Kil and Yun 1992). The water extracts of the 6 types of seedbed materials as well as of soils beneath them had no effect on seed germination of ponderosa pine and only a marginal effect on Douglas-fir. The water extract of big sagebrush litter, but not of Douglas-fir needle as previously reported (Daniel and Schmidt 1972), reduced seed germination in Douglas-fir. It is possible that allelopathy, even if it exists in some of the materials studied, could have been reduced during decomposition, since fresh needles or litter were mostly absent on the soil surface when samples were collected in the spring. Nevertheless, structural characteristics of these materials may provide a better explanation of the observed differences among seedbeds.

The effect of structural characteristics of seedbed materials on seed germination and seedling emergence has not received as much attention as allelopathy, possibly due to the difficulty of quantitative comparison among seedbeds. In general, litter materials buffer soil temperatures and help conserve soil moisture (Sydes and Grime 1981, Fowler 1986, Williams et al. 1990). On the other hand, seeds can be entrapped between layers of litter (Burbidge 1945), preventing germination by reducing the contact between seeds and surrounding materials. Even for the same type of litter, horizontal or vertical arrangement pro-

duced a different architecture, modifying temperatures under the litter layer (Bristow 1988). Mineral soil and manure fragments had the highest bulk density and relative volume among the 6 types of materials in our study, providing maximum contact with seeds and subsequently optimal water supply for seed germination. On the other hand, ponderosa pine needle and fescue litter were characterized by low bulk density and low relative volume. Therefore, seeds are not likely trapped in their loose structure, but fall through, contacting mineral soil. Douglas-fir needle and big sagebrush litter had moderate bulk density and relative volume and seeds are more likely to be trapped within these materials, resulting in low seedling emergence. The 2 factors, namely structural and chemical characteristics, may interactively affect seed germination as reported in the effect of oak litter on seedling emergence of table mountain pine (*Pinus pungens* Lam.) (Williams et al. 1990).

The effect of structural characteristics of seedbeds is related to moisture availability, which is highly variable in the field and may result in different results from controlled experiments such as the current study. Regardless of seedbed types, over 50% of seedlings of Douglas-fir and ponderosa pine emerged in the first 4 weeks (data not shown). Seedlings emerging early in the season have survival advantage (Miller 1987, Streng et al. 1989). Grasslands of British Columbia are characterized by low annual precipitation and extremely dry summers (Spilsbury and Tisdale 1944, Tisdale and McLean 1957) and conifer seedling establishment usually occurs when moisture conditions were close to or above the long-term average (Arno and Gruell 1983, 1986). Successful encroachment of these 2 tree species may therefore depend on the ability of seeds to germinate early in the season when soil moisture conditions are favorable and on seedbeds that can provide sufficient moisture.

In conclusion, seedbeds in grasslands of British Columbia, such as mineral soil, fescue litter and cattle manure fragment, favor seed germination and seedling establishment of Douglas-fir and ponderosa pine compared to those on forest floors, such as Douglas-fir needle. Differences among seedbeds are most likely due to their structural, but not chemical characteristics. Fire suppression, grazing and tree logging will modify the soil surface, and other factors such as weather conditions and competition will interactively influence seedling establishment of the 2

species. Field studies are therefore necessary for isolating factors causing tree encroachment for specific areas.

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Grassland biomass dynamics along an altitudinal gradient in the Pampa

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Abstract

Above and below-ground biomass and necromass dynamics were assessed for 3 grassland sites located at 550, 850, and 1,025 m elevation in Sierra de la Ventana range (38°1'S 62°2'W) in Argentina. The objective was to determine if differences existed in dry matter structure, mycorrhizae infection, net primary productivity (NPP) partitioning to aboveground and belowground tissues, senescence and litter fall, and seasonal patterns of dry matter fluxes with altitude. Soil properties, water budgets and temperature at the sites were also assessed. Biomass plus necromass (without litter) was $1,184 \pm 41$, $1,208 \pm 70$, and $1,507 \pm 63$ gDM m⁻² for the lower, intermediate and upper sites, respectively. The below:aboveground biomass ratio increased with elevation. Total NPP was 1,131, 1,280, and 1,157 gDM m⁻² year⁻¹, respectively, for the 3 grassland sites. belowground allocation of net productivity increased with altitude. Both mass and proportion of thin roots increased with elevation, and so did mycorrhizae infection. The aboveground and belowground turnover rates decreased with altitude, but rates were faster for aboveground tissues. We found different temporal patterns in productivity, senescence and disappearance among grassland sites despite similar total NPP. Water holding capacity of soils and temperature were important factors related to several of the observed trends in structure and function. Differences in grassland structure and fluxes are discussed as related to soils and local climate at each site.

Key Words: aboveground, belowground, litter, phytomass, productivity, roots

Natural grasslands dominate the landscape of the Sierras Australes (Buenos Aires, Argentina). The grass genera with more native species in the area are *Stipa* and *Piptochaetium*; other important species because of their abundance include *Briza*, *Sorghastrum* and *Festuca*. These hills (spanish *sierras*) are a gondwanic folding system extending NE to SW, 170 km in length x 65 km maximum width. The highest point in the Pampas is

Resumen

Se evaluó la dinámica de la biomasa y necromasa, aéreas y subterráneas, de tres sitios de pastizal ubicados a 550, 850, y 1,025 m de elevación en la Sierra de la Ventana (38°1'S 62°2'O), Argentina. El objetivo fue determinar si existían diferencias en la estructura de la materia seca, la micorrización, la asignación de la producción primaria neta (NPP) a tejidos aéreos y subterráneos, la senescencia y caída al mantillo, y los patrones de los flujos de materia seca con la altitud. También se consideraron las propiedades del suelo, los balances de agua y la temperatura de cada sitio. La biomasa más la necromasa (sin broza) fue de $1,184 \pm 41$, $1,208 \pm 70$ y $1,507 \pm 63$ gMS m⁻² para los sitios inferior, intermedio y superior, respectivamente. El cociente biomasa subterránea:aérea se incrementó con la elevación. La NPP total fue 1,131, 1,280 y 1,157 gMS m⁻² año⁻¹, respectivamente, para los tres sitios de pastizal. La asignación subterránea de la productividad primaria neta se incrementó con la altitud. La masa y la proporción de raíces finas, como también el porcentaje de micorrización, aumentaron con la elevación. Las tasas de renovación aérea y subterránea decrecieron con el aumento de la altitud, pero las tasas fueron más rápidas para los tejidos aéreos. Nosotros encontramos distintos patrones temporales en la productividad, senescencia y desaparición entre pastizales a pesar de su similar NPP. La capacidad de retención de agua del suelo y la temperatura fueron importantes factores relacionados a varias de las tendencias observadas en la estructura y funcionamiento de los pastizales. Las diferencias en la estructura y los flujos de los pastizales son comentadas en relación a los suelos y clima local de cada sitio.

peak Tres Picos (1,243 m elevation) (Harrington 1947, Suero 1972). The macroclimate at this area has been described elsewhere (Burgos 1968, Cappanini et al. 1971, Frangi and Bottino 1995). According to Thornthwaite (1948) the climate is C2 B'2 r a' -humid-subhumid, mesothermal, with a small to null water deficit, and a summer thermal concentration <48 %. Because of the low elevation of the hills, and being perpendicular to the atmosphere general circulation, they are not an effective condenser of atmospheric humidity but are effective in temperature reduction. Precipitation diminishes from NE to SW. Sierra de la Ventana (249 m asl), the nearest town to the study area, has an annual-long term mean temperature of 14.5°C and 809 mm precipitation. In the Pampas, the interannual variation of rains is ca. $\pm 50\%$ of the mean (Vervoorst 1967, Cappaninni et al. 1971).

The local geology is characterized by siliciclastic sedimentites of the Ventana Group, Lower Devonian age, containing fossils of *Brachyopoda* (Andreis et al. 1989, Von Gosen et al. 1990). They

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mostly consist of cross-bedded quartzites and sandstones, with grain-size diminishing upward cycle. Group thickness is about 1,400 m. Wide and shallow platforms and littoral zones constituted the paleoenvironment. Rocks were deformed by folding and internal faulting. The resulting sierras profile was asymmetric, with the eastern flank more extended and formed by steps motivated in the structural repetition by folding of more resistant lithological levels. The soils are lithic Hapludols, typic and lithic Argiudols and lithic Hapluudols developed on quaternary loessoid sediments sometimes mixed with fragments of base rock or intercalated CaCO_3 rock layers (Cappanini et al. 1971, Vargas Gil and Scoppa 1973, Frangi et al. 1980a, 1980b, Pérez 1996).

Grassland communities have been linked to differences in biotope and mesoclimate (Frangi and Bottino 1995, Kristensen and Frangi 1995). The greatest dissimilarity in local climates was between lowland and mountain grassland sites. The former are warm, anisothermic with higher diurnal evaporative capacity. They are covered by medium-sized feather grasses (*Stipa* and *Piptochaetium* species) in the piedmont and medium-sized tussocks of *Stipa caudata* Trinius or *S. ambigua* Spegazzini and *S. caudata* Trinius grasslands in deep soils of the valley bottoms¹. Steep SW slopes differ markedly in local climate and grass flora compared with gentle slopes (Frangi and Bottino 1995, Kristensen and Frangi 1995). Steep SW slopes are cold, isothermic, and very humid, receive low solar radiation during most of the year and are covered by *Festuca pampeana* Spegazzini tussock grasslands.

The NE and SW gentle slopes are covered by *Sorghastrum pellitum* (Hackel) Parodi and *Stipa filiculmis* Delile short grassland. They show intermediate conditions between the upper and lowland sites. The thermal gradient supported the existence of a montane bioclimatic belt above 750 m.

Mountain summits and high ridges are covered with short grasses and cushion plants. Fine textured soils give rise to high sierra meadows with *Briza subaristata* Lamarck, *B. brizoides* (Lamarck) O. Kuntze and *Festuca ventanica* Spegazzini in concave to flat more humid sites, with *Sorghastrum pellitum* and *Stipa filiculmis* short grassland on upper slopes. Stony soils are covered by *Grindelia chiloensis* Cabrera an evergreen dwarf

shrub. Climatic conditions are more extreme; they are colder and windy with the highest evaporative air capacity (Piche method) that is reduced in the winter because of clouds and mist.

Vegetation differs in physiognomy, species composition, and phytogeographic relationships among plant species (de la Sota 1967, Frangi and Bottino 1995). Biomass structure changes as well with elevation, slope and aspect (Barrera and Frangi 1994). Aboveground biomass decreases and belowground biomass increases with altitude. Aboveground net primary productivity (ANPP) has only been measured in low altitude grassland sites (Frangi et al. 1980a, 1980b).

Mountain grasslands are used as grazing lands (Ricci 1992). Overgrazing encourages bush encroachment (Barrera 1991, Barrera and Frangi 1996). Non-disturbed grasslands are important in erosion control and water quality of tributaries of the Sauce Grande river, a source of consumption water for the city of Bahía Blanca (Dascanio and Bianchi pers. com.). Exotic tree plantations are assumed by local people to protect steep slopes but symptoms of overland erosion under forest canopy are common (Frangi and Bottino 1995, Barrera and Frangi 1996).

The compositional, physiognomical and structural changes in biomass with topography, soil and local climate caused us to select an altitudinal gradient with a more limited complexity to answer the following questions: Are differences in dry matter structure correlated with net primary productivity (NPP) changes or only with partitioning among above- and belowground tissues? Do seasonal patterns in dry matter fluxes change along the altitudinal gradient? The hypotheses were: (1) Above- and belowground community biomass structure changed with elevation to reflect adaptations to improve available resource absorption; (2) NPP diminished with altitude because of less favorable local climate and soil conditions; (3) NPP allocation changed with elevation toward a greater proportion of roots at higher elevations; and, (4) Community differences in temporal patterns of dry matter fluxes indicated differences in plant strategies to changes in temperature and water availability along the elevational gradient.

The objectives were to determine the biomass and necromass structure including root sizes and mycorrhizae infection, net primary productivity partitioning to above- and belowground tissues, senescence and litter fall, and seasonal patterns of above- and belowground net productivi-

ty, senescence and disappearance at 3 grassland sites located at 550, 850, and 1,025 m asl. Soil properties, water budgets, and temperature at these sites were also determined.

Methods

Study sites

The 3 sites were located on an eastern secondary divide at peak El Destierro I (38°1'S 62°2'W), Ernesto Tornquist Nature Reserve. Slope was about 3% at all sites. Plant communities (Frangi and Bottino 1995) were described as short grassland with *Piptochaetium hackelii* (Arechavaleta) Parodi and *P. napostaense* (Spegazzini) Hackel, with *Briza subaristata* Lamarck dominating the low site (550 m). Short grassland with *Sorghastrum pellitum* (Hackel) Parodi and *Stipa filiculmis* Delile dominate the intermediate and high sites (850 and 1,025 m). In this paper we refer to the sites as lower (LS) 550 m elevation, intermediate (IS) 850 m elevation, and upper (US) 1,025 m elevation.

Soils

Six to 9 soil cores (0–20 cm depth) were obtained at random from a 0.5 ha area, in spring, fall and winter, from each site. These samples were immediately cleaned of roots and air-dried. A mixed composite soil sample for each site and date was prepared for physico-chemical analysis (n = 3 per site). Traditional methods were employed for texture using a sieving machine and densimeter (Duchaufour 1970). Soil pH was determined in a 1:1 (soil:water) paste using a pH meter with a combination electrode. Total soil nitrogen (N) and carbon (C) were determined using the CNS LECO 2000 procedure (Tabatabai and Bremner 1991). Available P was analyzed with the Bray & Kurtz #1 method (Page 1982). The cation exchange capacity (CEC) was assessed using 1N neutral ammonium acetate extraction (Page 1982). Exchangeable Ca, Mg, and Na were determined using 1N KCl extraction method and exchangeable K with Olsen EDTA procedure (Hunter 1982). Additionally, during the spring sampling, apparent density (AD) was estimated for 3 soil cores of known volume (6.5 cm diam. x 10 cm height) at 0–10 and 10–20 cm depth per site and dried at 70°C to constant weight. An average apparent density for 0–20 cm soil depth was calculated for each site (n = 3) discarding weight of pebbles. Soils were classified according to the Soil Survey Staff (1992).

¹Species nomenclature follows Cabrera (1963, 1970).

Water budgets

Thornthwaite's (Thornthwaite and Mather 1957) water budgets were calculated for each site using a computer program. Water retention maximum capacity (WRM) at each site was estimated according to:

$$\text{WRM (mm)} = (0.023 \times \text{sand fraction} + 0.25 \times \text{silt} + 0.61 \times \text{clay}) \times \text{AD (g cm}^{-3}) \times \text{depth (cm)} \times 10.$$

Monthly temperatures were estimated with data from the Sierra de la Ventana weather station (SMN 1981), altitudinal thermal gradients for each season (Kristensen and Frangi 1995) and site elevation. Weekly precipitation during the study period was measured with 1 standard US Weather Bureau type rain gauge per site.

Biomass and necromass

We used the following definitions: biomass was dry weight of live plant material; necromass was dead plant mass (standing dead, litter, and dead roots); aboveground dry matter was aboveground biomass plus standing dead; belowground dry matter was the sum of live and dead roots and, total dry matter was biomass plus necromass.

Sampling was done in 0.5 ha grazing exclosures, at 9 dates between July 1988 and July 1989. A stratified randomized design was used for sampling above- and belowground live and dead mass compartments. The aboveground dry matter was estimated by the harvest method (Milner and Hughes 1970). At each grassland site and on each date we collected ten, 0.25 x 1 m pseudoreplicates (according to Hurlbert 1984). Plant matter and litter were collected in separate bags. To avoid resampling a plot, we put a stake in each clipped quadrat. Plant matter was hand-separated into categories: green grasses, green dicotyledonous herbs, standing dead material, and reproductive tissue.

The belowground dry matter in 0–10 and 10–20 cm soil depth was estimated using a 6.5 cm diam. x 10 cm height soil core. On each date and site we extracted 10 cores from each soil depth at each aboveground harvest unit. Cores were processed by wet sieving over a 1-mm² mesh screen (Böhm 1979). Collected roots were washed free of soil, visually classified, and separated with tweezers into live (soft, translucent, white to brownish) or dead (brittle, opaque, and grayish) according to Böhm (1979) and McLaugherty et al. (1982) and subdivided according to diameter as thin (<1mm) or thick (>1mm)

roots. Plastic bags containing sampled plants, litter, or soils were stored in a freezer (–12°C) until they were separated, classified and dried to constant weight at 70°C.

Mycorrhizae

We estimated arbuscular (A-) mycorrhizae fungal infection of roots in each grassland in December 1988. Six soil samples were taken from each soil depth. Roots were extracted, clarified with KOH (7.5%) at 90°C for 20-minutes and stained employing the procedure of Phillips and Hayman (1970). Infection was measured with a line-intercept method under a 40X stereomicroscope (Giovannetti and Mosse 1980). A-mycorrhizal spores were extracted with the wet-sieving and decant technique (Gerdemann and Nicolson 1963) and counted under a 10X stereomicroscope.

Fluxes

For aboveground net primary products (ANPP), senescence, litterfall, and disappearance calculations we used the sum of differences between live and dead compartments (Frangi et al. 1980 a). Likewise we modified the equations to calculate belowground fluxes (Table 1). We used only the significant differences (Student t, $P < 0.05$) between the extremes of intervals with increasing or decreasing values trends of each compartment.

Total net primary products (NPP) was the sum of ANPP and belowground net primary products (BNPP). Aboveground and belowground turnover rates were calculated as the ratio between productivity and the annual mean of biomass of above and belowground compartments, respectively (Frissel 1981). Dry matter turnover rates were calculated employing the equivalent dry matter values.

Statistics

The differences in soil parameters among sites were compared with a one-way ANOVA. The plant compartment differences among sites and dates were evaluated using a repeated measure ANOVA. Previously we corroborated the variance homogeneity. To compare percentages of aboveground and belowground biomass compartments with total biomass we transformed the data to $\arcsin (\%^{1/2})$. We employed the F-test to determine significant differences between dates and sites and the studentized rank test of Tukey ($P < 0.05$) for mean comparisons (Sokal and Rohlf 1969). Multiple regression analysis was applied to explain relationships among plant mass compartments or ratios and independent variables. This analysis was performed with the pooled data of the 3 sites. The partial correlation of this variable was calculated after fitting other independent variables into an equation. When a non-significant partial correlation was found, it was interpreted that the other independent variables accounted for most of the differences among sites.

Results

Soils and water budget

Soils at all sites were classified as Lithic Hapludolls, notwithstanding a lower base saturation of some samples that indicated at intermediate site (IS) and upper site (US) there were Lithic Haplumbrepts also present. The texture was clay loam to loam at lower site (LS), loam at IS and sandy loam at US. Clay decreased by 50% between LS and US (Table 2). The organic carbon values were very high and the C:N ratios are similar and common to Pampa grassland soils. Soil pH decreased with elevation and was moderately acid at

Table 1. Formula to calculate aboveground and belowground dry matter fluxes, net primary productivity (ANPP = aboveground; BNPP = belowground), senescence (M), litterfall (C) and disappearance (D).

Aboveground			
ANPP =	$B^+ + (M - B^-) = B^+ + m$		
M =	$B^- + m$	being m =	$S - B^- + H^+$ (whenever $m > 0$)
C =	$H^+ + c$	being c =	$B^- - S - H^+$ (whenever $c > 0$)
D =	$d - H$	being d =	$B^- - S$ (whenever $D > 0$ and $d > 0$)
Where: B^+ : Positive increment in biomass, B^- : Decrease in biomass, S : Change in standing dead stock, H^+ : Positive increment of litter, H : Change in litter stock.			
Belowground			
BNPP =	$RV^+ + (M - RV^-) = RV^+ + m$		
M =	$RV^- + m$	being m =	$RM - RV^-$ (whenever $m > 0$)
D =	$RV^- - RM$		(whenever $D > 0$)
Where: RV^+ : Positive increment in live roots, RV^- : Decrease of live roots, RM : Change in dead roots stock.			

LS and moderately to very acid at both other sites. The CEC was similar at all sites, but its variation increased with elevation. Base saturation was high at low altitude and moderate at high elevation (Table 2). A traditional fertility data interpretation indicated that these soils were very well supplied in total N, moderately supplied in P, and adequately supplied in exchangeable K. Exchangeable Ca was well supplied at LS, but its CEC-saturation was significantly lower at IS and US. Magnesium was high at all sites and showed the same trend as Ca.

Low values of apparent soil bulk density can be related to the high organic matter content, with inter-site differences attributable to texture changes and also to a greater fraction of discarded pebbles at IS and US (Table 2).

Annual precipitation (P) increased with elevation, with 745, 786, and 828 mm at the LS, IS, and US, respectively. Days with rains were 29, 30, and 25 at LS, IS, and US, respectively, and maximum consecutive days without rains during the sampling intervals were about 17 days. Potential (PET) and actual evapotranspiration (AET) decreased with elevation whilst P/PET and P/AET ratios increased with elevation. The P/PET ratio was 1.1, 1.2, and 1.4 for LS, IS, and US, respectively, and the P/AET ratio was 1.41, 1.56, and 1.78 at the same site sequence. Maximum water retention capacity of soil diminished with elevation, with upper site 50% of lower site. The values observed were influenced by the shallow soil depth considered (20 cm) that corresponded to the rooting zone but also to the total profile at IS and US. The water budget showed clearly the alternation of humid and dry periods in the soils (Fig. 1). The humid periods

Fig. 1. Thornthwaite's water budgets in grasslands sites located at different altitudes from July 1988 to July 1989. WRM = maximum water retention capacity; PET = potential evapotranspiration; AET = actual evapotranspiration.

Table 2. Physico-chemical characteristics of soils at lower (550 m asl), intermediate (850 m asl) and upper (1,025 m asl) grassland sites. Values are ranges or means for composite samples (n = 3) per site. Different letters indicate significant differences among the 3 sites (Tukey, $P < 0.05$).

Soil parameter	Lower	Intermediate	Upper
Apparent density (g cm^{-3})	0.850 a	0.649 b	0.606 b
pH (soil/water 1:1)	5.4 to 5.9 a	4.3 to 5.4 a	4.1 to 5.2 a
Texture (%)			
Sand	40.50 b	44.40 b	58.40 a
Silt	30.70 a	39.00 a	28.00 a
Clay	28.90 a	16.60 b	13.60 b
Organic Carbon (%)	4.91 a	5.64 a	5.90 a
Total Nitrogen (%)	0.44 a	0.48 a	0.55 a
C:N ratio	10.9 a	11.8 a	10.9 a
P available (ppm)	12.17 a	10.50 a	11.45 a
CEC ($\text{cmol}_c \text{ kg}^{-1}$)	22.20 a	22.30 a	20.15 a
Exchangeable bases ($\text{cmol}_c \text{ kg}^{-1}$)			
Ca^{+2}	15.43 a	9.07 b	6.19 c
Mg^{+2}	6.56 a	4.31 b	2.78 c
Na^{+}	0.44 a	0.29 a	0.28 a
K^{+}	0.84 a	0.53 a	0.43 a
Base saturation (%)	90.0 to 98.6 a	50.0 to 92.2 a	39.0 to 68.3 b

occurred during early spring and fall at all sites. The late-spring water deficit was greater at both IS and US. Summer is clearly the main water consumption period but some recharge also happened; however, most recharge occurred in the autumn. Temperatures favored water consumption during winter at all sites but at US there was a water surplus.

Plant compartments mass

Total dry matter was greater at the upper site (US) ($1,552 \text{ g m}^{-2}$) by 20% more than either of the other 2 sites ($1,260 \text{ g m}^{-2}$ at IS and $1,225 \text{ g m}^{-2}$ at LS). The belowground dry matter increased with altitude and was 52, 62, and 73% of total dry matter at the lower site (LS), intermediate site (IS), and upper site (US), respectively. Litter

Fig. 2. Annual mean dry weight for different plant compartments in grasslands sites: a) aboveground (A-), belowground (B-) and total dry matter, all in (g m⁻²); b) Aboveground (A-) biomass and live thin and thick roots (%) with respect to total biomass (g m⁻²). Different letters indicate significant differences among compartment mean for the 3 sites (Tukey, $P < 0.05$). Least squares trend lines are indicated with broken line.

attained only about 3% of total dry matter at all sites.

Above- and belowground dry matter differed according to location and sampling dates. aboveground dry matter decreased with elevation, while belowground dry matter increased with elevation (Fig. 2a). The rate of decrease in aboveground dry matter was more pronounced (43 g m⁻² per 100 m elevation) between LS and IS than between IS and US (21 g m⁻² per 100 m). The rate of increase in belowground dry matter was greater between IS and US (199 g m⁻² per 100 m) than between LS and IS (47 g m⁻² per 100 m).

Although aboveground dry matter was mainly standing dead and aboveground biomass was similar at all sites, the relative contribution of live tissue increased with elevation (27, 34, and 36% at LS, IS, and US, respectively). belowground dry matter was mainly contained in the 0-10 cm soil layer: 71% at IS, 64% at LS and

68% at US; the last 2 were not significantly different.

Normalized proportions of each live compartment with respect to total biomass changed significantly among sites and dates. The green fraction decreased with increasing elevation. Thin roots were the main contributing root compartments to belowground biomass and were responsible for the increase in total live roots with increasing elevation (Fig. 2b). Roots colonized by endophytes forming A-mycorrhizae changed significantly from 40 to 57% with elevation (Fig. 3). Spores showed a non-significant decreasing trend in the same direction (20, 19, and 14, respectively).

Inter-site differences in biomass and dry matter compartments over time resume a distinct balance of functional processes at each site and date, as indicated by statistically significant interactions between location and sampling dates (Fig. 4). The US showed smooth changes in plant compartments over time, whereas both other sites manifested more noticeable stock peaks at different months.

Plant mass and the physical environment

The multiple regression analyses performed for aboveground dry matter, belowground dry matter, belowground biomass, or above-/belowground biomass ratio with independent variables of monthly mean minimum temperature, monthly available soil water, and monthly actual evapotranspiration were significant (Table 3). The regression coefficients of monthly

Fig. 3. Thin-/thick live roots ratio and mycorrhizae infection (%) in grasslands sites at different altitudes from July 1988 to July 1989. Vertical lines indicate $\pm$ SE.

Fig. 4. Above- and belowground dry weight (g m^{-2}) for various compartments at 3 grasslands sites located at different altitudes from July 1988 to July 1989.

actual evapotranspiration were non-significant for aboveground dry matter and above/belowground biomass.

The variable site was significantly correlated with all the dependent variables. When these correlations were partialled out by the independent variables of the regression models, no significant correlations were obtained with aboveground dry matter and above/belowground biomass. Monthly available soil water and mean minimum temperature (in that order of importance) mainly explained the differences in dependent variables among sites. The similar range of aboveground biomass at all sites, together with asynchronic inter-site variation, appears to explain the absence of correlation with the monthly independent variables (Fig. 4).

Fluxes and turnover rates

Annual net primary products (NPP) was similar at all sites (ca. 1,131 to 1,280 g m^{-2}) but the partitioning between above- and

belowground tissues changed among sites (41–59% at lower site, 46–54% at intermediate site and 33–67% at upper site, respec-

tively) (Table 4). Total NPP was bimodal, with one peak during the winter and spring and, another, in summer and autumn. The winter-spring NPP peak was more noticeable at IS and US (73 and 64% of annual NPP, respectively), since productivity was more evenly distributed at the LS (46% in winter-spring and 54% in summer-autumn). Reproductive tissues showed a major period of production during spring and lesser production at the beginning of autumn. The spring period showed 2 peaks of reproductive productivity at LS; one at the end of October comprised mainly by the winter exotic annual *Vulpia dertonensis* (Allioni) Gola, and another at the beginning of December composed of feathers (*Stipa* and *Piptochaetium*). Annual grasses were unimportant at both other sites.

Total senescence was greater and similar at LS and US. The root contribution to total senescence increased with site elevation (61, 64, and 68%). Litterfall increased slightly with elevation and represented about 10% of total senescence. Total disappearance of above- and belowground plant parts was greater in both elevational extreme sites (LS and US), where the main contribution came from belowground mass (88 and 68%, respectively). Total disappearance at IS was nearly 50% of both other sites and equally distributed between below- and aboveground tissue (Table 4). As a consequence of differences in litterfall and aboveground disappearance dynamics among sites the LS accumulated a maximum of litter at the end of February, whereas both the other sites had maximum accumulation at the end of December (Fig. 5).

Table 3. a) Multiple regression analysis of dry matter and biomass (g m^{-2}) in grassland sites to water, temperature and evapotranspiration. Only significant equations are given; the non-significant contribution ($P > 0.05$) of individual variables are indicated as (ns). b) Correlation and partial correlation of the site variable with the dependent variables. W = monthly available water (mm); T = minimum monthly temperature ($^{\circ}\text{C}$); ET = monthly actual evapotranspiration (mm); A- = aboveground; B- = belowground.

a)								
Dependent variables	Equation		Adjusted R ²	P	n			
Above-ground dry matter	Y = 275 + 8 W + 19 T - 1.4 ET ^(ns)		0.55	<0.0001	27			
Above-ground biomass			-0.075	0.759	27			
Below-ground dry matter	Y = 989 - 14 W - 38 T + 8 ET		0.35	<0.009	24			
Below-ground biomass	Y = 661 - 13 W - 64 T + 14 ET		0.42	<0.002	24			
B/A biomass ratio	Y = 6 + 0.14 W - 0.8 T - 0.2 ET ^(ns)		0.54	<0.0004	24			
b)								
	Dependent variable							
	A-dry matter		B-dry matter		B-biomass		A/B biomass	
Site variable	r	P	r	P	r	P	r	P
Correlation	0.59	<0.001	-0.80	<0.001	-0.77	<0.001	-0.67	<0.001
Partial correlation	0.006	0.98	-0.81	<0.001	-0.84	<0.001	-0.21	0.36

Table 4. Above- and belowground biomass, productivity, senescence, litterfall, disappearance and turnover rates at lower (550 m asl), intermediate (850 m asl) and upper (1,025 m asl) grassland sites. NPP = net primary productivity.

Parameter	Site		
	Lower	Intermediate	Upper
Biomass (g m^{-2})			
Aboveground	146 a	138 a	131 a
Belowground	410 c	615 b	904 a
Total biomass	556 c	753 b	1035 a
Net primary productivity ($\text{g m}^{-2} \text{y}^{-1}$)			
Aboveground	462	585	378
Belowground	669	695	779
Total NPP	1131	1280	1157
Senescence ($\text{g m}^{-2} \text{y}^{-1}$)			
Aboveground	434	374	319
Belowground	685	368	691
Total senescence	1119	742	1010
Litterfall ($\text{g m}^{-2} \text{y}^{-1}$)	107	210	232
Disappearance ($\text{g m}^{-2} \text{y}^{-1}$)			
Aboveground	103	200	210
Belowground	756	275	731
Total disappearance	859	475	941
Dry matter turnover rate (y^{-1})			
Aboveground	0.9	1.4	1.0
Belowground	1.0	0.9	0.7
Biomass turnover rate (y^{-1})			
Aboveground	3.2	4.2	2.9
Belowground	1.6	1.1	0.9

Turnover rates for aboveground biomass were higher than for belowground biomass at all sites (Table 4). The US presented the slowest turnover rates of live tissues.

Discussion

Soils and water budget

The reduction of the mineral colloidal fraction with elevation was buffered by the high content of soil organic matter and this explains similar CEC's at all sites. The lower base saturation and pH at higher elevation indicated that even though these were fertile soils, exchangeable nutrients were more limited at higher elevations. The relief heterogeneity and increased precipitation and runoff at the higher elevation site also influenced soil characteristics and helped to explain the increased variation in soil parameters. Thornthwaite's water budgets, estimation of runoff, and actual evapotranspiration gave comparable results to those empirically derived during the same period from the 158 ha watershed where the research sites were located (Bianchi and Dascanio pers. com.). The runoff at upper site and intermediate site were 44 and 36% of precipitation, respectively, vs 39–40% from the entire watershed above 550 m. Thornthwaite's water budget calculation did not include the wind effect in the evapotranspiration estimation. Although the upper slopes and

crest grasslands are colder and more humid with the lowest air saturation deficit, stronger winds provoke higher air evaporative capacity than found at lowlands (Kristensen and Frangi 1995). The wind effect should be important in increasing water vapor loss from soil surfaces and aboveground biomass at the upper site.

Biomass and necromass structure

Barrera and Frangi (1994) demonstrated that, between 350 and 1,100 m elevation, belowground dry matter increased linearly and aboveground dry matter decreased exponentially with elevation. Our sites were located within the elevational range studied by Barrera and Frangi (1994) and did not include the lowland tussock grasslands and high sierra meadows at the extremes of the gradient. Both independent studies showed similar trends in biomass with temperature change (Fig. 6). The results were consistent with the inverse relationship between belowground dry matter and temperature demonstrated by Sims et al. (1978).

Biomass distribution within plants is related to historic selective pressures and the present environment (Piper 1989). In a similar manner, the belowground/aboveground biomass ratio is an indicator of the allocation of energy to belowground and aboveground organs (Sims et al. 1978). In the sierra grasslands, this quotient

increased with elevation. Sims et al. (1978), in their studies of North American grasslands, indicated that it was not possible to assume a general relationship between aridity and high belowground/aboveground ratios. This ratio could be more related to life forms (Noy-Meir 1973, Liang et al. 1989) or temperature regime than with aridity (Noy-Meir 1973, Sims et al. 1978).

In Sierra de la Ventana altitudinal differences in belowground/aboveground biomass ratio could not be related to aridity as indicated by general climate and P/AET and P/PET ratios at each site. Lower soil water retention with elevation probably played an important role in magnifying the temporary water shortage derived from periods with several consecutive days without rain.

The relationship of the belowground/aboveground biomass ratio with life form has been recognized in tussock and non-tussock grasses of these sierra grasslands (Barrera and Frangi 1994); however, within each life form the ratio increased mainly as temperature decreased.

The belowground/aboveground dry matter ratio also increased with elevation. This ratio was 1.2 for the lower, 1.8 for the intermediate, and 3.0 for the upper site. These values are within the total range of physiognomic and altitudinal grassland types of Sierra de la Ventana, where the ratio varies between 0.13 (at 350 m with tussocks) to 4 (in the crests at 1,100 m elevation) (Barrera and Frangi 1994).

Körner and Renhardt (1987) have indicated for the Central Alps that the increased dicotyledonous herb belowground dry matter fraction at higher elevation resulted from shoot reductions and a proportional increase in thin roots. An extended thin root system at higher elevations could be a functional substitute for mycorrhizae that are more common at low elevations. Although mycorrhizal colonization directly with increases in soil temperature (Azcón-Aguilar et al. 1984), the degree of fungal colonization forming AMycorrhizae is also dependent on root system morphology, since thin roots are more susceptible to colonization (Hetrick et al. 1988, Reinhardt and Miller 1990). In sierra grasslands under a milder climate than the alpine, our results suggested a greater mycorrhizal activity coincidently with more thin roots rather than with temperature, as temperature decreased with elevation. belowground biomass and mycorrhizae abundance indicated greater soil volume

Fig. 5. Aboveground fluxes: net primary productivity (ANPP), senescence (ASEN), litterfall (FALL) and disappearance (ADIS); and belowground fluxes: net primary productivity (BNPP), senescence (BSEN) and disappearance (BDIS) in grassland sites at different altitudes from July, 1988 to July, 1989.

occupation when availability of soil resources decreased. Chapin (1991) has proposed that a more intense occupation of soil volume is a general response of plants to stress when resources are limiting.

Dry matter dynamics and fluxes

The 3 sites showed similar trends in dry matter and litter dynamics throughout the year. Aboveground compartments and live roots increased during spring and early autumn. Root growth during winter-spring preceded aboveground biomass increases.

Summer and winter were the seasons when necromass increased and biomass decreased. The aboveground dry matter increased during the spring as temperature and rainfall increased, but maximum stocks were found at different dates varying with elevation. The spring peak in growth occurred earlier in the lower grassland. Temperatures more favorable to aboveground growth were attained later at higher altitudes.

We found differences among altitudinal sites in the length of quiescence of vegetation. The cold period was more extended

in the upper grassland than in the lower one; in the intermediate grassland the rest period was during summer drought, not in winter. At the upper site, summer was not a true rest period but one with reduced production rates (Fig. 5). This behavior was consistent with seasonal changes in temperature and evaporative capacity that have been reported for this eastern slope (Kristensen and Frangi 1995).

Roots in the upper soil layer were the most dynamic component of belowground dry matter. The lesser variability in the deeper root mass has been attributed to the more constant thermal and hydric conditions of this layer relative to the surface layer (Dahlman and Kucera 1965, Fernández and Caldwell 1975, Ares 1976). Although live thin roots increased during favorable thermic and hydric periods, periods of high senescence followed during dry consecutive days.

The ecological differences among sites were not expressed by total net primary production (NPP), which was similar at all sites, but by its partitioning in space and time. The higher elevation grassland community invested a higher proportion of annual NPP in roots, independent of season. The allocation pattern changed seasonally at the other 2-sites. At the end of summer and beginning of autumn, which was more humid than in spring, above ground net primary production (ANPP) showed a decreasing trend with increase in altitude. The proportion of NPP allocated to photosynthetic tissues increased from the summits to the piedmont.

Turnover rates

Faster turnover rates for aboveground compartments than for belowground compartments have been reported in other grassland systems (Kucera et al. 1967, Sims and Singh 1978, Aerts et al. 1989, Soriano 1992). The differences in photosynthate partitioning and biomass distribution are shown by the different turnover rates (productivity/biomass) of aboveground and belowground live tissues at each site. Since mean aboveground biomass and total net productivity were similar at all sites, the lower turnover rate of

Fig. 6. Above (A-) (circle) and belowground (B-) (square) dry matter in sites located within the elevational range from 350 to 1,100 m asl. Sites from Barrera and Frangi (1994) (solid symbols) include the lowland tussock grasslands and high sierra meadows at the extremes of the gradient. Open symbols indicate data from our sites. Vertical lines indicate $\pm$ SE. Estimates of sites normal annual mean temperature (calculated with standard weather reports data for 1961–1970 period and 0.7°C thermal gradient) is indicated as a second x-axis.

aboveground biomass at higher elevation reflected the greater allocation of photosynthates to roots. In contrast, the lower turnover of roots at higher elevations indicated that although belowground productivity is greater, root replacement is slower because of its higher biomass compared to lower grasslands. The higher turnover rates and lower biomass of roots at the lower site suggested that more fertile soils were faster exploited during the humid periods, prolonged because of more loamy textures, while periods with scarce water availability may have stimulated root replacement. A texture that holds more water facilitates this strategy for sustaining a similar aboveground mass of live tissue to produce more aboveground tissues. Probably high temperatures and evapotranspiration at lower sierra slopes trigger a higher turnover rate of aboveground live tissue. As a consequence of higher productivity and senescence and lower disappearance of aboveground tissues, standing dead material accumulated more at the lower site and turnover rate of aboveground dry matter was slower. A similar annual absolute mass senescence and disappearance of roots at both extremes of

the elevational gradient indicated a higher belowground senescence rate and decomposition rate per mass unit of root, under soil conditions that prevailed at the lower site. Inversely, the markedly greater annual absolute aboveground disappearance suggested that aboveground disappearance rate per unit of aboveground dry mass was higher at the upper site, probably enhanced by higher humidity and lower saturation deficits.

Comparison with other temperate grasslands

aboveground dry matter and net primary production (NPP) values for these sierra grasslands fell within the range reported for USA ungrazed temperate grasslands (Sims et al. 1978, Sims and Singh 1978). belowground dry matter was lower than in USA comparable mixed-grass and tall-grass prairie sites. Although NPP of sierra grasslands was near the lower value of mixed-grass prairie, the above ground net primary production (ANPP) at sierra sites was higher than at USA sites reported by Sims and Singh (1978). Consequently, there was greater BNPP/NPP ratio at USA

than at Pampa sites despite the partial overlap in the quotient range (61 to 75% vs 54 to 67%, respectively). Since sites like Hays and Osage (Sims et al. 1978) were the most comparable to Sierra de la Ventana in latitude, mean temperature, precipitation, and vegetation parameters, we suggest that the harder seasonality (226 to 272 days length of thermal potential growth season, respectively) in the Northern Hemisphere compared to our sites, located in more oceanic climates (more than 300 days of estimated length of thermal potential growth season), influenced the structural and functional differences.

With respect to productivity, Laurenroth (1979) considered that the most productive grassland sites of the world were those with around 800 mm annual precipitation and a mean temperature $>15^{\circ}\text{C}$. His grassland group 6 included a wide set of sites characterized by a lack of a significant drought period at any time of the year and an ANPP in the range of $160\text{--}1,387\text{ g m}^{-2}\text{ year}^{-1}$ (mean = $525\text{ g m}^{-2}\text{ year}^{-1}$). The ANPP of the Sierra de la Ventana grasslands were $\pm 12\%$ to -28% of the grassland group 6 mean. The main difference appeared for the higher elevation site, where productivity was composed mainly of belowground tissues. Gómez and Gallopín (1991) modeled the productivity of Latin American biomes and the range for Pampean grasslands was $400\text{--}600\text{ g m}^{-2}\text{ year}^{-1}$. The sierra grasslands ANPP (378 to $585\text{ g m}^{-2}\text{ year}^{-1}$) fit within that range, as did those from Pampa lowland ungrazed sites like Salado River basin grasslands with $532\text{ g m}^{-2}\text{ year}^{-1}$ (Sala et al. 1981) and La Pampa grasslands with $410\text{ g m}^{-2}\text{ year}^{-1}$ (de Wysiecki 1993). The greater aboveground productivity ($700\text{ g m}^{-2}\text{ year}^{-1}$) estimated for the lower site a decade before (Frangi et al. 1980 a) suggested that annual productivity variation in the sierra grasslands is important.

Conclusions

The similar mean annual aboveground biomass at all sierra grassland sites suggested that a common threshold carrying capacity of green tissues had been attained. As total production was also similar among 3 elevational sites this suggested that photosynthetic efficiency was equivalent at all sites. The differences among sites observed in belowground biomass and proportion of fine roots that were linked to temperature and soil water holding capacity appeared to reflect an adaptive trend for improved water and nutrient absorption with eleva-

tion. As there were no differences in aboveground biomass, grass life forms or NPP among sites, and evapotranspiration could be similar at all sites, the below-ground biomass is probably satisfying a similar water demand. Because of a lower water holding capacity with elevation, a more intense occupation of soil is necessary to accomplish water absorption under colder conditions.

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Estimating grazing index values for plants from arid regions

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Abstract

The Ecological Index Method impacted directly on the estimation of grazing capacities in the Karoo, an arid region in South Africa. Due to inherent deficiencies in the ecological index method, index values formed a disjunct series, 10, 7, 4, and 1 and the fact that different value systems were employed to score plant species, necessitated that index values of species commonly encountered during botanical surveys be subjectively adjusted by means of a species by species comparison, forming a continuous series of index values. These index values were still subjective value judgements of the agronomic value of the Karoo plant species. The author felt that a method should be developed to objectively estimate grazing index values from certain plant variables, i.e. size, animal available dry matter production, and chemical properties of the species. The use of these properties would describe the agronomic value of the plant species, which would lead to agronomically sound current grazing capacities being estimated. The following 2 models were proposed to deal with the karoo subshrubs and the grasses of the karoo separately. Grazing index value for the karoo subshrubs = $\{(\text{canopy spread cover} + \text{available forage} + \text{TDN} + [\text{K} \div (\text{Ca} + \text{Mg})]) \div \text{ether extract}\} \div 100$, and grazing index value for the grasses = $\{(\text{canopy spread cover} + \text{available forage} + \text{TDN} + [\text{K} \div (\text{Ca} + \text{Mg})]) \times \text{ether extract}\} \div 100$.

Key Words: available dry matter production, canopy spread cover, current grazing capacity, $\text{K} \div (\text{Ca} + \text{Mg})$ ratio, total digestible nutrients

Publication of the Ecological Index Method by Vorster (1982) directly influenced the estimation of grazing capacities in the Karoo. He allocated index values to the karoo plants on the basis:

- 1) perennial climax grasses, index value 10; in close agreement with Tainton et al. (1980);
- 2) perennial sub-climax grasses and palatable karoo subshrubs, index value 7;
- 3) perennial pioneer grasses and the less palatable karoo subshrubs, index value 4; and
- 4) annual pioneer grasses, unpalatable karoo subshrubs and invader plants, index value 1.

This method has been used throughout the Karoo, with largely acceptable results. The ecological index values are used in the computation of range condition scores (see Tainton 1981), following surveys of sample sites. Grazing capacities for these sample sites are then estimated from the range condition scores. Since

Resumen

El método de Índice Ecológico impactó directamente en la estimación de la capacidad de apacentamiento del Karoo, una región árida de Sudáfrica. Debido a las deficiencias inherentes del método de Índice Ecológico los valores de los índices formaron un serie disyuntiva, 10, 7, 4 y 1, y el hecho de que se emplearon diferentes sistemas de valores para calificar las plantas, exige que los valores de los índices para las especies comúnmente encontradas durante los reconocimientos botánicos sean subjetivamente ajustados mediante la comparación de especies por especie formando series continuas de valores de los índices. Estos valores de los índices todavía son valores subjetivos del valor agronómico de las especies de plantas del Karoo. El autor sintió que se debería desarrollar un método para estimar objetivamente los valores del índice de apacentamiento a partir de ciertas variables de la planta, por ejemplo, el tamaño, la disponibilidad de materia seca para el animal y las propiedades químicas de las especies. El uso de estas propiedades describirá el valor agronómico de las especies vegetales, el cual conduciría a la estimación sensata de la capacidad de apacentamiento. Los siguientes 2 modelos fueron propuestos para tratar por separado los arbustos y zacates del Karoo. El valor del índice de apacentamiento para arbustos fue igual a: $\{(\text{cobertura de la copa extendida} + \text{forraje disponible} + \text{NTD} + [\text{K} \div (\text{Ca} + \text{Mg})]) \div \text{extracto etéreo}\} \div 100$ y el valor del índice de apacentamiento para zacates fue igual a: $\{(\text{cobertura de la copa extendida} + \text{forraje disponible} + \text{NTD} + [\text{K} \div (\text{Ca} + \text{Mg})]) \times \text{extracto etéreo}\} \div 100$.

Vorster (1982) scored the grasses on ecological attributes and karoo subshrubs on palatability, an agronomic attribute, the range condition score computed for the sample site represents the ecological state of health of the grass sward on one hand, but the agronomic state of health of the karoo subshrubs on the other (see Tainton 1981). Since the score is based partly on ecological principles and partly on palatability, it is inappropriate to estimate grazing capacities, which are agronomic values, from these range condition scores which are assumed to indicate the agronomic potential of the site to support livestock. Several other factors, for instance dry matter production (Botha et al. 1993) need to be considered when a realistic grazing capacity is to be estimated.

The ecological index method is largely dependent upon classical succession theory, similar to many methods currently employed elsewhere in South Africa (Foran et al. 1978, Tainton et al. 1980, Mentis et al. 1980, Hardy and Hurt 1989, Hurt and Bosch 1991). Another of the deficiencies was that some of the late developmental stage grasses, previously referred to as climax grasses, received too high an index value to be used in the computations when estimating the current grazing capacity (Tainton

et al. 1980, Edwards 1981, Vorster 1982). Research revealed that not all the late developmental stage grasses should have an index value of 10 (Du Toit and Botha 1993). Because of the above mentioned deficiencies, a committee investigated the apparent shortcomings in order to correct them in an effort to move away from the classical succession theory. The index values of all the species commonly encountered during botanical surveys, were adjusted subjectively by means of a species by species comparison. Each species being assessed on the basis of the following 6 variables:

- 1) The ability to produce forage, i.e. the amount of grazable dry matter produced per year: Low producers score 1, high producers score 10.
- 2) The nutritional value during the growing season: Species with a low nutritional value score 1, species with a high nutritional value score 10.
- 3) The nutritional value during the dormant season, as in No. 2.
- 4) Relative ease with which the species can be grazed i.e. presence or absence of spines: spiny species score 1, species without spines score 10. The presence of resins and aromatic oils downgraded the score due to anti-herbivory.
- 5) Perenniality: Annual species score 1, strong perennial sodforming grasses score 10.
- 6) Ability of the plant to protect the soil against surface soil erosion: Upright karoo subshrubs have a low score, decumbent bushes score fairly high, annual tufted grasses score 1, tufted perennial grasses, depending on productivity and habit, have an intermediate score due to the erosive channeling effect they may have on runoff water, sod forming grasses, where infiltration of rainwater is heightened, score 10.

These 6 agronomic properties of the species were chosen to ensure that individual species scores were comparable and the estimate free from bias. Each variable scored a maximum of 10. Individual variable scores were summed and the final species score calculated to occupy a position between 0 and 10. The average of the scores submitted by the members, and standard deviation was calculated for each species score. Values falling outside the range $\bar{x} \pm SD$ were discarded. A new mean was calculated for the remaining values. The resultant score called the subjective grazing index value was vetted taking into account scores of related species, as well

as unrelated species of known similar grazing value. The phases of the operational research study (Wilkes 1989) were followed.

These index values, however, still represent subjective value judgements of the actual agronomic value of the Karoo plant species. The author felt that a method should be developed to estimate grazing index values more objectively from certain agronomic plant variables; size, dry matter production, and chemical properties of the species. These properties were studied for a period of 3 years, to largely exclude extreme variations in productivity which is so characteristic of vegetation from semi-arid range types (Sneva and Hyder 1962). Species from distinct agro-ecological regions were studied. It was attempted to study related species in the different regions, to ascertain differences in grazing value between different species in an area and between related species of different areas. These objective grazing index values will replace the ecological index values. To avoid future confusion as to which index values have been used, and that an agronomic method of grazing capacity estimation was used, the ecological index method is replaced by the Grazing Index Method (Du Toit 1995).

Grazing index values estimated by the model, should reflect agronomic values of plant species more objectively and when used in conjunction with the Grazing Index Method, estimate more acceptable current grazing capacities. These grazing index values should furthermore verify the relative position of the species in the series, when compared to the subjective grazing index values developed earlier (Du Toit et al. 1995).

Methodology

Canopy spread cover

The canopy spread cover of a number of grasses and bushes was measured at random at each locality from 1990 to 1993. Fifty plants per species were selected from small to large plants, including the range of sizes normally found within the species. A frame 1 m x 1 m, subdivided into blocks of 50 mm x 50 mm for the large species and 25 mm x 25 mm for the smaller species, was used for this purpose. The canopy spread cover was estimated by counting the blocks of which half or more of each block was engaged by the perpendicular projection of the crown (Goebel et al. 1958). The number of blocks counted were then expressed as square centimeters

of canopy spread cover. The canopy spread cover of 50 plants per species obtained this way included a representative sample of sizes, from small plants to large plants. The 50 measurements gave a reliable average value (Roux 1963). The plants were harvested *in toto* at a height of approximately 20 mm to 50 mm above the soil surface. The plants were selected at random over an area of 1 hectare (Vlok 1963), to minimize variations in plant ecotypic differences. The harvested material was separated into potentially grazable and ungrazable material on the basis of the 2 mm rule of thumb (Botha 1981, Du Toit 1996a). The 2 mm rule of thumb states that stems thicker than 2 mm are not grazed. While stems thicker than 2 mm were regarded as ungrazable, thinner stems contributed to the available grazable forage (Botha 1981, Du Toit 1993). Grass tufts were harvested by clipping to a stubble height of 20–50 mm and the whole fraction was regarded as being grazable. Plant material was dried in a forced draft oven between 60°C to 80°C, for 24 hours.

Relation between canopy spread cover and mass

The canopy spread cover : total mass relation of specific species were determined by regression to determine the relation between plant cover and the available forage (Payne 1974).

Chemical analyses

The grazable material was chemically analyzed for N according to the Kjeldahl method (AOAC 1964), Ca, P, Na, Mg, K were analyzed by atomic adsorption spectrophotometer, (Homer and Parker 1961) and acid detergent fibre was analyzed according to a modified Weende method (Van Soest 1963).

Model development

The proposed model attempts to objectively allocate a grazing index value to each of the studied species, based on the agronomic variables; size of the species i.e. canopy spread cover, the cornerstone of the range condition assessment technique, animal available dry matter, and certain chemical properties. Stepwise regressions (Statistical Graphics Corporation 1991) of the subjective grazing index values on the values obtained for the different parameters of the studied species indicated the most important elements to be included in the model.

Taxonomy

Nomenclature follows Arnold and De Wet (1993). Species names used in this paper and in the tables with their authorities are given in Table 1.

Results and discussion

Available forage and canopy spread cover

The relation between available forage and canopy spread cover, for all values, has a coefficient of determination, $r^2 = 0.62$. The slope of the regression line is less than 45° . This means that as the plants increase in size, there is not the expected corresponding increase in available forage. With the available forage being over-estimated by about 25% (Du Toit 1993, 1996a), the regression relation should have a slope of much less than 45° . The available mass recovered from a plant with a certain canopy spread cover varies considerably. Therefore, cover on its own does not provide a reliable estimate of available forage, in contrast to the finding of Mueller Dombois and Ellenberg (1974). Uresk (1990) proposed that frequency and canopy spread cover be multiplied to render an index of forage mass, which would probably be a reliable indication of available forage. In this case the relation between plant cover, available forage and forage value was to be used to calculate a grazing index value for each species. Floristic composition measured by the grazing index method, together with the grazing index values of the species would then describe the grazing capacity.

Nutrient requirements of grazing animals

According to Du Toit et al. (1940), growing sheep needs approximately 0.16% calcium and 0.14% phosphorus in their diet, while Louw (1969) recommends that the diet must contain between 0.2% to 0.5% calcium and 0.2% to 0.46% phosphorus, which agrees with values quoted by Woods (1959). The calcium : phosphorus ratio must be in the region of 1.0 for normal growth and development.

Potassium, calcium, and magnesium are included as the $K \div (Ca + Mg)$ ratio. These elements have a direct influence on the grazing value since unfavourable ratios lead to tetany (Kemp and T'Hart 1957, Kidambi et al. 1989). Values of these macronutrients are included in the formulae for the objective estimation of the grazing index values. Low or high values and unfavourable ratios have detrimental

Table 1. Species names and their authorities used in this paper and in Tables 1 to 3.

<i>Chrysocoma ciliata</i> L.
<i>Eberlanzia ferox</i> (L. Bol.) L. Bol.
<i>Eriocephalus aspalathoides</i> DC.
<i>Eriocephalus ericoides</i> (L.f.) Druce
<i>Eriocephalus spinescens</i> Burch.
<i>Felicia fascicularis</i> DC.
<i>Felicia filifolia</i> (Vent.) Burtt Davy
<i>Felicia macrorrhiza</i> (Thunb.) DC.
<i>Felicia muricata</i> (Thunb.) Nees
<i>Galenia procumbens</i> L.f.
<i>Galenia secunda</i> (L.f.) Sond.
<i>Helichrysum dregeanum</i> Sond. & Harv.
<i>Helichrysum lucilioides</i> Less.
<i>Hermannia desertorum</i> Eckl. & Zeyh.
<i>Hertia pallens</i> (DC.) Kuntze
<i>Lycium cinerium</i> Thunb. (Sens. Lat.)
<i>Monechma incanum</i> (Nees) C.B.Cl.
<i>Nenax microphylla</i> (Sond.) Salter
<i>Osteospermum microphyllum</i> DC.
<i>Osteospermum spinescens</i> Thunb.
<i>Pentzia globosa</i> Less.
<i>Pentzia incana</i> (Thunb.) Kuntze
<i>Pentzia spinescens</i> Less.
<i>Phymaspermum parvifolium</i> (DC.) Benth. & Hook. ex Jackson
<i>Plinthus cryptocarpus</i> Fenzl
<i>Plinthus karooicus</i> Verdoorn
<i>Protasparagus suaveolens</i> (Burch.) Oberm.
<i>Pteronia adenocarpa</i> Harv.
<i>Pteronia glauca</i> Thunb.
<i>Pteronia glomerata</i> L.f.
<i>Pteronia sordida</i> N.E.Br.
<i>Pteronia staehelinoides</i> DC.
<i>Pterothrix spinescens</i> DC.
<i>Rhigozum obovatum</i> Burch.
<i>Rosenia humilis</i> (Less.) Bremer
<i>Rosenia oppositifolia</i> (DC.) Bremer
<i>Salsola calluna</i> Fenzl ex C.H.Wr.
<i>Salsola rabieana</i> Verdoorn
<i>Salsola tuberculata</i> (Moq.) Fenzl
<i>Walafrida geniculata</i> (L.f.) Rolfe
<i>Walafrida saxatilis</i> (E.Mey.) Rolfe
<i>Zygophyllum gilfillanii</i> N.E.Br.
<i>Zygophyllum lichtensteinianum</i> Cham. & Schlechtd.
<i>Zygophyllum microphyllum</i> L.f.
Grasses
<i>Aristida adscensionis</i> L.
<i>Aristida congesta</i> Roem. & Schult. subsp. <i>congesta</i>
<i>Aristida diffusa</i> Trin. subsp. <i>diffusa</i>
<i>Cymbopogon plurinodis</i> (Stapf) Stapf ex Burtt Davy
<i>Cynodon dactylon</i> (L.) Pers.
<i>Digitaria eriantha</i> Steud.
<i>Enneapogon desvauxii</i> Beauv.
<i>Eragrostis bergiana</i> (Kunth) Trin.
<i>Eragrostis chloromelas</i> Steud.
<i>Eragrostis curvula</i> (Schrad.) Nees var. <i>conferta</i>
<i>Eragrostis lehmanniana</i> Nees var. <i>lehmanniana</i>
<i>Eragrostis obtusa</i> Munro ex Fical. & Hiern
<i>Fingerhuthia africana</i> Lehm.
<i>Heteropogon contortus</i> (L.) Roem. & Schult.
<i>Hyparrhenia hirta</i> (L.) Stapf
<i>Merxmüllera disticha</i> (Nees) Conert
<i>Sporobolus fimbriatus</i> (Trin.) Nees
<i>Stipagrostis ciliata</i> (Desf.) De Winter var. <i>capensis</i>
<i>Stipagrostis obtusa</i> (Del.) Nees
<i>Themeda triandra</i> Forssk.

Table 2. Objective grazing index values (OGIV) calculated for species from the False Upper Karoo (Acocks 1988), compared to their corresponding subjective grazing index values (SGIV), illustrating the annual and seasonal variation.

	OGIV					SGIV
	May	Aug.	Nov.	Jan.	Mean	
1990/91						
<i>Chrysocoma ciliata</i>	1.22	0.31	1.29	0.51	0.83	1.50
<i>Eriocephalus ericoides</i>	2.44	1.67	3.44	4.16	2.93	5.00
<i>Pentzia incana</i>	1.64	1.33	2.01	1.94	1.73	5.70
<i>Aristida congesta</i>	3.36	1.92	0.94	1.07	1.82	1.30
<i>Digitaria eriantha</i>	19.59	7.72	13.51	6.46	11.82	8.90
<i>Themeda triandra</i>	15.04	10.19	8.31	6.69	10.06	9.30
1991/92						
<i>Eriocephalus spinescens</i>	3.09	2.75	0.29	2.73	2.22	4.50
<i>Pentzia incana</i>	1.67	1.17	1.42	1.93	1.55	5.70
<i>Rosenia humilis</i>	3.28	2.90	3.99	3.03	3.30	3.50
<i>Heteropogon contortus</i>	4.17	5.36	4.37	3.77	4.42	7.20
<i>Stipagrostis ciliata</i>	3.78	4.48	2.38	3.61	3.56	7.20
<i>Stipagrostis obtusa</i>	3.49	4.46	1.01	2.34	2.83	6.60
1992/93						
<i>Eriocephalus ericoides</i>	1.48	1.78	2.85	2.63	2.18	5.00
<i>Pentzia incana</i>	1.19	0.97	1.16	1.57	1.22	5.70
<i>Rosenia humilis</i>	3.16	4.56	4.60	3.65	3.99	3.50
<i>Aristida congesta</i>	1.82	1.58	0.78	0.85	1.26	1.30
<i>Heteropogon contortus</i>	3.77	5.06	4.15	3.98	4.24	7.20
<i>Themeda triandra</i>	6.64	6.26	5.65	4.70	5.81	9.30

effects on animal production (Van Hoven and Ebedes 1988). Low values lead to serious deficiencies in animal feeding (Woods 1959). Unfavourable values negatively affect index values.

In addition to the chemical properties mentioned above, the % ash and ether extract of the species were obtained from the literature for analyses previously carried out on plantspecies occurring in the same areas (Louw et al. 1968a, 1968b, 1968c, Steenkamp and Hayward 1979, Botha and Nash 1990, Botha et al. 1990a, 1990b, 1990c).

Total digestible nutrients (TDN)

Because of the prominence that total digestible nutrients receives in animal feeding ration formulations (Maynard and Loosli 1962), in the comparison of different feedstuffs (Swift 1957) and in this study, the comparison of different natural forages, it is included in these equations as a primary variable. The 2 variables incorporated in the determination of TDN (Glover et al. 1960, Bartholomew 1985, Bredon and Meaker undated), i.e. the percentages of nitrogen and acid detergent fibre, can be excluded from the model, since their influence on the index value is already taken into account.

The formula for the estimation of TDN using acid detergent fibre, is composed of the formulae developed by:

- 1) Glover et al. (1960) and Bredon and Meaker (undated) where : TDN =

$$75.1 + [(6.25 \times \log \% \text{ crude protein}) - 0.75 \times \% \text{ crude fibre}] \text{ and;}$$

- 2) Du Toit (1996b) where : Crude fibre = $-4.32 + 0.92 \times \% \text{ acid detergent fibre}$.

$$\text{TDN} = 75.1 + \{(6.25 \times \log \% \text{ N}) - (0.75 \times [-4.32 + (0.92 \times \% \text{ acid detergent fibre}])\} \text{ (Du Toit 1996b).}$$

Proposed model, used to estimate grazing index values

The model takes into account the size of the plant i.e. canopy spread cover, which is the cornerstone of the method of botanical survey for estimating grazing capacity, through the Grazing Index Method. Two approaches were followed with the formulation of the model. In the case of the karoo subshrubs the ether extract value negatively affects the grazing value, on account of it's contribution to the smell and taste of the karoo subshrubs. The higher the ether extract value of the karoo subshrub, the higher the resin and aromatic oil content. Experience teaches that plants with high resin and aromatic oil contents are the more unpalatable karoo subshrubs. Compare the unpalatable karoo subshrub *Chrysocoma ciliata* with ether extract values of 8.9 in summer and 9.2 in winter to the more palatable karoo subshrub *Pentzia incana* with ether extract values of 2.3 and 3.9 in summer and winter respectively (Botha et al. 1990c) (Table 2). High ether extract contents act as deterrents to herbivores, while the higher

the ether extract values of certain shrubs, the higher the loss of energy rich esters, ethers and aldehydes through the urine of sheep (Cook et al. 1952). The usable energy of these forages is not as high as their calculated TDN values indicate. Consequently the sum of the calculated values of the different variables is divided by the ether extract value, a lower index value for karoo subshrubs with high ether extract values are estimated, in accordance with their relatively low nutritional value.

Model a, grazing index value for karoo subshrubs

Grazing index value for the karoo subshrubs = $\{(\text{canopy spread cover} + \text{available forage} + \text{TDN} + [\text{K} \div (\text{Ca} + \text{Mg})]) \div \text{ether extract}\} \div 100$ (Du Toit 1996b) (Table 3).

In the case of grasses, ether extract values positively contributes to the grazing value, through the carotene content (Van Der Merwe 1985). Grasses with high ether extract values are late developmental stage species, they are more productive and assumed to be more nutritious, than early developmental stage grasses with normally low ether extract percentages and low carotene contents. High ether extract values indicate high carotene contents of the grasses and a more favourable vitamin A, B, E, and probably D content (McDonald et al. 1973). Late developmental stage grasses *Digitaria eriantha* and *Themeda triandra* have the highest ether extract values, 2.02

Table 3. Mean objective grazing index values (OGIV) calculated according to the model, compared to the subjective grazing index values (SGIV)

Karoobushes	OGIV				SGIV
	Min	Max	Mean	Std dev	
<i>Chrysocoma ciliata</i>	0.31	1.29	0.83	0.43	1.50
<i>Eberlanzia ferox</i>	1.07	3.68	1.96	0.67	2.70
<i>Eriocephalus ericoides</i>	0.57	7.67	2.54	1.67	5.00
<i>Eriocephalus spinescens</i>	0.29	5.77	3.65	1.20	4.50
<i>Felicia fascicularis</i>	0.22	0.95	0.48	0.23	6.20
<i>Felicia filifolia</i>	1.94	4.23	2.63	0.93	5.90
<i>Felicia macrorrhiza</i>	1.70	2.37	2.05	0.24	5.70
<i>Galenia secunda</i>	2.53	6.21	4.92	1.46	4.70
<i>Helichrysum dregeanum</i>	0.43	0.53	0.47	0.04	6.30
<i>Helichrysum lucilioides</i>	0.94	3.09	1.75	0.57	5.20
<i>Hermannia desertorum</i>	1.09	1.35	1.21	0.09	5.90
<i>Monechma incanum</i>	6.01	18.69	9.76	5.20	5.40
<i>Nenax microphylla</i>	0.50	4.07	1.16	0.83	7.00
<i>Osteospermum microphyllum</i>	1.51	1.79	1.66	0.10	7.00
<i>Osteospermum spinescens</i>	2.92	6.03	4.63	1.34	6.00
<i>Pentzia globosa</i>	0.71	1.73	1.26	0.30	4.80
<i>Pentzia incana</i>	0.97	2.01	1.50	0.33	5.70
<i>Pentzia spinescens</i>	0.44	6.16	2.43	1.12	4.80
<i>Phymaspermum parvifolium</i>	0.39	3.71	1.60	1.12	6.20
<i>Plinthus cryptocarpus</i>	0.54	4.70	1.95	1.35	6.70
<i>Plinthus karoocicus</i>	0.81	3.06	2.06	0.72	6.40
<i>Pteronia adenocarpa</i>	1.19	3.19	1.82	0.59	3.90
<i>Pteronia glauca</i>	1.89	3.81	2.77	0.80	3.20
<i>Pteronia glomerata</i>	1.15	2.63	2.06	0.55	3.90
<i>Pteronia staehelinoides</i>	0.14	0.22	0.18	0.03	4.00
<i>Pterothrix spinescens</i>	0.11	3.03	1.91	1.91	2.00
<i>Rosenia humilis</i>	2.44	6.06	4.00	0.89	3.50
<i>Rosenia oppositifolia</i>	0.50	1.24	0.82	0.30	3.10
<i>Salsola calluna</i>	4.24	5.71	5.11	0.62	7.20
<i>Salsola rabieana</i>	2.79	4.09	3.39	0.42	6.70
<i>Salsola tuberculata</i>	1.64	6.88	4.21	2.04	6.90
<i>Walafrida geniculata</i>	2.01	4.29	3.33	0.75	7.00
<i>Walafrida saxatilis</i>	0.54	0.86	0.69	0.12	2.00
<i>Zygophyllum lichtensteinianum</i>	1.20	1.62	1.43	0.17	4.00
<i>Zygophyllum microphyllum</i>	2.91	4.52	3.79	0.57	4.00
Grasses					
<i>Aristida congesta</i>	0.78	3.36	1.54	0.80	1.30
<i>Aristida diffusa</i>	2.56	11.00	5.75	2.36	5.10
<i>Digitaria eriantha</i>	4.82	19.59	8.58	4.47	8.90
<i>Eragrostis curvula conferta</i>	0.95	4.98	2.76	1.40	6.90
<i>Eragrostis lehmanniana</i>	1.87	5.64	2.70	0.89	5.40
<i>Fingerhuthia africana</i>	2.07	5.19	3.41	1.11	6.60
<i>Heteropogon contortus</i>	3.77	5.36	4.33	0.55	7.20
<i>Hyparrhenia hirta</i>	7.74	10.78	8.71	1.21	6.30
<i>Merxmüllera disticha</i>	4.91	12.24	7.46	2.82	5.00
<i>Sporobolus fimbriatus</i>	5.22	10.02	7.08	1.80	9.50
<i>Stipagrostis ciliata</i>	1.87	12.93	5.82	3.12	7.20
<i>Stipagrostis obtusa</i>	0.62	5.65	2.41	1.28	6.60
<i>Themeda triandra</i>	2.32	15.04	6.10	3.09	9.30

(summer) and 1.92 (winter) as opposed to the early developmental stage grasses *Aristida congesta* and *A. adscensionis* with a content of 1.34 in both summer and winter (Botha et al. 1990c) (Table 2) (Acoks 1988). Therefore the sum of the calculated values of the different variables is multiplied by the ether extract value. This action favours grasses with high ether extract values.

Model b, grazing index value for grasses

Grazing index value for the grasses = $\{(\text{canopy spread cover} + \text{available forage} + \text{TDN} + [\text{K} \div (\text{Ca} + \text{Mg})]) \times \text{ether extract}\} \div 100$ (Du Toit 1996b) (Table 3).

The estimated grazing index values

Although not all the plant species presented in the botanical surveys (Table 4) have objectively estimated grazing index values, the range condition scores and the resultant current grazing capacities result-

ing from the use of the objectively estimated grazing index values are closer to the accepted grazing capacity norms than where the subjectively estimated grazing index values have been used. Assuming that the grazing capacity norms set for the various areas are correct, the conclusion can be reached that it is more appropriate to use the objectively estimated grazing index values in the estimate of the grazing capacity, than either the ecological index values or the subjectively estimated grazing index values. It follows that the use of the objectively estimated grazing index values will result in more realistic estimates of the current grazing capacities of rangeland. Furthermore, the objectively estimated grazing index values verify the relative position of the subjectively estimated grazing index values of the different plant species on the grazing index value scale.

With this model, the grazing index value of any species can be estimated with a certain degree of confidence. Quality parameters can be gleaned from the literature, or be determined empirically. It may be possible to refine this model, by incorporating some of the parameters excluded at the moment. However, different grazing index values are estimated for species for the different seasons (Table 2) which in turn sheds more light on the concept of palatable and unpalatable species, as well as the seasonal palatability of a species.

The index value scale

It is questionable whether the top of the grazing index value scale should be 10. The use of a scale with values from 1 to 10 has become customary and is often proposed in biological work (cf. Curtis and McIntosh 1951, Brown and Curtis 1952, Vorster 1982, Hurt and Bosch 1991). It is clear that unbeknown to the estimators of the subjectively estimated grazing index values, the old ecological index method scale (Vorster 1982) and the climax adaptation values (Curtis and McIntosh 1951, Brown and Curtis 1952) played an important role in positioning the subjective estimates of the grazing index values. From the foregoing it then becomes clear that all the subjectively estimated grazing index values will have to be adjusted, mainly downwards, so as to fall into line with the objectively estimated grazing index values. Once this action is accomplished, current grazing capacities can be estimated much more reliably and realistically and different homogeneous areas can be directly compared to each other on a realistic and agriculturally sound scientific basis.

Table 4. Botanical composition, percentage canopy spread cover (CS), range condition scores (VCS) and the respective estimated current grazing capacities (CGC) presented for 7 sample sites from 4 reasonably homogeneous areas in the Karoo, i.e. the Bushmanland, the Eastern Mixed Karoo, the Great Karoo and the Central Upper Karoo. Sites follow a gradient from the arid northwest through the south and central Karoo to the relatively moist north eastern Karoo. The ecological, subjective grazing index and objective grazing index values of the different species are compared, as well as the results of their respective products with the percentage strikes on the species. Where no OGIV was available for a plant species, the SGIV was included as the OGIV score, this is indicated by an asterisk next to the species name. CGC is given in ha.LSU⁻¹. EIV = ecological index value, SGIV = subjective grazing index value and OGIV = objective grazing index value.

Grappies Farm (29° 25'S, 19° 57'E), Pofadder district; June 1992, median rainfall 82 mm.a⁻¹, grazing capacity norm 39 ha.LSU⁻¹, Bushmanland.

	%	EIV	Score	SGIV	Score	OGIV	Score
<i>Aristida congesta</i>	1	1	1	1.3	1.3	1.5	1.5
<i>Erioccephalus spinescens</i>	2	4	8	4.5	9.0	3.7	7.4
<i>Stipagrostis ciliata</i>	39	10	390	7.2	280.8	5.8	226.2
<i>Stipagrostis obtusa</i>	25	10	250	6.6	165.0	2.4	60.0
CS	67	VCS	649	VCS	456	VCS	295.1
CGC			7.2		10.2		15.7

Knolepark Farm (30° 38'S, 26° 20'E), Burgersdorp district; February 1992, median rainfall 450 mm.a⁻¹, grazing capacity norm 10 ha.LSU⁻¹, Eastern Mixed Karoo.

	%	EIV	Score	SGIV	Score	OGIV	Score
<i>Cymbopogon plurinodis</i> *	78	10	780	7.6	592.8	7.6	592.8
<i>Digitaria eriantha</i>	2	10	20	8.9	17.8	8.3	16.6
<i>Pentzia globosa</i>	1	4	4	4.8	4.8	1.3	1.3
<i>Themeda triandra</i>	9	10	90	9.3	83.7	6.1	54.9
CS	90	VCS	894	VCS	699	VCS	665.6
CGC			5.2		6.6		7.0

Diephoek Farm (30°07'S, 24° 15'E), Petrusville district; July 1992, median rainfall 312 mm.a⁻¹, grazing capacity norm 20 ha.LSU⁻¹, Eastern Mixed Karoo.

	%	EIV	Score	SGIV	Score	OGIV	Score
<i>Eragrostis lehmanniana</i>	30	7	210	5.4	162.0	2.7	81.0
<i>Pentzia globosa</i>	15	4	60	4.8	72.0	1.3	19.5
<i>Aristida congesta</i>	4	1	4	1.3	5.2	1.5	6.0
<i>Plinthus karoocicus</i>	8	7	56	6.4	51.2	2.1	16.8
<i>Enneapogon desvauxii</i> *	1	1	1	1.0	1.0	1.0	1.0
<i>Hertia pallens</i> *	2	1	2	1.2	2.4	1.2	2.4
<i>Lycium cinereum</i> *	1	1	1	3.0	3.0	3.0	3.0
<i>Protoparagus suaveolens</i> *	4	1	4	1.0	4.0	1.0	4.0
<i>Erioccephalus aspalathoides</i> *	1	4	4	4.0	4.0	4.0	4.0
<i>Galenia procumbens</i> *	5	4	20	4.3	21.5	4.3	21.5
<i>Eragrostis bergiana</i> *	3	4	12	2.8	8.4	2.8	8.4
CS	74	VCS	374	VCS	3.35	VCS	167.7
CGC			12.4		13.9		27.7

Hillstone Farm (31° 20'S, 25° 31'E), Middelburg district; July 1992, median rainfall 346 mm.a⁻¹, grazing capacity norm 16 ha.LSU⁻¹, Eastern Mixed Karoo.

	%	EIV	Score	SGIV	Score	OGIV	Score
<i>Sporobolus fimbriatus</i>	14	10	140	9.5	133.0	7.1	99.4
<i>Eragrostis obtusa</i> *	9	7	63	4.0	36.0	4.0	36.0
<i>Eragrostis lehmanniana</i>	1	7	7	5.4	5.4	2.7	2.7
<i>Erioccephalus ericoides</i>	15	4	60	5.0	75.0	2.5	37.5
<i>Pentzia globosa</i>	6	4	24	4.8	28.8	1.3	7.8
<i>Aristida congesta</i>	20	1	20	1.3	26.0	1.5	30.0
<i>Cynodon dactylon</i> *	4	4	16	4.5	18.0	4.5	18.0
<i>Lycium cinereum</i> *	8	1	8	3.0	24.0	3.0	24.0
<i>Eragrostis chloromelas</i> *	1	7	7	5.5	5.5	5.5	5.5
<i>Erioccephalus spinescens</i>	1	4	4	4.5	4.5	3.7	3.7
<i>Chrysocoma cilata</i>	1	1	1	1.5	1.5	0.8	0.8
CS	80	VCS	350	VCS	358	VCS	265.4
CGC			13.3		13.0		17.5

(Continued on Page 535)

(Table 4. Continued)

Swartgrond Farm (33° 04'S, 22° 56'E), Beaufort West district; August 1992, median rainfall 199 mm. a⁻¹, grazing capacity norm 32 ha. LSU⁻¹, Great Karoo.

	%	EIV	Score	SGIV	Score	OGIV	Score
<i>Aristida congesta</i>	2	1	2	1.3	2.6	1.5	3.0
<i>Protasparagus suaveolens</i> *	1	1	1	1.0	1.0	1.0	1.0
<i>Pentzia incana</i>	14	4	56	5.7	79.8	1.5	21.0
<i>Rhigozum obovatum</i> *	2	7	14	6.6	13.2	6.6	13.2
<i>Eberlanzia ferox</i>	1	1	1	2.7	2.7	2.0	2.0
<i>Hermannia desertorum</i>	5	7	35	5.9	29.5	1.2	6.0
<i>Stipagrostis obtusa</i>	2	10	20	6.6	13.2	2.4	4.8
<i>Erioccephalus ericoides</i>	1	4	4	5.0	5.0	2.5	2.5
<i>Felicia muricata</i> *	3	7	21	6.5	19.5	6.5	19.5
<i>Lycium cinereum</i> *	1	1	1	3.0	3.0	3.0	3.0
<i>Pteronia sordida</i> *	1	4	4	4.5	4.5	4.5	4.5
<i>Erioccephalus spinescens</i>	1	4	4	4.5	4.5	3.7	3.7
<i>Enneapogon desvauxii</i> *	1	1	1	1.0	1.0	1.0	1.0
<i>Stipagrostis ciliata</i>	2	10	20	7.2	14.4	5.8	11.6
<i>Felicia filifolia</i>	1	7	7	5.9	5.9	2.6	2.6
<i>Zygophyllum microphyllum</i>	1	4	4	4.0	4.0	3.8	3.8
CS	39	VCS	195	VCS	204	VCS	103.2
CGC			23.8		22.8		45.0

Abrahamskraal Farm (31° 46'S, 22° 40'E), Victoria West district; February 1992, median rainfall 227 mm.a⁻¹ grazing capacity norm 26 ha.LSU⁻¹,Central Upper Karoo.

Grass/karoo bush range	%	EIV	Score	SGIV	Score	OGIV	Score
<i>Eberlanzia ferox</i>	1	1	1	2.9	2.9	2.0	2.0
<i>Erioccephalus spinescens</i>	1	4	4	4.5	4.5	3.7	3.7
<i>Felicia filifolia</i>	2	7	14	5.9	11.8	2.6	5.2
<i>Pentzia incana</i>	34	4	136	5.7	193.8	1.5	51.0
<i>Pteronia glauca</i>	1	4	4	3.2	3.2	2.8	2.8
<i>Pteronia sordida</i> *	4	4	16	4.5	18.0	4.5	18.0
<i>Rosenia humilis</i>	1	1	1	3.5	3.5	4.0	4.0
<i>Salsola tuberculata</i>	1	7	7	6.9	6.9	4.2	4.2
<i>Stipagrostis obtusa</i>	20	10	200	6.6	132.0	2.4	4.8
<i>Walafrida geniculata</i>	1	7	7	7.0	7.0	3.3	3.3
<i>Zygophyllum gilfillanii</i> *	2	7	14	5.9	11.8	5.9	11.8
CS	68	VCS	404	VCS	395	VCS	154
CGC			11.5		11.7		30.0
Mean current grazing capacity of Abrahamskraal farm			17.2		14.1		29.3

Conclusions

The objectively estimated grazing index values verifies the relative position of the species in the series and they can be compared to the subjective grazing index values developed earlier at the Grootfontein Agricultural Development Institute (Du Toit et al. 1995).

It is possible to objectively estimate grazing index values for plant species of the arid areas by means of a suitable model. In the estimates used in the model, certain plant variables such as the canopy spread cover, the available forage on the plant and the chemical content of the available forage at that instant, play prominent roles.

The objective grazing index values have been successfully used in the computation

of range condition scores and in the calculation of current grazing capacities from these range condition scores (Table 4). These current grazing capacities have been estimated for widely differing areas. It is clear that they closely approximate the long-term grazing capacity norms prescribed for these areas by the South African Department of Agriculture.

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Tiller recruitment patterns and biennial tiller production in prairie sandreed

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Abstract

Tiller recruitment is an essential process for ensuring the perenniality of grasses. The timing and extent of tiller recruitment and the role of biennial tillers must be documented for key range species. Prairie sandreed [*Calamovilfa longifolia* (Hook) Scribn.] is an important grass in the Nebraska Sandhills for both ecological functioning and as a forage. The objective of this study was to document tiller recruitment patterns and the occurrence and contribution of current year and biennial tillers to biomass production in prairie sandreed at 2 locations in Nebraska. Tiller recruitment was monitored at 2-week periods throughout the growing season during a 2-year period. Newly emerged tillers were classified as intravaginal, extravaginal, or rhizomatous tillers and marked with colored wire. Prairie sandreed has an unimodal pattern of tiller recruitment and over 50% of the current year tillers emerged by mid-May and 80% by mid-June. Rate of tiller emergence and absolute number of emerged tillers were poorly correlated with short- and long-term precipitation totals ($r < 0.3$ $P > 0.20$). The year after new tillers were marked, biennial tillers and tillers initiated during the current-year were counted and clipped in September for biomass determination. Biennial tillers made up only 6 and 20% of the total tiller emergence at these locations and were generally only 30% as large as the new tillers. Extravaginal tillers composed over 78% of the biennial tiller population as a result of both their dominance in emerging populations and the higher percentage of tillers that survived the winter. Current year tillers contributed the most to prairie sandreed forage production and their emergence was largely completed by mid-June. The lack of a relationship between tiller recruitment and precipitation patterns, combined with previous studies of prairie sandreed, indicates that tiller recruitment involves a process that begins the previous growing season.

Key Words: Warm-season grass, tiller demography, *Calamovilfa longifolia* (Hook.) Scribn., grassland ecology, population ecology/biology

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Resumen

El renuevo de las macollas (número de macollas que brotan durante todo el periodo de crecimiento) es un proceso esencial para asegurar la perennidad de los pastos. La regulación del tiempo, la cantidad de renovación de las macollas, y el papel de las macollas bienales deben ser documentados para las especies claves de las praderas. Prairie sandreed [*Calamovilfa longifolia* (Hook) Scribn.] es un pasto importante en las lomas arenosas (sandhills) al oeste de Nebraska, no solo por su contribución ecológica sino también como forraje. Los objetivos de este estudio han sido el de documentar el patrón de renuevo de las macollas, la ocurrencia y la contribución de las macollas durante el presente año y las macollas bienales del año anterior en la producción de la biomasa del pasto prairie sandreed en dos localidades de Nebraska. El renuevo de las macollas fue determinado cada dos semanas durante la época de crecimiento del pasto y por un período de dos años. A medida que las macollas iban brotando fueron clasificadas en intravaginadas (crecimiento desde adentro de la vaina de la hoja) y extravaginadas (penetración de la vaina de la hoja) o rizomas e identificadas con alambres de colores. El pasto prairie sandreed posee un patrón unimodal en su renovación de las macollas; durante el presente año mas del 50% de sus macollas, brotaron a mediados de Mayo y el 80% a mediados de Junio. La proporción de la brotación de las macollas y el número absoluto de las macollas que brotaron estuvo pobremente correlacionado ($r < 0.3$ $P > 0.20$) con la precipitación total a corto y a largo plazo. En el segundo año, las macollas bienales y las macollas que brotaron durante el presente año fueron contadas y cortadas para determinar la biomasa. Las macollas bienales representaron de un 6 al 20% del total de las macollas en las dos localidades, y fueron por lo general 30% tan grandes como las macollas nuevas. Las macollas extravaginadas formaron mas del 78% de la población de macollas bienales, debido a su caracter dominante para brotar y también a su alto porcentaje de sobrevivencia durante el invierno. Las macollas del presente año fueron las que mas contribuyeron a la producción del pasto forrajero sandreed, completando la mayor parte de su brotación a mediados de Junio. La carencia de relación entre el renuevo de las macollas y los patrones de la precipitación, combinado con resultados obtenidos en años anteriores, indican que el renuevo de las macollas está involucrado en un proceso el cual se inicia en el anterior período de crecimiento del pasto.

Prairie sandreed [*Calamovilfa longifolia* (Hook) Scribn.] is a widespread rhizomatous perennial grass on sandy soils in the Northern Great Plains of the United States. It is one of the most

common grasses of the Nebraska Sandhills (Tolstead 1942) and together with sand bluestem [*Andropogon gerardii* var. *pau-cipilus* (Nash) Fern.] and little bluestem [*Schizachyrium scoparium* (Michx.) Nash] provides 50–60% of the available forage in most years (Northup 1993). Tolstead (1942) and Hendrickson et al. (1998) described the developmental morphology of prairie sandreed.

Knowledge of tiller dynamics contributes to greater ecological understanding and more effective management of grasslands (Briske and Silvertown 1993, McKenzie 1997). Understanding tiller dynamics is critical in developing appropriate grazing strategies for rangelands (Cullan et al. 1999). Most perennial grasses have bimodal recruitment patterns with flushes of new tillers emerging during the spring and fall (Langer 1956, Briske and Butler 1989, Briske and Richards 1995). However, crested wheatgrass [*Agropyron desertorum* (Fisch. Ex Link) Schult.], bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) A. Löve] (Mueller and Richards 1986), and big bluestem [*Andropogon gerardii* Vitmann var. *gerardii*] (McKendrick et al. 1975), only produced 1 annual cohort. These established patterns of tiller recruitment may be affected by defoliation which extends the recruitment period (Butler and Briske 1988), promotes additional tiller cohorts (Olson and Richards 1988a), and changes the timing of peak recruitment (Bullock et al. 1994). Tiller recruitment is also a major method of perennial grass persistence (Hendrickson and Briske 1997) and annual tiller replacement is necessary to maintain tiller density (Olson and Richards 1988b). Reduction in tiller density reduces both current and future productivity since tiller density represents a pool of meristematic tissue for future growth (Murphy and Briske 1992).

Timing of tiller recruitment has a direct effect on tiller longevity and tiller yield. Tillers recruited in the fall often overwinter in the vegetative stage and resume growth the following spring (Briske 1991). These “biennial tillers” have been reported for certain grasses in the plains states. In the Kansas Flint Hills, a majority of indiangrass tillers [*Sorghastrum nutans* L. (Nash)] were biennial but big bluestem tillers only lived for 1 year (McKendrick et al. 1975). In the Nebraska Sandhills, biennial tillers were reported in prairie sandreed but not its co-dominant sand bluestem (Bredja et al. 1988, Cullan et al. 1999) and prairie sandreed in Montana did not produce biennial tillers (White 1977). Biennial tillers are important because they

often have a greater dry weight, leaf number, and seed yield than tillers recruited during the growing season because they have more time for growth and development (Langer 1956).

Tiller type influences plant architecture (Briske 1991) and plant development (White 1977). Bunchgrasses are characterized by intravaginal tillers or tillers which arise from within the subtending leaf while sod forming grasses have more extravaginal and rhizomatous tillers (Briske 1991). Prairie sandreed has rhizomatous, intra- and extravaginal tillers similar to switchgrass (*Panicum virgatum* L.) (Bredja et al. 1988). Rhizomatous tillers in prairie sandreed have an increased probability of producing seed-heads (White 1977) which has an adverse affect on nutritive value and palatability (Reece et al. 1999).

Despite the importance of prairie sandreed to the Nebraska Sandhills in particular and the Northern Great Plains in general, relatively little is known about its basic demographic patterns and the role of biennial tillers in biomass determination. The objective of this study was to evaluate tiller recruitment patterns in prairie sandreed, estimate the contributions of intravaginal, extravaginal, and rhizomatous tillers to overall tiller recruitment and determine the importance and contribution of biennial tillers to forage production.

Materials and Methods

Research was conducted in 1990 and 1991 at 2 University of Nebraska research locations. The Gudmundsen Sandhills Laboratory (42° 07'N, 101° 43'W) is centrally located in the Nebraska Sandhills near Whitman, Nebr. and the Panhandle Experimental Range (42° 08'N, 103° 43'W) is located near Mitchell in the Nebraska Panhandle approximately 240 km west of the Gudmundsen Sandhills Laboratory. There were 3 and 6 study sites located at the Gudmundsen Sandhills Laboratory and the Panhandle Experimental Range respectively. Study sites were located on Valentine fine sands (mixed, mesic typic Ustipsamments) at the Gudmundsen Sandhills Laboratory and Valent fine sands (mixed, mesic, ustic Torripsamment) at the Panhandle Experimental Range in areas dominated or co-dominated by prairie sandreed (50% of the cover). Dominance or co-dominance by prairie sandreed is typical of a majority of Sandhills vegetation that is in mid to high seral stage.

Average annual precipitation at the Gudmundsen Sandhills Laboratory is 514 mm and 70% falls during the growing season (April through September). At the Panhandle Experimental Range, the average annual precipitation is 393 mm with the same distribution pattern. Precipitation from 1 April to 30 September was 76, 119, and 90% of the 30-year average for the Gudmundsen Sandhills Laboratory in 1990, 1991, and 1992 respectively. Precipitation during the same years, at the Panhandle Experimental Range, was 98, 138, and 96% of the 30-year average. Precipitation data were collected electronically during the growing season from a weather station at the Gudmundsen Sandhills Laboratory headquarters and from a rain gauge located 1.25 km south of the Panhandle Experimental Range study site. Thirty-year averages were taken from the closest U.S. Weather Service stations located 20 km northeast of the Gudmundsen Sandhills Laboratory and 10.5 km southeast of the Panhandle Experimental Range.

Study sites at the Gudmundsen Sandhills Laboratory were excluded from livestock grazing for 5 years previous to the initiation of the study. At the Panhandle Experimental Range, study sites were grazed as part of a deferred rotation for 15 years previous to the study at a stocking rate of 1.01 AUM/ha. However, livestock were excluded from the sites during the investigation.

Twelve permanent 0.5 m² quadrats (70.5 cm x 70.5 cm) were randomly located within the study sites during the first week of May 1990 at each location. There were a total of 4 quadrats within each of the 3 study areas at the Gudmundsen Sandhills Laboratory and 2 quadrats within each of the 6 study areas at the Panhandle Experimental Range. Quadrats were monitored for new tiller emergence at 2-week intervals, from mid-May through mid-September during the 1990 growing season. Newly emerged tillers were classified into 3 categories (intravaginal, extravaginal, or rhizomatous) based on the position of the emerging tiller. Tillers that emerged from within the subtending leaf sheath were considered intravaginal tillers while extravaginal tillers emerged through the subtending leaf sheath (Briske 1991). Tillers that emerged more than 3 cm from the nearest existing tiller were considered to be rhizomatous. Colored wires were placed on the base of each new tiller to indicate category and date of emergence.

In 1991, these same 12 quadrats at each location were evaluated to determine the

winter survival of the 1990 tillers by counting the number of live tillers. Surviving tillers were classified as biennial. Counts were done in mid-April, mid-May and at the end of September in 1991. In September, biennial and new tillers were clipped separately, separated into vegetative and reproductive tillers, dried for 3 days at 55°C, and weighed.

In 1991, 12 new 0.5 m² quadrats were randomly located in the same study areas at each location and monitoring was conducted in the same manner as in 1990 except that at the Panhandle Experimental Range, monitoring of tiller emergence began in mid-April rather than mid-May. Evaluation of these 12 quadrats for biennial tillers was conducted in April and September of 1992.

Daily tiller initiation rate was calculated as follows:

$$\text{Daily tiller initiation rate} = \frac{\text{number of new tillers } 1.0 \text{ m}^{-2}}{\text{number of days since previous sampling}}$$

The number of tillers emerged was converted from 0.5m² to the more recognizable 1.0 m². Based on the 1991 tiller emergence patterns at the Panhandle Experimental Range, 1 April was selected as the beginning date for calculating rate of tiller initiation for the first sampling period each year.

Tiller emergence was analyzed as a split plot in time with time being a sub-plot factor to allow for a greater resolution of time (Briske and Hendrickson 1998). Differences between locations were analyzed using study site nested within location as an error term and differences between time and location by time were analyzed using time by study site nested within location as an error term. A majority of tiller emergence occurred early in the growing season and so only the first 4 time periods were included in the data analysis. Tiller emergence data were log transformed to correct for a non-normal distribution. Results are presented using non-transformed data for clarity of presentation. Standard errors were calculated across the first 4 time periods. Tillers within each type category were pooled over time periods, because of small sample sizes in some time periods and categories, and analyzed for differences between locations and study sites within location. Analysis was conducted using the SAS PROC GLM module (SAS 1989). Means separation was done using the Student-Newman-Keuls' test.

The absolute number of tillers that emerged and the rates of tiller emergence were correlated with the sum of the precipitation received during the 14 and 30-

day intervals prior to the sampling period. Tiller emergence was also correlated with the 30-year average precipitation on a monthly basis. Correlations were done using the PROC CORR procedure in SAS (SAS 1989). Significance was determined at $P = 0.05$ unless otherwise noted. Standard errors were calculated averaged across sampling dates.

The Panhandle Experimental Range had relatively few biennial tillers. Therefore, most of the data used in evaluating the contribution of biennial tillers came from the Gudmundsen Sandhills Laboratory. Standard errors used in the comparison of the contributions of new and biennial tillers to biomass and tiller numbers were calculated across study sites and quadrats. Standard errors, used in evaluating the number and percent of biennial tillers from each sampling date, were calculated across study sites and quadrats within sampling dates.

Results

Emergence date and category:

There were no significant differences in tiller recruitment between locations in 1990 ($P > 0.10$); however, tiller emergence during the 1990 growing season was 160% greater at Gudmundsen Sandhills Laboratory than at Panhandle Experimental Range (Fig. 1). In 1991, tiller emergence declined by 25% at the Gudmundsen Sandhills Laboratory but nearly doubled at the Panhandle

Experimental Range so total tiller emergence was very similar between locations ($P > 0.75$) (Fig. 2). Over 50% of the total tiller emergence for the season occurred by mid-May for both years and locations (Fig. 1 and 2). After early June, tiller emergence generally declined and remained low for the remainder of the growing season.

Time, but not location by time, had a significant effect on tiller recruitment in 1990, thus tiller emergence was pooled over location (Fig. 1). Each of the first 3 sampling periods in 1990 had significantly greater tiller recruitment than the subsequent period (Fig. 1). In 1991, there was a location by time interaction (Fig. 2) and tiller recruitment patterns were analyzed separately at each location. The pattern of tiller emergence at the Gudmundsen Sandhills Laboratory was similar to 1990 although there were no significant differences between the mid and late June time periods (Fig. 2). At the Panhandle Experimental Range, tiller emergence was similar in early and mid June and those time periods were significantly greater than late June (Fig. 2).

The Gudmundsen Sandhills Laboratory had significantly more extravaginal and rhizomatous tillers than the Panhandle Experimental Range in 1990. However, intravaginal tiller number was influenced more by site within location than by location. In 1991, the Gudmundsen Sandhills Laboratory had significantly more intravaginal tillers than the Panhandle Experimental Range, but the number of

Fig. 1. Number of tillers that emerged (m⁻²) on each monitoring date in 1990 pooled across locations for the Gudmundsen Sandhills Laboratory (GSL) and the Panhandle Experimental Range (PER). Newly emerged tillers were classified as either intravaginal, extravaginal or rhizomatous at each monitoring date. Numbers in parentheses are the total number of tillers that emerged (tillers m⁻²). Data was pooled over locations for each emergence date. Bars with different letters represent significant differences ($P < 0.05$) in total tiller emergence among the first 4 dates.

Fig. 2. Number of tillers that emerged (m^{-2}) on each monitoring date in 1991 at the Gudmundsen Sandhills Laboratory (GSL) and the Panhandle Experimental Range (PER). Newly emerged tillers were classified as either intravaginal, extravaginal or rhizomatous tillers at each monitoring date. Number in parentheses is the total number of tillers that emerged (tillers m^{-2}) during the growing season at each location. Data was not pooled because of a location by time interaction. Bars with different letters represent significant differences ($P < 0.05$) in total tiller emergence between the first 4 dates for each location.

extravaginal tillers was similar between locations. The number of rhizomatous tillers, in 1991, was affected more by site within location than by location.

Over the 2-year period, extravaginal tillers made up more than 63% of all tillers recruited at the Gudmundsen Sandhills Laboratory and over 75% of all tillers recruited at the Panhandle Experimental Range. Extravaginal tillers comprised more than 50% of the emerged tillers at any single sample date (Figs. 1 and 2) and they were the only tiller category to emerge from 24 July to 28 August 1990 and from 6 August to 19 August 1991 at the Panhandle Experimental

Range. Rhizomatous tillers were the next largest category and they were 20 and 18% of total tiller emergence at the Gudmundsen Sandhills Laboratory and the Panhandle Experimental Range, respec-

tively. Intravaginal tillers contributed the least number of tillers at both locations with only 7% and 16% of the emerged tillers being intravaginal at the Panhandle Experimental Range and the Gudmundsen Sandhills Laboratory respectively.

Tiller initiation correlations

Absolute tiller recruitment and tiller initiation rate were poorly correlated with 14-day and 30-day precipitation amounts (Fig. 3). Correlation coefficients were less than 0.3 ($P > 0.20$). An exception was tiller initiation rate and 30-day precipitation at Gudmundsen Sandhills Laboratory in 1991 ($r = 0.43$, $P = 0.07$). Correlations between tiller emergence and longer-term precipitation data (monthly totals over 30 years) was also low ($r < 0.30$, $P > 0.20$).

Biennial tiller yield:

Most tillers did not survive the following winter. Only 22% of the tillers, which emerged during the 2-year study, became biennial tillers at the Gudmundsen Sandhills Laboratory and only 6% at the Panhandle Experimental Range. In 1991, less than 1% of all the tillers that emerged during the growing season at the Panhandle Experimental Range became biennial tillers. Because of their minimal contribution to numbers and biomass at the Panhandle Experimental Range, those biennial tillers were not included in any of the data analysis regarding biennial tillers. Approximately 30% of tillers harvested in 1991 from plots established in 1990 at the Gudmundsen Sandhills Laboratory were biennial tillers but this had declined to 20% in 1992 (Fig. 4). Biennial tillers made up 12% of the yield from all live prairie sandreed tillers in 1991 and 6% of the 1992 biomass at the Gudmundsen Sandhills Laboratory (Fig. 4).

Yields of biennial tillers may have decreased because of harvesting in September rather than earlier in the growing season. However, there were no significant differences ($P > 0.05$) at the Gudmundsen Sandhills Laboratory when the number of biennial tillers recorded

Table 1. Mean individual tiller weights for tillers surviving from the previous year (biennial) and tillers that emerged during the current year at the Panhandle Experimental Range (PER) and Gudmundsen Sandhills Laboratory (GSL). Biennial tillers recorded in 1991 and 1992 had emerged in 1990 and 1991 respectively.

Harvest Date	PER		GSL	
	Biennial Tillers	Current Year Tillers	Biennial Tillers	Current Year Tillers
	----- (mg.) -----			
1991	78 $\pm$ 4	759 $\pm$ 48	131 $\pm$ 3	443 $\pm$ 33
1992	321 $\pm$ 63	414 $\pm$ 21	93 $\pm$ 3	334 $\pm$ 8

early in the season was compared to biennial tillers recorded later in the growing season. Tillers that emerged during the current growing season were 30 to 880% heavier than the biennial tillers (Table 1). These extremes were both recorded at the Panhandle Experimental Range but at the Gudmundsen Sandhills Laboratory, current year tillers were 230 to 260% heavier than the biennial tillers.

At the Gudmundsen Sandhills Laboratory, tiller cohorts that emerged early in the growing season the previous year made up the largest percentage of biennial tillers (Fig. 5). However, tillers that emerged later in the growing season were more likely to become biennial tillers (Fig. 5). May tiller cohorts made up approximately 33% of the biennial tillers in 1991 and 60% of the biennial tillers in 1992. The 1991 biennial tiller population had a large contribution from tiller cohorts that emerged later in the season in 1990 because of increased tiller emergence later in the season combined with increased potential for these tillers to become biennial. Over 70% of the biennial tillers at Gudmundsen Sandhills Laboratory were from the extravaginal tiller category (Table 2) because of the greater number of extravaginal tillers. Extravaginal tillers had the highest survival rate in the 1990 cohort but survival rates were similar between the extravaginal and intravaginal categories in the 1991 tiller cohort (Table 2).

Discussion

The unimodal pattern of tiller emergence in prairie sandreed differs from the more commonly reported bimodal tillering pattern of other perennial grasses in temperate zones (Langer 1963, Butler and Briske 1988, Briske and Richards 1995). However, unimodal tillering patterns have been reported for the C₃ grasses, crested wheatgrass, and bluebunch wheatgrass, (Mueller and Richards 1986). In a Kansas study of 2, C₄ grasses, indiangrass had a

bimodal tiller recruitment pattern while big bluestem, had a unimodal pattern (McKendrick et al. 1975).

Regionally, patterns of tiller emergence may be linked to precipitation patterns or the length of the growing season (Briske 1991). In our more site specific study, tiller emergence during the growing season and the rate of daily tiller emergence were poorly correlated with either yearly or 30-year average precipitation events which was similar to reports from sideoats grama [*Bouteloua curtipendula* (Michx.)

Torr.] (Hendrickson 1996). Moreover, although both locations received more precipitation during the 1991 than in the 1990 growing season, total tiller emergence decreased from 1990 to 1991 at Gudmundsen Sandhills Laboratory while increasing by 100% at Panhandle Experimental Range. However, Cullan et al. (1999) suggested that soil moisture and the ability of plants to absorb soil moisture may be critical factors in determining recruitment in prairie sandreed. The sandy substrate at both locations complicates the response to precipitation because its coarse texture allows for deep percolation of even minor rainfall events (Barnes and Harrison 1982). Thus, frequency of precipitation events may be more important than total precipitation.

Biennial tillers did not make a large contribution to tiller recruitment (6 to 22%) or aboveground biomass, which was surprising since the longer season of growth and development is often considered to give a growth advantage to biennial tillers (Langer 1956, Briske 1991). However in our study, new tillers were 200% heavier

Fig. 3. Daily tiller initiation rates (tillers m⁻² day⁻¹) and precipitation events (cm) during the growing season at the Gudmundsen Sandhills Laboratory and the Panhandle Experimental Range during the 1990 and 1991 growing seasons. The numbers in parenthesis represent total precipitation received during the growing season at each location and each year.

Table 2. Percentage of tillers that emerged during the preceding year and survived to become biennial tillers from each tiller category and the percentage that each tiller category contributed to the composition of the biennial tiller population in 1991, 1992 and averaged over both years at the Gudmunsen Sandhills Laboratory. Data from the Panhandle Research Range not presented.

Tiller Category	Survival Rate			Composition of the Biennial Tiller Population		
	1990	1991	Average	1990	1991	Average
	-----(-)-----					
Extravaginal	27 ± 2.2	27 ± 3.8	27 ± 2.0	86 ± 2.7	70 ± 1.3	78 ± 3.9
Intravaginal	8 ± 2.7	25 ± 2.2	16 ± 4.2	6 ± 2.2	15 ± 1.3	10 ± 2.3
Rhizomatous	9 ± 4.7	17 ± 2.3	13 ± 2.9	8 ± 2.7	15 ± 2.6	12 ± 2.4

Fig. 4. Contribution of current year tillers and biennial tillers to biomass (g m^{-2}) and tiller numbers m^{-2} at the Gudmundsen Sandhills Laboratory in 1991 and 1992. Biennial tillers had emerged during the previous growing season (1990 and 1991 respectively) and survived overwinter. Current year tillers were tillers that emerged in the 1991 and 1992 growing seasons. Current year tiller biomass was separated into vegetative and reproductive components but biennial tiller biomass was pooled over both components.

than biennial tillers thus early emergence did not seem to give a growth advantage to biennial tillers. If biennial tillers died prior to the harvesting date in September, their numbers and biomass could have been underestimated. However, biennial tillers numbers were generally similar between the early (April and May) and September monitoring dates.

The largest percentage of biennial tillers were from tiller cohorts that emerged early in the previous growing season because of the larger tiller recruitment. However, later emerging tillers were more likely to become biennial. Although, tillers which emerge early in the growing season generally have the greatest probability of becoming reproductive (Briske 1991), in our study a majority of biennial tillers were still vegetative when they were harvested at the end of the second growing season. A study of morphological development in prairie sandreed conducted during the same time period at Gudmundsen Sandhills Laboratory also indicated a majority of tillers remained vegetative throughout the growing season (Hendrickson et al. 1998). This suggests that the limited number of biennial tillers in prairie sandreed may not be a result of the tillers completing their life cycle but rather because of the small number of tillers recruited late in the growing season when they were more likely to become biennial. In Montana, C_3 grass tillers took 2–3 years to flower and C_4 grass tillers took 1–2 years although the results varied by species (White 1977).

Biennial tillers may represent a small pool of long-lived tillers that provide

prairie sandreed with an alternative population maintenance mechanism. This observation is difficult to assess because of the limited time frame of the experiment but a majority of biennial tillers remained vegetative even at the end of their second growing season. Although the contribution of axillary buds and tiller recruitment to population persistence has been explored (Hendrickson and Briske 1997), there is limited information regarding the role of tiller longevity in this regard. There have been reports of tiller ages of up to 5 years in northern wheatgrass [*Agropyron dasystachyum* (Hook) Scribn.] in Saskatchewan, Canada (Zhang and Romo 1995) and 3-year old western wheatgrass (*Agropyron smithii* Rydb.) tillers were observed in Montana (White 1977). These reports are from areas with more severe winter climates and contrast with lifespan of 1–2 years in more moderate climates (Langer 1956, Briske 1991,

Fig. 5. The number and percent of new tillers m^{-2} marked on each monitoring date in 1990 and 1991 that survived overwinter and became biennial tillers the following year at the Gudmundsen Sandhills Laboratory.

Briske and Richards 1995). From a practical point of view, a majority of the prairie sandreed tillers appeared to function as annual tillers similar to reports of prairie sandreed tillers in Montana (White 1977).

The limited contribution of biennial tillers in our study emphasized the importance of tillers initiated during the current year to tiller density and productivity. However tillers, which emerge during the growing season, are often initiated early and make some limited subterranean growth in the previous growing season (Bredja et al. 1988). Therefore, stress that occurs during this crucial time period early in the growing season may affect tiller numbers into the following growing season. For example, tiller and axillary bud numbers of prairie sandreed per unit area decreased when prairie sandreed and its associated species were clipped early in the growing season (June) over a 3-year period (Mullahey et al. 1991). Organic reserves of prairie sandreed were also adversely affected by a single grazing event in June or July but not August (Reece et al. 1996). These responses collectively indicate that tiller numbers during the year may be determined relatively early in the previous growing season. Consideration of the effects of environmental variables and management over multiple years needs to be incorporated into current management decisions.

Conclusions

In prairie sandreed, the tillering pattern and role of biennial tillers contrasts with patterns observed in other species (Langer 1956, Briske 1991). Prairie sandreed has a unimodal tillering pattern and a majority of tillers do not survive over winter. The few biennial tillers that are produced are small and make a minor contribution to biomass production as opposed to tillers that emerge during the growing season. The developmental morphology of prairie sandreed and the low correlations with precipitation indicate current-year tiller production may be linked to conditions in previous years. Given the importance of prairie sandreed for ecological functions and as a forage resource, quantifying the effects of preceding and current-year management as well as environmental variables on tiller emergence is warranted.

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Seed biology of rush skeletonweed in sagebrush steppe

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Abstract

Rush skeletonweed (*Chondrilla juncea* L.) is an invasive, herbaceous, long-lived perennial species of Eurasian or Mediterranean origin now occurring in many locations throughout the world. In the United States, it occupies over 2.5 million ha of rangeland in the Pacific Northwest and California. Despite the ecological and economic significance of this species, little is known of the ecology and life history characteristics of North American populations. The purpose of this study was to examine seed germination characteristics of 2 populations of rush skeletonweed in Idaho. Seeds from rush skeletonweed plants in southwestern Idaho were collected during the 1994 and 1995 growing seasons. Mature seeds were harvested on 6 dates between early July and early October 1994, and on 5 dates between early July and late September 1995. Fresh seeds from each harvest period were measured to determine seed weight, total germination, rate of germination, and viability (tetrazolium staining [TZ]) of non-germinating seeds. An aliquot of seeds collected in 1994 was also stored for 1 year to examine the effects of seed storage on germination. In southwestern Idaho, rush skeletonweed produces seeds continuously from mid-July through October. Seeds were capable of immediate germination without scarification or wet prechilling. Total germination generally ranged from 60 to 100% throughout the entire seed production period. Germination was also rapid, reaching 50% of total germination in less than 12 days. In general, germination was higher at the lower incubation temperature regime (20/10°C), perhaps reflecting origins of this species in Mediterranean winter rainfall regions. The TZ testing indicated that 30 to 60% of non-germinating seeds were viable, suggesting that seeds may persist in the soil seed bank. Up to 60% of seeds remained viable following 1 year of storage. Stored seeds generally exhibited higher germination rates ($\bar{x}$ = 90%) than fresh seeds ($\bar{x}$ = 67%), indicating possible dormancy and afterripening effects. Germination characteristics of this species are consistent with those of other invasive alien species, and favor rapid population growth leading to community dominance.

Key Words: *Chondrilla juncea* L., Pacific Northwest, rangeland weed, cereal crop weed, invasive species, germination

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Resumen

Chondrilla juncea L. (nombre vulgar: yuyo esquelético) es una especie herbácea perenne e invasora de larga vida y origen eurasiático o mediterráneo que habita actualmente en muchos lugares del mundo. En los Estados Unidos, ocupa más de 2.5 millones de hectáreas de tierras ganaderas en el Noroeste Pacífico y California. A pesar del significado ecológico y económico de esta especie, poco se sabe sobre la ecología y las características de la historia de vida de las poblaciones norteamericanas. El objetivo del presente trabajo fue examinar las características de la germinación de semillas de dos poblaciones de *C. juncea* en Idaho. Se colectaron semillas de plantas en el suroeste de Idaho durante la estación de crecimiento en 1994 y 1995. Se coleccionaron semillas maduras en 6 ocasiones entre principios de julio y principios de octubre de 1994, y en 5 ocasiones entre principios de julio y fines de septiembre de 1995. Se midieron semillas frescas de cada cosecha para determinar el peso de las semillas, la germinación total, la tasa de germinación, y la viabilidad (teñido con tetrazolio [TZ]) de semillas que no germinaron. Una alícuota de semillas colectadas en 1994 se almacenó por un año para examinar los efectos del almacenamiento sobre la germinación. En el suroeste de Idaho, *C. juncea* produce semillas continuamente desde mediados de julio hasta octubre. Las semillas fueron capaces de germinar inmediatamente sin escarificación o mojado y enfriado previos. La germinación total varió generalmente del 60 al 100% durante el período completo de producción de semillas. La germinación también fue rápida, alcanzando el 50% de la germinación total en menos de 12 días. En general, la germinación fue mayor en el régimen de temperatura de incubación más bajo (20/10°C), lo cual quizás refleja el origen de esta especie en regiones mediterráneas de lluvias invernales. Las pruebas con TZ indicaron que del 30 al 60% de las semillas que no germinaron eran viables, sugiriendo que las semillas podrían persistir en el banco de semillas. Hasta el 60 % de las semillas seguían viables después de un año de almacenamiento. Las semillas almacenadas generalmente mostraron proporciones de germinación mayores ($\bar{x}$ = 90%) que las frescas ($\bar{x}$ = 67%), indicando posibles efectos de la dormancia y postmaduración. Características de germinación de esta especie son consistentes con las de otras especies exóticas invasoras, y favorecen un crecimiento rápido de las poblaciones que la lleva a dominar en la comunidad.

Rush skeletonweed (*Chondrilla juncea* L., Asteraceae: Cichorieae), an apomictic, perennial forb with Eurasian and Mediterranean origins, has been introduced to other regions of the world, including Australia, South America, and the United

States (Cullen and Groves 1977, McVean 1966, Panetta and Dodd 1987). In North America, it was first discovered in the western United States near Spokane, Wash. in 1938. By 1981, its rate of spread was approximately 40,000 ha year⁻¹ (Cheney et al. 1981). It now dominates more than 2.5 million ha of rangeland in the Pacific Northwest and California (Sheley and Hudak 1995).

Rush skeletonweed grows in dense monocultures and displaces native plants, thereby reducing biodiversity and forage production for both domestic and native herbivores (Carroll 1980, Sheley and Hudak 1995). Seeds are wind-dispersed. New infestations establish on coarse, well-drained soils along roadways and on overgrazed rangelands, abandoned croplands, and other disturbed sites. The species exhibits a wide range of adaptability, occurring at elevations from less than 225 m to over 1,830 m that receive 250 to 1,500 mm annual precipitation (Moore 1964, Sheley and Hudak 1995).

Although rush skeletonweed is spreading primarily on rangelands, its potential threat to agricultural crops is also a major concern as it competes aggressively for light, water, and nutrients (Schirman and Robocker 1967, Zimdahl 1980). In some parts of Oregon and northern Idaho, rush skeletonweed has reduced annual wheat

yields by 26 to 42% (Cheney et al. 1981). It is one of the most serious weeds of cereal cropping in Australia where it has reduced wheat yields by as much as 80% (Piper 1983, Sheley and Hudak 1995, Sheley et al. 1999).

Current technology is largely ineffective at curtailing the spread of rush skeletonweed. Although the weedy characteristics of Australian populations have been described, a better understanding of the reproductive potential and germination characteristics of North American populations is essential if we are to identify the biological characteristics that contribute to the ecological success of this species, and develop more effective management methods (Wapshere et al. 1974, Lee 1986, Sheley et al. 1999). The objective of this study was to evaluate the effects of environmental conditions, maturation date, and dry storage on seed germination and viability of 2 rush skeletonweed populations in southwestern Idaho.

Materials and Methods

Study Sites

Populations of rush skeletonweed were identified at 2 locations in southwestern Idaho. The Orchard Research Site

(Orchard) is located 32 km southeast of Boise, Ada Co., Ida. (116° 04' W 43° 33' N), at an elevation of 955 m (NOAA 1993, Kitchen 1995). Mean annual temperature is 10.5°C (Fig. 1) (NOAA 1993). Mean annual precipitation is 250 mm with 81% occurring between November and June (Fig. 1). The frost-free period ranges from 140 to 190 days. This site supports a degraded Wyoming big sagebrush (*Artemisia tridentata* Nutt. var. *wyomingensis* [Beetle & A. Young] Welsh)/mixed bunchgrass community. Soils are sandy, mixed, mesic Xeric Torriorthents with deep, well-drained profiles. The rooting zone extends to a depth of 1.5 m or more and available water capacity is high (Collett 1980).

The Shrub Garden site is located near the Boise River, about 27 km northeast of Boise, Ada Co., Ida. (116° 04' W 43° 33' N), at an elevation of 1,033 m. Mean annual temperature is 9.2°C (Fig. 1) (NOAA 1993). Mean annual precipitation is 430 mm, and the frost-free period averages 126 days (Fig. 1). The site supports an antelope bitterbrush (*Purshia tridentata* [Pursh] DC.)/mountain big sagebrush (*Artemisia tridentata* Nutt. var. *vaseyana* [Rydb.] J. Boivin) community with a diverse grass-forb understory (Shaw and Monsen 1982). Soils are loamy-skeletal, mixed, mesic Aridic Argixerolls that are moderately deep and well-drained, developing from weathered granite (Collett 1980).

Seed Collection and Testing

Sixty plants at each study location were randomly selected and marked for seed collection in spring 1994. Mature seeds were hand harvested at 2-week intervals from the time of earliest maturation in late July through early October in 1994. In 1995, seeds were harvested on days within the same 7-day periods as in 1994, with the exception that no collections were made in October 1995. Weeks of harvest were: late July (22 to 28), early August (6 to 12), late August (18 to 24), early September (3 to 9), late September (22 to 29), and early October (7 to 13). Seeds were pooled among plants within a location on each harvest date.

Seeds were cleaned by hand-rubbing and sieving to remove the pappus and debris. Subsamples of each cleaned seed lot were used to determine seed weight, germinability, and viability. On each collection date, 3 subsamples of 100 seeds from each location were weighed to estimate average seed weight. Three additional subsamples of 100 seeds from each

Fig. 1. Air temperature and precipitation profiles for the Orchard and Shrub Garden sites, 1993-1995. Climatic data were based on NOAA information from the Boise Airport (Orchard) and Lucky Peak (Shrub Garden) Idaho weather stations. Long term averages encompass 1961-1990. (NOAA 1993, 1994, 1995).

location were immediately placed in incubation trials (1 to 2 days after collection). Remaining seeds from each 1994 collection date not used in germination trials were stored in sealed glass containers at room temperature in darkness for a period of about 1 year. Three subsamples of 100 stored seeds from each location and collection date were placed in incubation about 1 year later in late August 1995 to examine the effects of dry storage on seed germination characteristics. Because the effects of storage on seed germination were only examined for seed produced in a single growing season (1994), inferences are not broadly applicable to seed generated in another year.

Germination trials were conducted by placing each subsample of 100 seeds on 2 blue blotters saturated with distilled water in an 11 x 11 cm germination box. Germination boxes were then incubated at either 20/10 or 30/20°C (12 hrs/12 hrs). Seeds were exposed to light (PAR = 15 $\mu\text{M m}^{-2} \text{ s}^{-1}$) during the high temperature alteration. Germination counts were made at 2-day intervals for 14 days. Germination boxes were rearranged randomly in the incubation chambers after each count. Seeds were considered germinated when the radicle had emerged and the cotyledons were green and spreading. After 14 days, non-germinated seeds were tested for viability using a 1% solution of 2,3,5-triphenyl tetrazolium chloride (Moore 1973). Maximum germination was calculated as number of seeds germinated divided by the number of germinated seeds plus the number of viable nongerminated seeds determined by TZ testing. Rate of germination was expressed as days to 50% of 14-day germination.

Statistical Analyses

Experimental design was a randomized, complete block with site as the blocking factor. An ANOVA was used to evaluate differences in germination, germination rate, and viability of nongerminated fresh and stored seeds attributable to the main effects of year of collection, harvest date, storage treatment, and incubation regime and all possible interactions (SAS Institute 1988). Where significant interactions precluded direct interpretation of main effects, pairwise comparisons were made using the Bonferroni t-test (Milliken and Johnson 1992). All differences reported were significant at $p = 0.05$. Regression analyses were used to examine the relationship between seed weight and environmental conditions preceding each harvest date, germination, and rate of germination.

Results

Climatic Conditions

Total 1994 precipitation was 4% below average at Orchard and 33% below average at the Shrub Garden (Fig. 1). By contrast, 1995 was a relatively wet year. Total precipitation was 43% above average at Orchard and 12% above average at the Shrub Garden. In 1994 and 1995, the 14-day mean maximum air temperature prior to each harvest date ranged from 27 to 32°C at both locations, while the mean 14-day minimum air temperature ranged from 8 to 16°C.

Seed Weight

Weight of individual rush skeletonweed seeds ranged from 0.1 to 0.5 mg (Fig. 2). Seed weight was greater in 1994 than in 1995 for the early harvest dates ($p < 0.01$) (Fig. 2). In 1994, seed weight was positively correlated with total precipitation received during the 4-week interval prior to each harvest date ($R^2 = 0.75$, $p < 0.05$) and with the mean air temperature during the 2-week period preceding each harvest date ($R^2 = 0.98$, $p < 0.05$). No significant correlations between seed weight and precipitation or air temperature were found in 1995.

Germination of Fresh 1994 and 1995 Seeds

Germination of fresh seeds varied with year of collection, harvest date, and incubation regime (Fig. 3A) (Table 1). Seeds collected in early August exhibited lower total germination percentages than seeds collected on other harvest dates. Total germination percentage was not affected by incubation regime in 1994. However, total germination percentage of seeds collected on 1995 harvest dates was greater when incubated at the 20/10°C compared to the 30/20°C regime.

Fresh seeds harvested in 1994 and 1995 germinated rapidly, generally reaching 50% germination within 2 to 8 days (Fig. 3B). Germination rate was affected by a significant 3-way interaction between collection year, week of harvest, and incubation temperature (Table 1).

Days to 50% germination was similar for seeds harvested on the early dates in 1994 and incubated at either 20/10°C or 30/20°C. In 1995, seeds collected on the late harvest dates germinated more rapidly when incubated at 20/10°C compared to 30/20°C. In both 1994 and 1995 rate of germination was more rapid for seeds collected later in the season and incubated at 20/10°C. There were no significant relationships between seed weight and total germination percentage or germination rate.

Viability of nongerminating seeds differed between years (Table 1). In 1994 less than 10% of the nongerminating seed were viable following incubation, while in 1995 more than 30% were viable (Fig. 3C).

Fig. 2. Mean weight of *Chondrilla juncea* L. seed (mg) collected on 1994 and 1995 harvest dates from the Orchard and Shrub Garden sites in southwestern Idaho.

Table 1. Degrees of freedom (df), MS values, and probability levels (p) for ANOVA models used to statistically analyze total germination, days to 50% germination, and viability [TZ] of nongerminating fresh rush skeletonweed seed from 1994 and 1995 harvest dates and for fresh and stored seed from 1994 harvest dates in southwestern Idaho. Seeds were stored in sealed containers at room temperature from harvest to August 1995.

Model	Total Germination			Days to 50% Germination		Viability	
	df	MS	p	MS	p	MS	p
----- fresh 1994 vs fresh 1995 seed -----							
Collection Site (Block)	1	167.6	*	5.9	ns	562.6	*
Year of Collection (Year)	1	1879.9	***	18.7	*	8444.5	***
Week of Collection (Date)	4	1025.0	***	83.7	***	117.8	ns
Germination Temperature (Temp)	1	894.3	***	6.4	ns	101.2	ns
Year*Date	4	452.4	***	12.3	**	105.0	ns
Year*Temp	1	980.1	***	28.9	***	160.6	ns
Date*Temp	4	105.3	ns	0.9	ns	73.7	ns
Year*Date*Temp	4	134.4	*	6.1	*	25.4	ns
----- fresh 1994 vs stored 1994 seed -----							
Collection Site (Block)	1	121.8	ns	1.6	ns	266.0	ns
Week of Collection (Date)	5	480.8	*	31.1	***	198.7	ns
Germination Temperature (Temp)	1	154.8	ns	0.6	ns	0.0	ns
Storage	1	150.7	ns	60.7	***	351.4	ns
Date*Temp	5	31.2	ns	0.7	ns	198.2	ns
Date*Storage	5	229.2	ns	24.4	***	210.7	ns
Temp*Storage	1	196.8	ns	22.3	*	10.6	ns
Date*Temp*Storage	5	28.8	ns	3.9	ns	159.6	ns

* p < 0.05

** p < 0.01

***p < 0.001

Germination of Fresh and Stored 1994 Seeds

Total germination percentage of seeds harvested in 1994 and incubated immediately or stored in sealed containers at room temperature until August 1995 varied with harvest date (Table 1). For stored seeds, those collected mid-season exhibited greater total germination percentages than collections harvested at earlier or later collection periods (Fig. 3D). Stored seeds were as germinable as fresh seed, generally exceeding 80% germination following 1 year of dry storage.

Days to 50% germination for 1994 seeds varied with storage treatment and harvest date (Table 1). Stored seeds generally germinated more rapidly than fresh seeds with the exception of seeds collected at the later harvest dates and incubated at 30/20°C (Fig. 3E). Days to 50% germination also varied with storage treatment and incubation regime (Table 1). The germination rate was similar for fresh or stored seeds when incubated at 30/20°C. However, stored seeds germinated more rapidly than fresh seeds when incubated at 20/10°C. The viability of nongerminating seeds was similar for fresh and stored 1994 seed collections averaging 13% (Table 1).

Discussion and Conclusions

Many weedy species of Eurasian and Mediterranean origins are well-adapted to the climatic conditions of the interior western United States (Mack 1986). These invasive plants occupy broad niches and exhibit a large degree of phenotypic plasticity (Baker 1986, Bazazz 1986). They are generally capable of flowering and setting seed under a wide range of environmental conditions (Pimentel 1986).

The adaptability of rush skeletonweed to climatic conditions in areas of the western United States has been demonstrated by its rapid expansion. In addition, it shares many characteristics of highly successful invader species. Its apomictic habit eliminates dependence on insect pollinators and promotes genetic stability. Plants are capable of establishing, reproducing, and dispersing seeds in areas where environmental factors may be limiting for plant growth and development (Duke 1985, Bazazz 1986).

The southwestern Idaho rush skeletonweed populations flowered and produced seeds continuously from July to October during the driest and warmest portion of the season. Despite the environmental limitations, rush skeletonweed produced viable seeds that germinated rapidly at

both temperatures tested. Most seeds were capable of immediate germination without pretreatment to relieve dormancy. In both years, seeds reached total germination percentages in excess of 60% regardless of incubation regime.

Grant-Lipp (1966) reported that rush skeletonweed seeds from Canberra, Australia reached 90% germination within 24 hours when incubated at temperatures between 18 and 30°C. Germination was complete within 48 hours. Slower rates reported in this study were attributed to differences in criteria used to define successful germination. Radicle emergence was used by Grant-Lipp; criteria used for this study were believed to provide a more realistic index of seedling survival in the field.

Even in the drier year (1994) when precipitation was considerably less than the 30 year average, rush skeletonweed produced seeds that were highly germinable, reaching total germination percentages generally in excess of 80% (Fig. 3A). These seeds also exhibited more rapid germination than seeds from 1995. Studies have found that when subjected to mild drought stress, some plant species display higher germinability (Hilhorst and Toorop 1997). Dodd and Panetta (1987) found that a large numbers of seeds are produced even under drought conditions. Rush skeletonweed may be producing viable seeds even under hot, dry conditions because flowering and seed production are independent of summer rainfall (Panetta and Dodd 1987). Plants acquire soil water through deep roots that may penetrate several meters into the soil profile (Panetta and Dodd 1984, 1987). Elevated temperatures during the seed production period in 1994 may have increased the germinability of rush skeletonweed seeds in this study.

In both years, across all dates, there appeared to be a trend toward greater germination rates and faster germination at the lower incubation temperature regime (Fig. 3). Germination of rush skeletonweed seeds was generally rapid in both incubation regimes. Plants reached 50% of total germination within 2 to 8 days for most dates in both 1994 and 1995. For seeds produced in 1995, germination was slower for seeds incubated at the higher temperature regime. This trend may reflect origins of rush skeletonweed in Mediterranean winter rainfall regions where cool-season germination may ensure access to winter precipitation. The ability to germinate during the cooler portions of the growing season would be advantageous throughout

Fig. 3. Germination, germination rate, and viability of non-germinated rush skeletonweed seeds immediately following 1994 and 1995 harvest dates from the Orchard and Shrub Garden sites in southwestern Idaho. The legend in figure 3E applies to the entire graph. Figures 3A, B, and C are results for fresh seed incubated in 1994 and 1995. The effects of storage on germination were evaluated for seed collected in 1994 only. Figures 3D, E, and F represent results of stored seed collected in 1994 and germinated in August 1995.

much of the northwestern United States where most precipitation occurs during the winter. Conversely, lower germination at higher temperatures may reduce the risk of germination during the warmest, driest portion of the season when soil moisture may be insufficient for seedling survival, establishment, and growth (Baskin and Baskin 1985).

About 10% of non-germinating seeds from 1994 and more than 30% of non-germinating seeds from 1995 were viable. Viability of non-germinating seeds may be an indication of some seeds possessing a primary dormancy. Germination results from seeds collected in 1994 and stored for 1 year indicated that storage did not

have a detrimental effect on germination of rush skeletonweed seeds. Cuthbertson (1970) reported that germination percentages of mature rush skeletonweed seeds remained unchanged after 12 months of dry storage.

The increased germination total and rate for stored 1994 seed indicates that some fresh seeds may indeed possess a primary dormancy. Seeds with primary dormancy may undergo an afterripening process during storage that releases dormancy and results in increased germination rates and percentages under a broader range of incubation conditions (Beckstead et al. 1995). Primary dormancy in rush skeletonweed seeds ranges from 0 to 40% among studies

(Grant-Lipp 1966, McVean 1966, Cuthbertson 1970, Panetta and Dodd 1987). Cuthbertson (1970) stated that there appeared to be a short-lived dormancy in some field samples, while others suggest that rush skeletonweed seeds lack primary dormancy (Grant-Lipp 1966, Coleman-Harrell et al. 1979). Rush skeletonweed seeds may be exhibiting germination polymorphism, a common characteristic of successful weeds. It may be a survival strategy whereby the range of conditions favorable for germination varies among seeds. This mechanism permits some seeds to germinate immediately whereas others may germinate at a later date (Pimentel 1986).

A small percentage of non-germinating stored seeds, especially seeds produced later in the season, were still viable, indicating that rush skeletonweed seeds may acquire a secondary dormancy which could potentially enable some seeds to persist in the soil seed bank. Lonsdale et al. (1988) stated that persistence of seeds in soil seed banks is a critical component for maintaining populations of weedy species. Grant-Lipp (1966) indicated that rush skeletonweed seeds may acquire a secondary dormancy when exposed to high temperatures. Other studies have found that in some plant species, dispersed seeds are readily germinable immediately after shedding, if conditions are favorable. However, when conditions for germination are not met, seeds may acquire a secondary dormancy (Hilhorst and Toorop 1997). Subjecting rush skeletonweed seeds collected in 1994 to storage conditions may have induced a secondary dormancy in some seeds. The findings in this study suggest that a portion of rush skeletonweed seeds may have a primary dormancy and that others may be acquiring a secondary dormancy, enabling seeds to persist in the soil.

In addition to germination polymorphism, rush skeletonweed seeds also showed seed polymorphism in producing seeds of different weights. Although seed weight is positively correlated with germinability in many plant species (Saner et al. 1995), this relationship was not evident with rush skeletonweed in this study.

Seed weight was positively correlated with both temperature and rainfall during the growing season in 1994, but not in 1995. Because 1995 was a wetter year, environmental conditions may have been conducive to greater seedling establishment in the earlier portions of the growing season. Rush skeletonweed density was obviously higher in 1995 than in 1994

(personal observation). We speculate that plants establishing early in the 1995 growing season may have allocated more carbon to growth while conditions were favorable. However, those plants may have experienced greater intraspecific competition in the latter portion of the growing season when hot, dry conditions ensued. This may have in turn reduced the amount of carbon available for plants to allocate to seed production.

In conclusion, we found that germination characteristics of rush skeletonweed were consistent with those of other successful alien invaders. Rapid germination, without any afterripening requirements, favors rapid explosive population growth and allows rush skeletonweed to spread, persist, and dominate disturbed communities. Secondary dormancy may allow some skeletonweed seed to persist in the soil and possibly reestablish a stand if unfavorable environmental conditions or management activities eliminate an initial population. Due to these characteristics, the control or eradication of rush skeletonweed in most infested areas may prove difficult.

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Seed production in sideoats grama populations with different grazing histories

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Abstract

Frequent and intense defoliation of grasses has been associated with the evolution of "grazing morphotypes" that exhibit a variety of vegetative traits correlated with improved grazing resistance. While recovery from a seed bank is not considered an important grazing resistance mechanism, relatively little is actually known regarding seed (caryopsis) production in grazing morphotypes of caespitose grasses. The goal of this research was to compare components of seed production in 2 populations of sideoats grama (*Bouteloua curtipendula* var. *caespitosa* Gould & Kapadia) from nearby sites with different histories of livestock grazing. This was done using vegetative propagules of genotypes from both populations in a greenhouse study. The study was conducted in 2 flowering seasons under conditions considered favorable for seed production. The population exposed to livestock grazing showed a genetically based decrease in seed production relative to the ungrazed population. Lower seed production per plant in the grazed population was at least partially due to reduced numbers of tillers and panicles per plant and spikes per panicle that may be associated with selection for grazing tolerance. The grazed population also exhibited lower average seed production per spike indicating lower inherent floral fertility. Seed production was not closely correlated with vegetative traits associated with increased grazing tolerance, nor was there evidence of obvious physiological trade-offs related to decreased seed production in the grazed population. Lower seed production potential in populations of sideoats grama intensively grazed by livestock may lead to reduced potential for seedling colonization.

Key Words: *Bouteloua*, defoliation tolerance, evolution, grazing resistance

Grasses that are exposed to herbivores often possess unique life history, morphological and physiological traits (Carmen and Briske 1985, Briske and Richards 1995, Briske 1996). When defoliation has been frequent over long periods of time, these traits may be associated with the evolution of genetically based defoliation tolerance and the emergence of "grazing morphotypes" in the plant populations affected (e.g., Detling and Painter

Resumen

La frecuente e intensa defoliación de los zacates ha sido asociada con la evolución de "morfotipos de apacentamiento" que presentan una variedad de características vegetativas correlacionadas con una mejor resistencia al apacentamiento. Mientras que la recuperación a partir del banco de semillas no se considera un mecanismo importante de resistencia al apacentamiento, actualmente poco se sabe respecto a la producción de semilla (cariópside) de los "morfotipos de apacentamiento" de zacates cespitosos. La meta de este estudio fue comparar los componentes de la producción de semilla de dos poblaciones de "Sideoat grama" (*Bouteloua curtipendula* var. *caespitosa* Gould & Kapadia) de sitios cercanos con diferentes historiales de apacentamiento por ganado. Esto se realizó a través de un estudio de invernadero utilizando propágulos vegetativos de genotipos de ambas poblaciones. El estudio se condujo durante 2 estaciones de floración bajo condiciones consideradas favorables para la producción de semilla. La población expuesta al apacentamiento por ganado mostró una disminución (genéticamente basada) en la producción de semilla en relación a la población sin apacentamiento. La baja producción de semilla por planta de la población con apacentamiento se debió parcialmente a el reducido número de hijuelos y panículas por planta y espigas por panícula, lo que puede estar asociado con la selección por tolerancia al apacentamiento. La población apacentada también exhibió un promedio menor de producción de semilla por espiga, indicando una menor fertilidad floral inherente. La producción de semilla no se correlaciono estrechamente con las características vegetativas asociadas con el aumento en la tolerancia al apacentamiento, ni hubo evidencia obvia de cambios fisiológicos relacionados con la disminución de producción de semilla de la población apacentada. La potencial baja producción de semilla de poblaciones de "Sideoat grama" apacentadas intensivamente puede conducir a una reducción potencial de colonización por plántulas.

1983, Aarssen and Turkington 1985, Carmen and Briske 1985, Painter et al. 1989, 1993, Smith 1998). Defoliation tolerance in caespitose grasses is commonly correlated with a series of vegetative traits including reduced plant height, a less upright growth form, fewer and smaller leaves, and increased tiller number (Briske 1996).

Previous research (Smith 1998) compared vegetative responses under varying defoliation regimes of genotypes from 2 populations of sideoats grama (*Bouteloua curtipendula* var. *caespitosa* Gould & Kapadia) with different livestock grazing histories. In

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these studies, a population with long-term exposure to cattle grazing (approximately 100 yr) exhibited traits associated with improved defoliation tolerance (primarily increased tiller survival and reduced tiller mass) compared to a population that was not exposed to grazing by livestock. Evidence of reduced genetic variation within the grazed population was also noted for various vegetative traits associated with defoliation tolerance. While the environments the 2 populations inhabited differed in ways other than the presence of livestock, the response of genotypes from both populations was consistent with the evolution of increased grazing tolerance in the population from the grazed site.

Increased seed production and expansion of a soil seed bank may represent an additional defoliation resistance mechanism (Briske 1996), but the effects of livestock grazing on the evolution of this resistance mechanism are not well characterized. Reduced production of reproductive tillers has been observed in populations of perennial grasses derived from sites exposed to contrasting grazing regimes (e.g., Trlica and Orodho 1989, Painter et al. 1989, 1993). Nevertheless, little information is available regarding any differences in seed (caryopsis) production between such populations. Scott and Whalley (1984) found that the mean number of seeds produced per inflorescence was significantly lower in genotypes from populations of 2 species of *Danthonia* that had been exposed to heavy grazing by sheep compared to relatively less grazed populations. However, protection from livestock grazing for more than 50 years did not result in altered seed production in Indian ricegrass (*Achnatherum hymenoides* (Roemer & J.A. Schultes) Barkworth) genotypes taken from grazed or ungrazed sites when these genotypes were grown in a common environment (Orodho et al. 1998). A lack of additional data on seed reproduction and the evolution of grazing morphotypes prevents a more integrated understanding of demographic processes that may be affected by the presence of grazing animals.

The primary objective of this research was to determine whether exposure to different livestock grazing regimes is associated with genetically based changes in seed production in sideoats grama. This was done under conditions of minimal defoliation stress using genotypes from 2 populations with contrasting livestock grazing histories (Smith 1998). Secondary objectives were to determine whether variation in seed production was associated with other traits related to defoliation tolerance.

Materials and Methods

This research utilized genotypes from 2 populations of sideoats grama from the semidesert grassland biotic community in southeastern Arizona (Brown 1994). One population ("ungrazed") occurs atop a steep-walled butte (32° 42' N, 110°, 29' W 1,655 m asl) near Mammoth, Ariz. that probably has never been grazed by large (>100 kg) herbivores, including most domestic livestock (Hadley et al. 1991). The other ("grazed") population occurs on a site (1,338 m asl) that has been regularly grazed by cattle since before 1900 (V. Mercer, Mammoth, Ariz., personal communication) that is located 4.8 km from the ungrazed population. Deer (*Odocoileus* spp.) and small mammalian herbivores are able to reach both sites and may graze on sideoats grama (Krausman et al. 1997). Prairie dogs (*Cynomys* spp.) occurred in southeastern Arizona (Hoffmeister 1986) and may have also grazed on both sites until about the late 1930's. No description of fire history or precipitation is available for either site. Both sites are on 20–35% slopes with numerous rock outcrops and shallow Haplargid soils (D. Robinett, USDA-NRCS, Tucson, Ariz., personal communication). Sideoats grama occurs sporadically in the area between the 2 sites, most commonly in drainages on the slopes of the butte, and this may permit gene flow between the populations.

Twenty randomly selected genotypes (basal area >15 cm) were dug from along a 400-m transect at each site in 1994. Individual genotypes were separated by at least 3 m and were assumed to represent the products of separate established seedlings. Genotypes from both populations are high polyploids with $2n = 75-92$ (D. Showalter, University of Arizona, unpublished data, Gould and Kapadia 1964). These genotypes were grown in 4-liter pots in a shadehouse in Tucson, Ariz. for 6 mo before a minimum of 6 ramets were established for each genotype from single rooted tillers (Smith 1998). Individual ramets were grown in 4-liter pots in an evaporatively cooled greenhouse and treated uniformly until June 1997 with defoliation 5 cm above the soil surface every 6 to 12 weeks. The resulting ramets were placed on greenhouse benches using a modified split-plot arrangement with 4 replications with population as the main plot and all 20 genotypes from each population placed randomly as sub plots within the main plots. Ramets within each main plot were grouped together within an area of 1 m² to concentrate pollen from

that population and were isolated from the other main plot in that replication or from other replications by at least 80 cm.

Mean daily temperature in the greenhouse during the study was 32.7°C (mean low of 27.7°C, mean high of 35.6°C). Fans were used to circulate pollen during anthesis. Ramets were irrigated individually when leaf curling and color indicated drought stress. Soil moisture content was ~20 to 30% of field capacity at this point.

Ramets were allowed to grow from June through October in 1997 and 1998, a period exceeding the entire flowering season for sideoats grama in southern Arizona. Inflorescences in sideoats grama are panicles with up to 50 short, pendulous spikes. As panicles matured, at least 3 were harvested individually from each ramet in each main plot. Spikes were counted for each panicle and individual seeds per panicle determined following threshing. Mean seed mass was determined from 50-seed samples dried at room temperature. The mean number of spikelets per spike was determined by dissecting 5 spikes from each ramet. Spikelets were assumed to contain 1 floret (Cronquist et al. 1977). Tiller number was recorded for each ramet 8 weeks after defoliation in a regrowth cycle that began 5 June 1998. Tillers that showed any sign of a mature spike were counted as reproductive.

Some of the genotypes used in this study were also included in a greenhouse study that evaluated vegetative response to different defoliation frequencies (Smith 1998). Seed production per spike in ramets from these genotypes (ungrazed: $N = 10$, grazed: $N = 9$) was rank correlated (Sokal and Rohlf 1995) with various traits associated with vegetative growth from the previous study where defoliation occurred every 14, 28, or 56 days over a 168-day period. These traits were: plant height, root dry weight, shoot dry weight, total plant dry weight, and tiller number and dry weight.

Mixed-model analysis of variance was used to compare traits among genotypes of the 2 populations. Proc MIXED of SAS (Littell et al. 1996) was used with replications, years, and genotypes within populations considered random effects. For comparisons of the components of seed production (Table 1), significance of differences between populations were assessed using single-degree of freedom contrasts. Least-squares means are reported throughout for these traits. Distribution of mean seed production per spike in the 2 populations was evaluated for each year separately using frequency histograms and two-

Table 1. Least squares means for components of seed production by structural unit in ungrazed and grazed populations of sideoats grama.

Population	Structural unit								
	Spike			Panicle			Plant ¹		
	(Seeds spikelet ⁻¹)	(Seeds spike ⁻¹)	(Spikelets spike ⁻¹)	(Seeds panicle ⁻¹)	(Spikes panicle ⁻¹)	(Tillers ramet ⁻¹)	(% reproductive tillers)	(Panicles ramet ⁻¹)	(Seeds ramet ⁻¹)
Ungrazed	0.050*	0.200*	3.37	6.3*	31.3	33.7*	40.9*	9.2*	284*
Grazed	0.013*	0.140*	3.75	4.1*	28.4	29.2*	37.6*	6.8*	197*

¹Estimated from tiller counts made in 1998.

*Population means significantly different by single degree of freedom contrast ($P \leq 0.05$).

tailed Fisher's exact tests. The same approach was used to compare the number of spikes per panicle but data from both years were combined since means were not significantly different between years for this trait. Relationships between components of seed output could be evaluated using rank correlation coefficients which do not assume a linear relationship between the 2 variables examined (Sokal and Rohlf 1995). The numbers of seeds produced per spike and spikes produced per panicle were also rank correlated with various vegetative traits associated with response to defoliation using data from a previous study (Smith 1998) for genotypes that were included in that study and the present one. Conservative rank correlation procedures were also used in this case, again because linear relationships could not be assumed but also because data originated from separate experiments for some pairs of variables.

Genetic analysis was done using Box-Cox transformed values for the number of seeds per spike (Sokal and Rohlf 1995) and untransformed values for the number of spikes per panicle. Broad-sense heritability was estimated for both traits within each population using a split-plot in time design after Nyquist (1991). When the estimates were significantly greater than 0, standard errors were calculated using the method of Gordon (1979). Phenotypic correlations were utilized throughout since the array of genotypes and experimental design utilized did not permit accurate estimation of additive genetic variance which would be required for calculation of genetic correlations (Lynch and Walsh 1998). Statistical significance was assigned at $P \leq 0.05$ in all cases.

Results

Ramets from the ungrazed population produced significantly more seeds per spikelet and spike overall than did those from the grazed population (Table 1). Since the 2 populations did not differ in

the average number of spikelets per spike, the number of seeds per spike may be considered as the primary component explaining differences in floral fertility between the populations. This resulted in significantly higher mean seed production per panicle in the ungrazed population. Using tiller count data, it was possible to estimate additional components of seed output on a whole-plant basis. This showed that in the absence of significant defoliation, ramets from the ungrazed population would generally be expected to produce significantly more tillers overall and reproductive tillers, and therefore more panicles and spikes than ramets from the grazed population (Table 1). Combination of tiller data with that from individual spikes and panicles further revealed that significantly more seeds would be expected per ramet under these conditions in an entire flowering season within the ungrazed population than within the grazed population.

There was no significant difference between the populations in average seed mass (ungrazed: 0.62 ± 0.05 mg [least-squares mean $\pm$ SE], grazed: 0.70 ± 0.08 mg). Because ramets from the ungrazed population would produce more seeds, the mean total mass of seeds produced per ramet was significantly higher in the ungrazed population (34.2 ± 5.7 mg) than

in the grazed population (23.6 ± 4.8 mg). Still, the mass of seeds produced by each ramet would represent less than 2% of the aboveground biomass productions of these ramets based on results for the 2 populations from previous research (Smith 1998).

Over all genotypes in both populations, seed production per spike was significantly correlated between years ($r_s = 0.66$, $P \leq 0.05$) and the genotype $\times$ year, and population $\times$ year interactions were not significant. However, the mean number of seeds produced per spike was significantly greater in 1998 (0.26 ± 0.02) than in 1997 (0.12 ± 0.01) based on a Wilcoxon signed rank test. Analysis of frequency histograms of seeds produced per spike over genotypes (Fig. 1) in each year also suggested differing distributions of this variable between the populations. This led to separate analyses of the distribution of seed production for the 2 years. These distributions differed significantly between the 2 populations in both years with seed production in the ungrazed population consistently skewed toward higher values (Fig. 1). In 1997, the median number of seeds produced per spike was 0.125 in the ungrazed population compared to 0.064 seeds per spike in the grazed population. In 1998, medians for the 2 populations were 0.320 and 0.091 seeds per spike. The

Fig. 1. Distribution of mean seed production per spike for genotypes from ungrazed and grazed populations of sideoats grama. Population distributions significantly different ($P \leq 0.05$) based on Fisher's exact test for experiments conducted in 1997 and 1998.

mean number of spikes per panicle did not differ between years, nor was there a significant population x year interaction for this trait. The distributions of this trait also did not differ significantly between populations (Fig. 2). Medians for the ungrazed and grazed populations were 31.6 and 28.6 spikes per panicle, respectively.

The number of seeds per spike was significantly and negatively correlated with the number of tillers per ramet in the ungrazed population as measured in this study (Table 2). The number of spikes per panicle was also positively correlated with tiller number in this population. Overall seed production per ramet was positively associated with the number of seeds produced per spike in both populations. In the grazed population, the number of seeds per ramet was also positively correlated with both the number of tillers and the number of spikes produced per ramet. This would be expected given the lower mean seed production per spike in this population. The average mass of an individual seed was not significantly correlated with any other primary reproductive measures in either population.

Combining data from this study with those from Smith (1998), the number of seeds produced per spike was significantly correlated only with mean tiller weight with defoliation every 28 days ($r_s = 0.52$, $P = 0.05$). No other significant phenotypic correlations were observed between any measures of reproductive output and vegetative growth under different defoliation regimes for the 19 genotypes common to both studies.

Overall variability in the number of seeds per spike appeared greater in the grazed population than in the ungrazed population ($CV = 84$ vs 121%). Broad-sense heritability of the number of seeds per spike over years was significantly greater than 0 in both populations, but did not differ significantly between the populations (ungrazed: $24.5 \pm 6.0\%$, grazed:

$35.8 \pm 11.3\%$). Broad-sense heritability of the number of spikes per panicle was less than 2% and did not differ significantly from 0 in both populations.

Discussion and Conclusions

As was the case with vegetative traits (Smith 1998), this research shows that 2 sideoats grama populations from nearby sites with contrasting livestock grazing histories differed in reproductive characteristics that may be associated with plant demography (Table 1, Fig. 1). While the grazed population displayed evidence of selection for vegetative traits associated with increased grazing tolerance in previous research, the current study indicates that this population also exhibits decreased average seed production potential per plant. Observation of significant broad-sense heritability for the number of seeds per spike in both populations demonstrates a genetic basis for the variation among genotypes within these populations.

Because the 2 populations occupy environments that may differ in ways other than their livestock grazing history, it is not possible to definitely conclude that differences in reproductive biology are solely the result of exposure to livestock grazing in 1 population. For example, fire history and weather may differ at the 2 sites and could explain the differences in vegetative traits (Smith 1998) and reproductive biology between the populations. The 2 populations may have also diverged genetically before livestock were introduced to the grazed site. Nevertheless,

Fig. 2. Distribution of mean spike production of spikes per panicle for genotypes from ungrazed and grazed populations of sideoats grama. Population distributions are not significantly different ($P > 0.05$) based on Fisher's exact test.

given that sideoats grama occurs in the area between the sites, that many native herbivores are able to reach both sites, and that genotypes from the grazed population exhibit vegetative characteristics that are consistent with selection for tolerance to defoliation (Briske 1996), it appears reasonable to speculate that exposure to livestock may have affected reproductive characteristics of the grazed population.

As in this research, Scott and Whalley (1984) found that plants from populations of *Danthonia linkii* Kunth and *D. richardsonii* Cashmore that had been exposed to intense grazing by sheep produced fewer seeds per panicle on average when grown without defoliation stress compared to plants from populations from sites with lower grazing stress. These results are also consistent with the observation that increased seed production to expand the seed bank is apparently not a common mechanism of defoliation resistance in perennial caespitose grasses (Pyke 1990).

Reduced average seed production potential per plant in the grazed population is due in part to a combination of traits that lead to a reduction in overall plant size. These include a reduced number of tillers and panicles compared to the ungrazed population (Table 1). This morphology and its effects on seed production is consistent with findings from previous research on the evolution of grazing-adapted morphotypes in caespitose grasses (e.g., Detling and Painter 1983, Painter et al. 1989, 1993). These morphological adaptations affecting seed production may therefore represent simply secondary consequences of strong selection for vegetative traits associated with defoliation tolerance.

Table 2. Rank correlation coefficients between components of seed production ungrazed (upper values and grazed (lower) populations of sideoats grama.

	Spikes panicle ⁻¹	Tillers ramet ⁻¹	% reproductive tillers	Spikes ramet ⁻¹	Seeds ramet ⁻¹	Seed mass
Seeds spike	—	-0.50*/0.40	—	—	0.68*/0.93*	—
Spikes panicle	—	0.56*/0.04	—	0.48*/0.22	—	—
Tillers ramet	—	—	—	0.68*/0.81*	0.04/0.56*	—
% reproductive tillers	—	—	—	0.85*/0.58*	—	—
Spikes ramet ⁻¹	—	—	—	—	0.31/0.55*	—
Seeds ramet ⁻¹	—	—	—	—	—	—

*Significant at $P = 0.05$,

— = $P > 0.05$;

Ungrazed population/Grazed population, $N = 20$ for both.

The observation of reduced floral fertility (number of seeds per spike) in the grazed population suggests that selection under grazing stress may have affected the production of seeds within an individual spikelet. This could be driven by competitive advantages afforded to genotypes that allocate additional photosynthetic resources to vegetative growth and less to seed production (Bazzaz et al. 1987, Ashman 1994). Physiological trade-offs of this sort (Stearns 1992) would be expected to lead to negative correlations between the life-history traits affected although these have been difficult to document in perennial grasses (Reekie 1991, Cheplick 1995). While this research was not designed to identify physiological trade-offs, there is some evidence for such a trade-off in the ungrazed population where the number of tillers per plant is negatively correlated with the number of caryopses per spike (Table 2). However, this is not conclusive since seed production traits are not correlated with the number of spikes produced either by individual panicles or whole plants in this population as might be expected with this trade-off.

A commonly discussed physiological trade-off related to seed production involves linkage of decreases in seed number per plant with increases in seed mass, and with increases in the latter trait presumably leading to improved seedling establishment (Westoby et al. 1992). This does not appear to be the case here as mean seed mass did not differ between the populations and this trait was not correlated with any components of seed output (Table 2).

Available evidence suggests that the polyploid sideoats grama populations native to southern Arizona are facultatively apomictic (Harlan 1949, Freter and Brown 1955, Gould 1951). The existence of facultative apomixis and complex sexual/apomictic cycles (Richards 1986) in this taxon would seem likely given current understanding of its reproductive biology. Recent research (Overath and Asmussen 1998) suggests that it may be incorrect to assume that populations of facultatively apomictic plants are necessarily depauperate genetically and therefore less responsive to selection than non-apomictic species. Canfield (1957) showed that individual sideoats grama plants did not live longer than 3 years on sites grazed by cattle in southern Arizona. Together, these findings indicate that significant genetic variation may have existed and sufficient mortality and seedling establishment could have occurred to permit selection of traits

associated with grazing resistance in the grazed population in the roughly 100 years that it has been exposed to livestock.

Reduced seed production would have negative consequences most noticeably in reducing propagules available for colonization of open sites (Richards 1990). Reduced seed production as demonstrated here could also affect genetic structure within the grazed population since the production of fewer seeds would result in reduced opportunities for sexual reproduction should it occur. Indeed, previous genetic analyses of these 2 populations (Smith 1998) suggests that the grazed population is less variable genetically in vegetative traits associated with defoliation tolerance. The grazed population may therefore be more susceptible to local extinction (O'Connor 1991) due to either the direct demographic effects of reduced contribution to the soil seed bank, or to the more indirect genetic effect of limiting available genetic variability due to reduced potential for outcrossing.

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Hoary cress reproduction in a sagebrush ecosystem

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Abstract

Field studies were undertaken to evaluate hoary cress (*Cardaria draba* (L.) Desv.) reproduction and spread in a sagebrush ecosystem. Hoary cress germination, emergence, and survival were restricted to moist environments. These conditions occurred 2 out of 8 years. Hoary cress germination under field conditions was greatest on toe slope positions and areas of soil disturbance. Number of shoots varied annually for established hoary cress populations. Shoot propagation was reduced when early spring growth was followed by frost or drought. Shoot numbers were increased when spring growth was delayed and warm, moist growing conditions occurred in May. Seed reproduction did not increase plant density in monitored populations. Established populations relied upon vegetative reproduction to sequester resources and increase plant density.

Key Words: Noxious weeds, *Cardaria draba* (L.) Desv., rangeland weeds

Hoary cress (*Cardaria draba* (L.) Desv.), also known as white-top or heart-podded whitetop, was introduced to North America in the 1800's (Mulligan and Franklin 1962). The earliest collections of hoary cress in the United States were made in California in 1876 (Groh 1940). Hoary cress, a perennial weed of forage crops, has extended its range into the sagebrush ecosystem of the Northern Great Basin.

Hoary cress reproduces by seed and creeping rootstock (Whitson et al. 1992). Two seeds develop in each heart-shaped capsule. Adult plants can produce 1,200 to 4,800 seed with over 80% viability (Selleck 1965). Seed rain occurs as individual seeds are released through ruptures in the capsule sidewall, as individual capsules, and as capsule clusters which break away from the parent plant. Hoary cress seed exude mucilage when moistened (Kiemnec and Larson 1991). Mucilage produced by other species increases germination under conditions of low osmotic potential (0 to -0.2 MPa) (Harper and Benton 1966). Germination occurs in the fall or spring and non-germinated seed can remain viable in the soil seed bank for 3 to 4 years (Bellue 1946, Pryor 1959). Shoots develop on adult plants at the root crown and along creeping root stock (Mulligan and Findlay 1974). Shoot development begins in the fall or spring, as a loose rosette, and culminates with the production of a flowering stalk.

Understanding the expression of reproductive characteristics of hoary cress in a sagebrush ecosystem would aid in the evaluation

Resumen

Se condujeron estudios de campo para evaluar la reproducción y diseminación de "Hoary cress" [*Cardaria draba* (L.) Desv.] en un ecosistema de "Sagebrush". La germinación, emergencia y sobrevivencia de "Hoary cress" ocurrió solo en ambientes húmedos. Estas condiciones se presentaron en 2 de 8 años. La germinación de "Hoary cress" bajo condiciones de campo fue mayor en posiciones de la punta de la pendiente y en áreas con suelo disturbado. En las poblaciones establecidas de "Hoary cress", el número de tallos varió anualmente. La propagación de los tallos se redujo cuando el crecimiento temprano de primavera fue seguido de una sequía o helada. El número de tallos se incrementó cuando el crecimiento de primavera se retrasó y en Mayo se presentaron condiciones de calor y humedad. La reproducción por semilla no incrementó la densidad de plantas en las poblaciones establecidas. Las poblaciones establecidas dependieron mas de la reproducción vegetativa para adquirir los recursos necesarios e incrementar la densidad de plantas.

of its spreading potential. The objective of this research was to evaluate the contribution of vegetative and seed reproduction to hoary cress spread in a sagebrush ecosystem by measuring germination, emergence and shoot density.

Materials and Methods

Field studies were conducted between 1986 and 1994 in north-eastern Oregon (44° 43' N, 117° 45' W) in the foothill range of the Wallowa mountains. Study sites lie within the Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Nutt.)—bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. & Smith = *Pseudoroegneria spicata* (Pursh) Scribn. & Smith) habitat type (Daubenmire 1970). At each study site the sagebrush component was intact but the bluebunch wheatgrass had been lost and later replaced by crested wheatgrass (*A. cristatum* (L.) Gaertn.) seeded during the 1960's. The predominant soil in the study area is an Encina gravelly silt loam (fine, montmorillonitic, mesic Aridic Calcic Argixeroll).

Temperature and precipitation data obtained from the Baker City airport (10 k from study area, 1,050 m elevation) were used to calculate average precipitation (mm), maximum/minimum temperature (C) and growing degree day (Miller and Donahue 1990) estimates (threshold: 4°C). Precipitation and temperature frequency estimates were obtained from the Baker County Soil Survey (Laird et al. 1988) and represent data recorded in the period 1951 to 1981.

Seed reproduction - germination

Hoary cress seed was collected at the study area during July 1988. Seed were separated from capsules, cleaned and counted into lots of 50. Shriveled seed was discarded. Each lot (50 seed) was sealed with 5 ml of silt loam soil in a nylon mesh packet (8 cm x 8 cm; mesh opening = 0.015 cm) and placed in the field in October 1988.

Seed packets were located in 4 topographic positions (ridgetop, toe slope, mid-slope north aspect, and mid-slope south aspect). Seed packets were placed on the surface and at 1- and 3-cm depths and were retrieved at 6-week intervals beginning on 15 December 1988 and ending on 1 May 1989. Each treatment was replicated 5 times (4 topographic positions, 3 soil depths, 4 retrieval dates, 5 replicates = 240 seed packets/experiment). The experiment was conducted at 2 sites within the study area.

Seed packets were opened on the retrieval date and number of germinated seed (emerged radicle) recorded. Remaining seeds were placed on filter paper moistened with distilled water in a sealed Petri dish and placed in an environmental chamber (16-hour dark period at 15°C, 8-hour light period at 20°C). Germination was evaluated for 16 days with germination counts occurring at 4-day intervals.

Data analyses were performed on 2 categories of seed germination: (1) field germinated seed—seeds germinated in the seed packet prior to the retrieval dates of 15 December, 1 February, 15 March, and 1 May and (2) total germination—seeds germinated in the field plus seeds germinated in the environmental chamber after each retrieval date. Data from the 2 sites were combined after it was determined there were no site differences. The experimental design was a complete randomized block. Data analysis (Dowdy and Wearden 1983) included Hartley's data normality test, analysis of variance, and mean separation by least significant difference ($P = 0.05$).

Seed reproduction - emergence

Hoary cress emergence was studied at 2 sites in 1986 and 1987. Seed were collected in July 1986 and 1987 using the procedures described previously. Seed were broadcast (50 seed/plot) in November 1986 and 1987 onto 0.1-m² plots in both Wyoming sagebrush-crested wheatgrass and annual grass communities (toe slope topographic position). Tilled (churned with a shovel) and undisturbed seedbed treatments were compared in a complete

randomized block design. Treatments were replicated 3 times within each community at each site (2 years, 2 sites, 2 treatments, 3 replications). Emerged seedlings were counted at weekly intervals in May 1987 and 1988. Emergence data were analyzed using analysis of variance procedures with mean separation by least significant difference ($P = 0.05$). Data were blocked by years, and sites were combined after it was determined that there were no site differences.

Vegetative reproduction

Hoary cress shoot density was estimated by counting live shoots along 8 permanent transects (30-m length) in 2 infested Wyoming big sagebrush-crested wheat-

Results and Discussion

Germination

Germination in buried seed packets in 1989 was restricted to the time period between 1 February and 15 March. Air temperatures during the months of October through April were near normal (avg. max./min.; 16/-1, 7/-4, 2/-8, 1/-9, 4/-6, 9/-3, 14/0 °C). Precipitation was below normal in October (13 mm) (frequency < 2 yr in 10), whereas precipitation was above normal in November (44 mm), December (35 mm), January (33 mm), and March (35 mm) (frequency < 2 yr in 10). Precipitation amounts during February and April were near normal.

Germination was affected by topographic position and burial depth (Table 1).

Table 1. Field germination of hoary cress seed associated with topographic position and soil depth.

Position	Soil Depth (cm)			Mean
	0	1	3	
	----- (%) ¹ -----			
Toe slope	56 c	43 b	34 a	45 C
North Aspect	16 a	34 c	28 b	26 B
Ridgetop	19 a	27 b	26 b	24 B
South Aspect	6 a	16 b	20 c	14 A

¹Horizontal letter changes indicate significance (LSD = 4; $P = 0.05$) within a topographic position. Upper case letters indicate significance of means across topographic positions (LSD = 6; $P = 0.05$).

grass communities. Parallel transects were established at each infestation (diameter approximately 70 m); 2 transects dissected the infestation and 2 transects (non-infested) were tangent to the infestation. Shoot densities were tallied mid-May from 1987 through 1994. Density counts were taken using 0.2-m² quadrats placed at 1.5 m intervals along the transect. Data were not collected in 1991.

Twenty excavations (0.25 m² X 20 cm deep) within hoary cress infestations were made in 1988. Counts of vertical root extensions and shoots were taken.

Differences in shoot density were determined by analysis of variance with mean separation by least significant difference ($P = 0.05$). Precipitation and growing degree day estimates were determined bi-monthly for the months of March, April, and May during the period of 1987-1994. Stepwise linear regressions (Statsgraphics, Cambridge, Mass.) were performed to select the periods of precipitation and growing degree day accumulation that accounted for the variation in annual shoot density.

Germination was greatest on the toe slope with minimal soil coverage. Germination at the other topographic positions improved with some seed burial. Micro- and macro-topographic characteristics influence seed germination (Harper 1983). These influences largely reflect the degree of contact between the seed and soil surface and the matric potential of the soil water (Fenner 1985). Osmotic potential can also be a factor, especially in arid areas where salt influences are more common. Kiemnec and Larson (1991) reported hoary cress germination rates of 82, 55, 11 and 0% at osmotic potentials of 0, -0.5, -1.0, and -1.5 MPa. The process of soil freezing and thawing may have also benefited germination through vertical redistribution of soil moisture upward toward the freezing layer (Heidmann and Thorud 1976). In finer textured soils, freezing and thawing can increase moisture levels at the soil surface to near saturation (Krumbach and White 1964, Harlan 1973). We speculate that some or all of these processes were present during our study and likely contributed to the pattern of field germination.

Seed germination (field + lab) achieved rates of 71 to 94%. Compared to field germination these germination rates suggest

Table 2. Hoary cress emergence in 2 plant communities with 2 levels of seedbed preparation.

Year	Seedbed	Community	
		Sagebrush	Annual Grass
1987		--- (shoots 0.2 m ⁻²) ¹ ---	
	tilled	0.68 a	14.68 b
	undisturbed	0.0 a	0.0 a
1988			
	tilled	3.32 a	9.32 b
	undisturbed	0.0 a	0.0 a

¹Horizontal letter changes within each year indicate significance (P = 0.05)

that moisture and/or temperature rather than seed viability or dormancy were limiting germination in this study.

Emergence

Seedling emergence occurred only on plots that were tilled and was greatest in the annual grass community (Table 2). None of the seedlings that emerged during the study survived beyond May. This was likely due to a lack of available soil moisture.

Vegetative reproduction

Shoot density fluctuations occurred within monitored hoary cress populations. Shoot densities ranged from 12 shoots 0.2m⁻² (1989 and 1993) to 5 shoots 0.2m⁻² (1990 and 1994). These changes did not result in a measurable expansion or contraction of the area occupied by the hoary cress populations. Hoary cress seedlings were observed in the monitored populations in 1989 and 1993, but did not survive beyond their first growing season (data not shown).

Excavations of hoary cress showed the creeping root system averaged 19 vertical extensions arising from lateral roots and each extension averaged 2.5 shoots with numerous dormant buds. These excavations suggest that the creeping root system is the primary source of the observed density fluctuations.

Precipitation amounts and the number of accumulated growing degree days during 16–30 April and 1–15 May accounted for 76% (R²) of the observed variation in shoot density (Table 3). Precipitation (44%) and accumulated degree days (22%) for April 16–30 contributed 66% of the R² value. Precipitation (22%) and accumulated degree days (12%) for May 1–15 contributed the remaining 34% of the R² value.

Table 3. Regression model of shoot density association with precipitation amount and accumulated degree days in 16–30 April and 1–15 May during the period 1987–1994.

Variable ¹	Coefficient (b)	t-value	P
Intercept (a)	17.14	5.20	0.01
Degree Day ²			
16–30 April (X ₁)	–0.12	–4.82	0.01
1–15 May (X ₂)	0.09	3.25	0.01
Precipitation; cm			
16–30 April (X ₃)	–2.68	–5.04	0.01
1–15 May (X ₄)	1.22	4.01	0.01

¹Regression model: $Y = a + b_1X_1 + b_2X_2 + b_3X_3 + b_4X_4$

²Growing degree day = $\frac{\text{max temp} + \text{min temp}}{2} - \text{threshold}$

Precipitation and degree day accumulation for 16–30 April were negatively associated with shoot density (Table 3). Precipitation and degree day accumulated during the first half of May were positively associated with shoot density. These relationships suggest cool, dry weather in the later half of April and/or warm, moist conditions in the first half of May are associated with years of increased hoary cress density.

We speculate that rapid above ground growth in April is susceptible to frost or drought damage in May. In 1990, warm, moist conditions in April were followed by frost damage from 5 nights below freezing in May. These cold conditions were associated with a 56% reduction in shoot density compared to shoot density in 1987. Low temperatures of 2°C or lower occur later than 10 May in 5 out of 10 years and temperatures below 4°C occur later than 4 May in 2 out of 10 years. In 1994, rainfall total was 30 mm and average temperature (max/min) was 58/34°C in April. These conditions were followed by below normal (0.8 mm) early May precipitation and 6 days in which maximum temperatures ranged from 24 to 29°C. These growing conditions were associated with a 36% reduction in shoot density.

By contrast a cool, dry April in 1989 and 1993 was followed by several rains (> 6 mm) during the first 15 days of May. Mean daily maximum temperatures in May both years was near 18°C and lows were above 1°C. These conditions were associated with 31 and 41% increases in shoot density.

Implications

Hoary cress germination is limited by dry environmental conditions (Kiemnec and Larson 1991). The xeric nature of the sagebrush ecosystem restricts seed germination, emergence, and survival to

microsites where moist conditions are present. These conditions most likely occur on toe slope positions and soil disturbance areas where direct seed-to-soil contact is maximized. Reproduction by seed occurred 2 out of 8 years and was associated with warm, moist weather in May.

Shoot densities in established hoary cress populations vary annually. Densities are increased by early cool, dry periods followed by warmer, wetter conditions and decreased by frost or drought damage. Measured changes, however, did not result in a measurable expansion or contraction of hoary cress populations.

We speculate that the spread of hoary cress, controlled primarily by environmental conditions, is occurring at a relatively slow rate. Soil moisture conditions needed for seed germination occur relatively infrequently. However, established plants appear to readily sequester resources via a creeping root system thus reducing the risk of shoot mortality. Factors such as irrigation, disking established populations, foraging by pocket gophers, and other influences that increase soil moisture or fragmentation of existing root systems will tend to increase the rate of spread.

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International Center for Agricultural Research in the Dry Areas (ICARDA) RANGE/FORAGE SCIENTIST/ECOLOGIST VACANCY ANNOUNCEMENT

Arabian Peninsula The Organization

ICARDA is a non-profit international agricultural research center in a worldwide consortium of 16 centers, supported by the Consultative Group on International Agricultural Research (CGIAR). The CGIAR is co-sponsored by the World Bank, the Food and Agriculture Organization of the United Nations, the United Nations Development Programme and the United Nations Environment Programme. With a staff of over 400 scientists and support personnel, representing more than 40 nationalities, ICARDA addresses two key areas of agricultural research: germplasm improvement (cereals and legumes) and natural resource management.

The Position

ICARDA wishes to recruit a dynamic Range Ecology/Forage/Management Scientist to work as part of ICARDA's Arabian Peninsula Regional Program (APRP) whose main office is located in Dubai, UAE. The overall objective of the position is the development of integrated range/forage/livestock production systems and management practices for rangeland regeneration, through conservation and sustainable management of rangeland vegetation and the production of stress tolerant and water use efficient forage crops. In collaboration with the Range Management Scientist at ICARDA headquarters, the incumbent will be responsible for the execution of the research strategy of the rangeland program, which will focus on the following: collection and evaluation of indigenous and exotic forage and rangeland species for the purpose of rangeland regeneration (restoration and rehabilitation) and as sources for alternative forage crops; identification of the appropriate technical options for forage seed/crop production in different agroecological zones in the region; identification of the appropriate technical options for the regeneration of degraded rangelands; adoption and demonstration of rangeland management practices in target areas and pilot sites.

Required Qualifications & Experience

- PhD in Range Science/Ecology, or related discipline, with strong background and scientific experience in range plant ecology and forage production in arid and salt-affected environments. Knowledge of animal/plant interactions and ecophysiology is important.
- Minimum of five years' experience, preferably with knowledge of the region and with international research organizations, demonstrated field orientated skills, and ability to work in an inter-disciplinary team.
- Statistical skills to analyze range dynamics—including overgrazing.
- Ability to communicate in spoken and written English (knowledge of Arabic is desirable).

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Book Review

Old Fences, New Neighbors. By Peter R. Decker. 1998. The University of Arizona Press, Tucson, Arizona [www.uapress.arizona.edu]. 159 p. US\$40.00 hardbound, US\$20.00 paper. ISBN 0-8165-1771-1 hardbound, ISBN 0-8165-1905-6 paper.

On the cusp of middle age I find that change, especially change I don't like, begins to seem inevitable. Growing up in the Midwest I saw farms become shopping malls; as an adult living in the Southwest I see ranches becoming subdivisions. *Old Fences, New Neighbors* has given me hope that we can preserve our ranches as open space.

Decker's book, which he calls a partial biography of a place, is his attempt "...to bring some order and understanding to the chaotic changes..." that have occurred in Ouray County, Colorado during the past 20 years. Rapid population growth in this ranching community led to higher land prices, which drove many ranchers out of business. Decker traces this area's waves of invasions over the past 150 years, from the U.S. military driving out the Utes, through Anglo miners, farmers, and ranchers, to the latest newcomers, beginning in the 1980s. This last group was able to pay more for land than the land could produce from ranching, shifting the area from an agricultural to a largely residential one.

Old Fences, New Neighbors weaves together several themes. First is isolation, as the San Juan Mountains slowed settlement and made transportation difficult. Its corollary is the influence of outside forces, over which the residents have no control. Historian Patricia Limerick, in her 1987 book *Legacy of Conquest: The Unknown Past of the American West*, described western immigrants as denizens of an "Empire of Innocent" driven by heartfelt motives but the victims of forces beyond their control. In Ouray County these forces have included the federal government, which instituted grazing fees on public land in the 1930s, and had planned to flood the town of Ridgway behind a dam in the 1960s. National and world economies have determined the prices of minerals, farm produce, and cattle; big businesses, including mines and railroads, began and ended operations. During the past 20 years low cattle prices and high land prices, driven by changing demographics and increasing affluence, have forced many ranchers to sell out. Decker also describes the relationship that each wave of immigrants has had with the land. The Utes hunted and gathered and miners, farmers, and ranchers made their living directly from the land. Most of the current residents were drawn by the land's beauty, but make their living outside the county.

Decker argues that higher cattle prices would be the best protection for ranchers. Although it is possible to receive above-market prices with a specialty product, such as "natural beef" (Voynick, 1998, Coleman, Saguache, Colorado), the vast majority of ranchers must accept market prices for their cattle. Although land values also are beyond the control of individual ranchers, the residents of Ouray County have been able to preserve open space by regulating land values indirectly. The county had instituted unusually strict zone regulations in the 1970s, which included low housing density limits, visual impact specifications, and protection of irrigated hay meadows. In response to increased pressure for development in the 1980s, density limits were increased, but open space requirements were added. This limited the return from subdividing ranches, reducing their appeal to developers and leaving wealthy individuals from outside the county as the main ranch buyers.

Cash from outsiders, drawn by the area's outstanding scenic beauty, has protected the ranches of Ouray County, illustrating how stewardship of private lands and working landscapes can be an important part of preserving our open spaces (Knight, 1998, Wildl.

Sci. Bull. 26:725-731). Newcomers have preserved almost 80,000 acres of open land, which is almost half of the private land in the county. This has maintained the critical mass of ranches needed for their continued survival and minimized rough edge effects between ranches and developments (Huntsinger and Hopkinson 1996, J. Range Manage. 49:167-173).

Old Fences, New Neighbors contains no warning that the zoning that was instrumental in maintaining open spaces and ranches in Ouray County can be transitory, as the populace and politics change. Not all of the current landowners have made a commitment to preserve their ranches in perpetuity. Conservation easements offer permanent protection for open spaces, but require an agency with large amounts of cash, and, as Decker points out, are of limited use to small ranchers with little income to offset.

Although the physical landscape has largely been preserved, Decker now sees a different human landscape in Ouray County. The present community is less unified than before, as the residents no longer share common goals. But this area has reinvented itself many times, as Decker documents; the transition periods are painful, but the community has survived. For Decker, Ouray County is "...losing its cows, but...gaining in human strength to sustain and comfort its citizens".

Decker's love of the West is evident, as he describes being a camp Jack, the lowest form of life on a Montana sheep ranch as a teenager, rediscovering the West as a young adult, and later, ranching in Ouray County. He simply and richly describes the joy at the birth of a calf, the camaraderie of neighbors at branding time, and his battles with the Dry Creek meadow with its "...steep slope and thin soils...".

In a book with many dichotomies, Decker himself is a gray area. Neither old timer nor newcomer, he bought his ranch in 1974 but continued to hold an academic position until he began ranching full-time in 1980. He seems to have been accepted by the ranchers and to have been able to write, without rancor, from both sides. But ranching has never been his sole source of income. Few ranchers receive National Endowment for the Humanities or Rockefeller Foundation grants, and their books are rarely published. Decker also served as Chair of the County Planning Commission and State Commission of Agriculture for Colorado. But these additional sources of income could not protect him against falling cattle prices and soaring land prices; Decker sold most of his ranch and moved to Nebraska in 1993.

An egregious oversight of the book is the lack of any mention of estate planning or trusts, other than those supporting some of the county's new residents. Although Decker and the other ranchers bemoan estate taxes and recite stories of cash-poor ranches sold to pay the taxes, he never mentions the simple steps to avoid this occurrence. This is difficult to bring up with one's parents or to accuse a neighbor of having foolishly overlooked. The onus is on the cattle industry to encourage and educate ranchers in the use of estate planning, as a recent article in *Rangelands* does (McCann, 1999:21:3-4).

Although not a blueprint for preserving cattle ranches and open spaces in the New West, *Old Fences, New Neighbors* is for anyone concerned about ranching and open lands. This book is not a call to caring, but is for those who care: ranchers, environmentalists, planners, resource managers, and the citizens of Ouray County. It tells the story of a difficult place, hit hard by demographic and economic changes, and its ability to reinvent itself. The book gives us hope that open spaces can be preserved and that ranching can continue, although perhaps in a different form.—Lucinda F. Salo, School of Renewable Natural Resources, University of Arizona, Tucson, Arizona.

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