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TABLE OF CONTENTS: Vol. 40, No. 1, January 1987

ARTICLES

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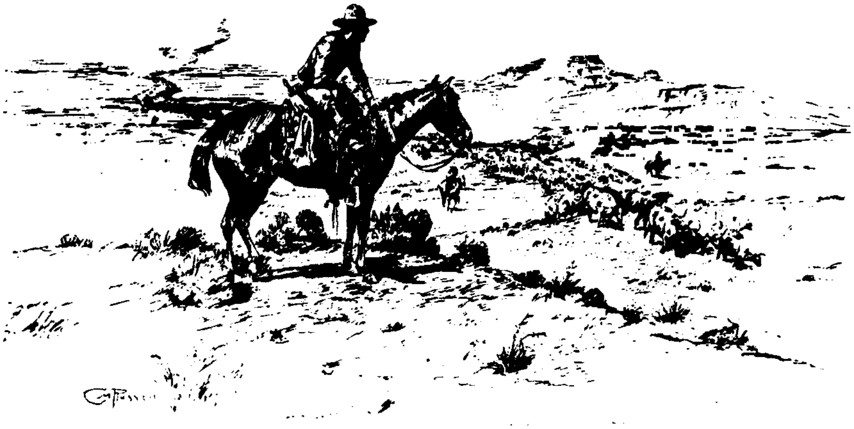

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Wet-dry Cycle Effects on Warm-season Grass Seedling Establishment

G.W. FRASIER, J.R. COX, AND D.A. WOOLHISER

Abstract

A series of 14-day field experiments were conducted to evaluate seedling establishment characteristics of *Bouteloua, Erogrostis,* and *Panicum* grass species with controlled wet-dry watering combinations. The objective of the study was to validate previously published greenhouse data of Frasier et al. (1985) on the effects of the first wet-dry watering sequence following planting on seedling emergence and survival. Seedling survival numbers were different between the field and greenhouse experiments but the same general responses to watering sequences were measured. With short wet periods (2 days), seeds generally did not germinate but survived the subsequent dry period as viable seeds. Most seeds germinated with 5 wet days and produced seedlings that were able to survive drought periods of 5 to 7 days. Fewer seedlings survived with 3 days wet than with either 2 or 5 days wet. High rates of soil moisture evaporation in a spring field experiment made it difficult to maintain adequate soil moisture for seed germination, and seeds which germinated failed to produce seedlings. Seedlings were successfully established in 2 experiments conducted later in the summer following the onset of summer rains, which increased the relative humidity and reduced the rate of soil moisture evaporation. This effect was verified in a greenhouse study. In both the greenhouse and field experiments, seedlings were established when the relative humidity exceeded 50% for over one-half of the time during the initial wet-dry period.

Key Words: *Eragrostis* sp., *Panicum antidotale, Bouteloua curtipendula,* drought tolerance, plant survival, seeding

The development of improved techniques for plant establishment under rainfed conditions in semiarid regions requires an understanding of seed germination and seedling responses to water quantity and frequency following planting. Cox and Jordan (1983) found that the amount and distribution of precipitation during the first growing season affected plant densities and forage production 10 years later.

There are several intervals during plant establishment when water availability is critical to seedling establishment. Wilson and Briske (1979) found that blue grama (*Bouteloua gracilis* (Willd. ex. H.B.K.) Lag. ex. Griffiths) requires 2 to 4 days of moist soil conditions for seed germination and initial root growth. A similar wet period, 2 to 8 weeks later, was necessary to ensure plant establishment. In a greenhouse study, Frasier et al. (1985) identified 2 factors that affected the survival of warm-season grass seedlings during the first wet-dry watering sequence following planting. They are: (1) the number of seedlings which developed sufficient vigor in the wet period to survive the subsequent dry period: and (2) the number of ungerminated but viable seeds which remain after the initial wet and dry periods following planting. Frasier et al. (1984) showed how seedling emergence and seedling survival probabilities, evaluated under various wet-dry watering sequences, could be combined with estimates of the joint probabilities of the lengths of the first wet and dry periods after planting to select the optimum time for seeding in a specific area, or identifying plant species which are best suited for a given climatic regime.

The objectives of the study were: (1) determine the effects of selected combinations and lengths of initial wet-dry watering sequences on the germination, emergence, and survival of 5 grasses in the field; and (2) determine if seedling establishment and survival responses to the initial watering sequences were qualitatively the same in the field as those observed in previously reported greenhouse studies (Frasier et al. 1984, Frasier et al. 1985). Following completion of the field study, a greenhouse study was conducted to evaluate the effect of air humidity on initial seedling establishment.

Materials and Methods

Field Study

Site Preparation

The field experiments were conducted on a Sonoita fine-loamy mixed thermic, Typic Haplargid soil (Gelderman 1970) at an elevation of 1,330 m (MSL) on the Walnut Gulch Experiment Watershed near Tombstone, Ariz. A 10 × 50-m area was cleared of all vegetation, smoothed with a road grader, and the top 12 cm of soil loosed with a rototiller. The entire area was covered with black polyethylene sheeting and methyl bromide injected under the sheeting for 48 hr to kill any plant propagules remaining in the soil surface.

Plot Installation and Seeding

The study consisted of three, 14–16-day experiments conducted at different times during the summer of 1983. Experiment 1 was initiated on 25 May 1983, experiment 2 on 22 July 1983 and experiment 3 on 15 August 1983. There were 120 plots, 30.5 × 30.5 cm square with a 5-cm high wooden border in each experiment. Plots were grouped 10 cm apart in rows of 5. Rows were spaced 1 m apart. The grasses used in the study were 'Premier' sideoats grama [*Bouteloua curtipendula* (Michx.) Torr.], 'A-68' Lehmann lovegrass (*Eragrostis lehmanniana* Nees), 'Catalina' boer lovegrass (*E. curvula* var. *conferta* (Schrad.) Nees), 'Cochise' lovegrass (*E. lehmanniana* Nees × *E. trichophora* Coss & Dur.), and 'SDT' blue panicgrass (*Panicum antidotale* Retz). Each grass species was randomly located in each row.

All plots were wetted with 3 mm of water and the surface smoothed. One hundred small depressions, 0.6 cm deep and 2.5 cm apart on a 10 × 10 grid, were made on each plot surface with an impression plate. Each plot was seeded with 100 seeds, one seed in each depression, with a vacuum chamber seed planter (Frasier 1985) and covered with a 2- to 3-mm layer of soil.

Water Sequences and Application

The watering sequences consisted of: (1) an initial wet period, (2) a dry period, and (3) a final wet period. Three separate wet-dry-wet watering sequences and an everyday wet sequence were used simultaneously in each experiment (Table 1). Ten to 12 mm of water were applied immediately following seeding which wetted the soil to a depth of approximately 10 cm. A single fan-shaped deflector nozzle on a reciprocating spray bar sprayed water downward onto a single row from a height of 25 cm. The nozzle applied 0.8 mm of water per pass. All plots in a row received the same water quantity and distribution. In Experiment 1, the quantity of water applied on each subsequent day was determined by gravimetric measurement of the water lost from 4 small plastic cones (3.8-cm D. by 20-cm

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Table 1. Wet-dry-wet watering sequences used in the three field experiments.

Experiment No.	Water sequence identification	Period Wet	Period Dry	Period Wet
		(days)	(days)	(days)
1 and 2	2–5	2	5	7
	3–5	3	5	6
	5–5	5	5	4
	14–0	14	0	–
3	2–7	2	7	7
	3–7	3	7	6
	5–7	5	7	4
	16–0	16	0	–

long) filled with soil and buried level with the soil surface between the plots. In Experiments 2 and 3 the daily water application quantity was equal to a Standard Class A evaporation pan, next to the plots, loss that had occurred during the previous 24 hours. On the first day following the dry period the plots received 12–14 mm of water to insure adequate soil moisture below the depth of the rooting zone.

Soil water contents were measured in depth increments of 0–5 mm, 5–10 mm, 10–30 mm, and 30–60 mm by gravimetric sampling on separate unplanted plots, 1 plot for each watering sequence. Prior to water application, soil samples from 3 random locations within each plot were collected and combined into a single composite sample for each depth increment for each watering sequence.

A moveable translucent corrugated fiberglass roof was used to prevent wetting of the plots by rainfall. The roof was pulled over the plots at sunset or when a rainfall event was imminent and removed at sunrise the next morning or after the rainfall stopped. Air temperature and humidity were recorded at ground level with a hygrothermograph.

Data Collection and Analysis

Seedlings were counted daily at 0600 hours. A grid template was used to pinpoint the location of the planted seeds (Frasier 1985). Any visible sign of a plant was recorded as a seedling. Seedling counts were normalized relative to pure live seed (PLS) using 10-day filter paper and germination percentages determined in a constant temperature incubator at 29.5° C and 100% relative humidity.

The experimental design was a randomized block with 6 replications, 4 watering sequences, and 5 species. Five plots were aligned into a single row. Four rows were grouped into a block. Results of separate experiments were not directly compared because of different climatic conditions. Seedling count means for each experiment and each data set period were subjected to analyses of variance. When "F" values were significant, ($P<0.05$), Duncan's new multiple range test was used to determine differences among species and water sequences.

Greenhouse Study

The study was conducted in 2 separate greenhouses using the procedure reported by Frasier et al. (1984). The grass species were the same as used in the field study. Tapered plastic cones, 3.8 cm in diameter by 20 cm long, were filled with 210 g of dry 60-mesh silica sand. Ten seeds were placed on the dry surface of each cone and covered with a 2- to 3-mm layer of dry sand. Ten cones were prepared for each grass species per watering treatment for each greenhouse.

Watering sequences used in the study were the same as in field Experiments 1 and 2 (Table 1). Water was applied to the cones with an overhead reciprocating spray system. Ten percent of the total number of cones in an experiment were randomly selected and marked for daily weighing to determine evapotranspiration losses and verify the quantity of applied water. All cones were initially wetted to field capacity with 20 g of water (10% moisture by weight). In wet periods, the cones were sprinkled daily with sufficient water to bring the average moisture content to the original weight.

One greenhouse (high humidity) was cooled by a standard evaporative cooler. The other greenhouse (low humidity) had the same ventilation system but without water applied to the evaporative pads. Air movement was provided by an oscillating fan. The cones in the low humidity greenhouse were moved to the high humidity greenhouse for watering. Following the end of the dry period of each watering sequence, the cones were permanently moved to the high humidity greenhouse. Cones in the 14–0 watering sequence were moved into the high humidity greenhouse on Day 8.

Live plants in each cone were recorded daily. The plant count of 10 cones for each species was averaged for the replication mean. The study consisted of 3 identical experiments conducted during the summer of 1985. No attempt was made to make direct comparisons of plant counts in the field study to the greenhouse study. Analysis of variance was used to determine differences among species and watering sequences. When "F" values were significant ($P<0.05$), Duncan's new multiple range test was used to separate means.

Results and Discussion

Field Study

Experiment No. 1

No seedlings emerged in this experiment on any watering sequence. This period of the year was characterized by high air temperatures and low relative humidities which rapidly dried the soil. One hour after sprinkling, the measured soil moisture contents in the top 60 mm were 11 to 12% by weight (field capacity). Twenty-three hours later, the soil moisture in the seed zone (0–5mm) was less than 1.5% (approximately -1.5 MPa), (Table 2).

Table 2. Climatic and soil moisture parameters for the three field experiments.

Item	Units	Experiment No. 1		Experiment No. 2		Experiment No. 3	
Length of experiment	(days)	14		14		16	
Starting date		25 May		22 Jul		15 Aug	
Pan Evaporation							
Daily (24 Hour)	(mm)	13	2.1	9	2.9	9	2.2
Nighttime (1800–0600)	(mm)	——[1]		3	1.3	3	0.8
Air temperature							
Maximum	(C)	35	2.2	35	1.3	35	2.6
Minimum	(C)	14	4.4	20	0.9	17	3.0
Humidity							
Maximum	(%)	73	14	100	1	95	5
Minimum	(%)	30	4	33	10	33	6
Soil Moisture[2]							
0–5 mm	(% by weight)	1.2	0.4	7.4	3.9	4.4	1.4
5–10 mm	(% by weight)	1.2	0.4	9.1	2.8	6.1	1.4
10–30 mm	(% by weight)	4.8	0.9	10.4	1.6	7.8	1.9
30–60 mm	(% by weight)	5.7	1.9	10.5	1.4	8.1	1.9

[1] Value not determined.

[2] Mean values for the experiment duration from the 14–0 watering sequence plot at 0600 each day prior to water application starting with Day 2.

Following the 14-day experiment, water was sprayed on the plots with a set of low-pressure lawn-soaker hoses for 4 hours daily for 6 days. A seedling count on Day 6 of this post-experiment watering period showed that less than 50% (PLS) of the seeds had survived the initial wet-dry watering sequences.

Experiment No. 2

Seedlings of all species were established with all watering sequences during this mid-summer experiment. This experiment was conducted after the onset of the summer "rainy" season and late afternoon or evening thunderstorms were common. The relative humidity increased and the evaporative demand on soil moisture decreased. These conditions are conducive to seedling establishment, but there were fewer seedlings with the 3 wet-dry watering sequences than with the 14–0 water sequence (Table 3).

Table 3. Mean seedling counts (PLS), for the initial wet period and Day 14 for field experiment No. 2 with 4 watering sequences (5-day dry).

Water sequence	Cochise lovegrass	Catalina Boer lovegrass	A-68 Lehmann lovegrass	SDT blue panicgrass	Premier sideoats grama	Water Sequence Means
	Maximum Initial Plant Count					
2–5	5.4[1]	12.7	6.2	5.3	51.9	16.3 c[2]
3–5	19.2	19.2	32.6	30.8	75.7	35.5 b
5–5	35.0	21.3	29.2	50.2	73.2	41.8 b
14–0	100.4	30.9	43.3	54.3	87.0	63.2 a
Species Means	40.3 b[3]	21.0 c	27.8 c	35.2 bc	72.0 a	
	Day 14 Plant Count					
2–5	71.7	35.9	34.2	33.8	60.8	47.3 ns
3–5	62.9	33.4	51.8	43.9	75.3	53.5 ns
5–5	85.5	32.4	36.6	54.3	71.0	56.0 ns
14–0	115.0	37.6	49.9	63.2	84.1	69.8 ns
Species mean	83.8 a	34.8 b	43.1 b	48.6 b	72.8 a	

[1] Mean seedling count of 6 blocks normalized for germination percentage (PLS).
[2] Water sequence means with the same letter are not significantly different ($P<0.05$).
[3] Species means with the same letter are not significantly different ($P<0.05$).

Two seedlings count data sets are of major interest for evaluating seedling survival characteristics (Frasier et al. 1985). These are: (1) the maximum number of seedlings from the initial wet period; and (2) the final seedling count at the end of the experiment. The 14-day wet treatment does not include a dry period; therefore the maximum seedling count on Day(s) 6–8 were used for the initial period data set (Table 3).

Water treatment and species interactions were not significant for either the initial or Day 14 counting periods ($P<0.05$). Species means in both the initial maximum and the Day 14 counting periods were different (Table 3). In the initial count there were 10 times more sideoats grama seedlings with the 2-day wet watering sequence than with the other 4 species. With 5 days wet, there were twice as many sideoats grama seedlings compared to the other species. These differences were not present in the Day 14 count period. There were no changes in the number of sideoats grama seedlings between the 2 counting periods, indicating that the final sideoats grama seedlings were plants that had been established during the first wet period. Conversely, with the SDT blue panicgrass, Catalina lovegrass, and A-68 Lehmann lovegrass, seedling numbers increased approximately 1.5 times and the Cochise lovegrass doubled between the initial and Day 14 counting periods. This indicates that the seeds of these 4 species did not germinate in the first wet period but remained viable through the 5-day dry period.

Seedling counts on several Cochise lovegrass plots on Day 14 were greater than 100% PLS. Germination percentages at 10 days on filter paper in the constant temperature incubator were: Premier sideoats grama–73%, A-68 Lehmann lovegrass–87%, Catalina lovegrass–87%, Cochise lovegrass–40%, and SDT blue panicgrass–81%. The germination percentage and/or germination rate of some of the species were evidently higher in soil than on filter paper.

Mean seedling counts differed among water sequences in the initial count period but not on day 14 ($P<0.05$) (Table 3). The 2 days wet watering treatment initially produced less than 50% as many seedlings as the other water treatments. The exception was sideoats grama, which had a threefold increase in seedling numbers with the 2 days wet treatment between the 2 counting periods. This indicates that many of the final seedlings of the other 4 species were from seeds that survived the dry period. There were smaller increases in seedling counts between the 2 counting periods with the 3 and 5-day wet treatments. The final seedlings with these watering sequences were from plants established in the initial wet period which survived the dry period.

Experiment No. 3

There were no significant interactions of water sequence and species for either the initial maximum period or on Day 14 ($P<0.05$). There were no significant differences in mean seedling counts among species and among watering sequences in both the initial wet and Day 14 periods (Table 4).

Table 4. Mean seedling counts (PLS), for the initial wet period and Day 14 for field experiment No. 3 with 4 watering sequences (7-days dry).

Water sequence	Cochise lovegrass	Catalina Boer lovegrass	A-68 Lehmann lovegrass	SDT blue panicgrass	Premier sideoats grama	Water Sequence Means
	Maximum Initial Plant Count					
2–7	0.0[1]	0.0	0.2	0.2	36.3	7.3 b[2]
3–7	1.3	0.4	4.0	1.0	56.2	12.6 b
5–7	66.3	25.0	59.3	40.6	78.7	54.0 a
14–0	96.7	39.7	52.0	41.6	81.6	62.3 a
Species Means	41.0 b[3]	16.3 d	28.9 c	20.9 c	63.2 a	
	Day 14 Plant Count					
2–7	97.1	23.0	25.0	12.5	49.4	41.4 b
3–7	39.2	13.1	13.1	6.4	57.6	25.9 c
5–7	67.5	23.6	57.5	38.3	80.3	53.4 b
14–0	118.7	43.5	62.3	48.4	87.5	72.0 a
Species Mean	80.5 a	25.8 b	39.5 b	26.4 b	68.7 a	

[1] Mean seedling count of 6 blocks normalized for germination precentage (PLS).
[2] Water sequence means with the same letter are not significantly different ($P<0.05$).
[3] Species means with the same letter are not significantly different ($P<0.05$).

Final seedling counts were lower in the wet-dry water sequences compared to the 14-day wet treatment, indicating a seed/seedling mortality during the 7-day dry period. Some specific similarities in the results to Experiment 2 were: (1) high initial counts of sideoats grama seedlings which survived the dry period as seedlings; and (2) low initial seedling counts of the other 4 species with 2 and 3-day wet watering sequences, and a subsequent increase in seedling count at Day 14 from seeds surviving the dry period. With the exception of sideoats grama, there were fewer surviving seedlings in the Day 14 plant count period with the 3-day wet sequence than with the other watering sequences. One possible interpretation, is that the species were vulnerable to an extended dry period if the first wet period initiated germination but there is insufficient moisture for subsequent seedling development (Frasier et al. 1984).

Effect of Time of Year on Seedling Establishment

Cox et al. (1982) reported that a common recommendation in the southwestern United States is to seed prior to the summer rains. In the same report it was also stated that the success rate of seeding trials in many areas was only 1 in 4. Schreiber and Sutter (1972) showed that the probability of water availability for plant growth in southeastern Arizona, defined as 'four consecutive days of wet soil,' was best from 5 July to 10 Aug. Smith and Schreiber (1973) showed that the peak summer rainfall frequency occurs in the period 15 Jul–15 Aug. This would indicate that soil moisture conditions may be more favorable for plant establishment with later planting dates.

In our later summer studies (Experiments 2 and 3), successful seedling establishment was achieved with the same length of wet periods as used in Experiment 1. While these experiments were not dependent upon natural rainfall, a micro-climate favorable for seedling establishment was created during the "rainy period." This is evidenced in the climatic data collected at the site (Table 2). The maximum air temperatures and minimum relative humidities were similar in all 3 experiments. There were differences in the maximum relative humidity and the length of time during the day that the high relative humidity persisted. In Experiments 2 and 3, the relative humidity exceeded 50% for more than half the time, compared to 20% of the time during Experiment 1 (Table 5). The high relative humidities with the onset of the summer storms from increased cloud cover during Experiments 2 and 3 contributed to a lower evaporative demand as reflected in the soil moisture measurements. The higher soil moisture in the upper soil profile for a longer time was sufficient to stimulate seed germination and aid in seedling establishment.

Table 5. Percentage of time the relative humidity was greater than 30%, 50% and 70%, and air temperatures greater than 21° C, 27° C, and 32° C for the three field experiments.

Experiment Number	Percent of Time					
	Relative Humidity			Air Temperature		
	>30%	>50%	>70%	>21° C	>26° C	>32° C
	(%)	(%)	(%)	(%)	(%)	(%)
1	60	19	4	64	39	8
2	93	64	39	79	32	11
3	93	58	36	62	31	8

Greenhouse Study

The everyday wet (14–0) watering sequence was the only sequence which produced any plants in the initial wet period in the low humidity greenhouse (Table 6). Water treatment and species interactions were not significant in the initial plant count for either greenhouse condition ($P<0.05$). In the high humidity greenhouse there were significantly fewer seedlings in the initial wet period with the 2 day wet water sequence. There were differences among species with the A-68 Lehmann lovegrass having approximately twice as many initial seedlings as the other 4 species. There were no differences among species in the low humidity greenhouse.

Table 6. Mean seedling counts (PLS), for the initial wet period for the greenhouse experiment with 4 watering sequences (5-day dry).

Water sequence	Cochise lovegrass	Catalina Boer lovegrass	A-68 Lehmann lovegrass	SDT blue panicgrass	Premier sideoats grama	
	Wet Greenhouse					Water Sequence Means
2–5	7.7[1]	16.3	58.3	28.7	29.7	28.1 b[2]
3–5	40.3	49.0	97.0	48.0	47.7	56.4 a
5–5	82.7	79.0	105.7	68.0	55.0	78.1 a
14–0[3]	62.3	66.7	111.0	61.3	47.3	69.7 a
Species Means	48.3 b[4]	52.8 b	93.0 a	51.5 b	44.9 b	
	Dry Greenhouse					
2–5	0.0	0.0	0.0	0.0	0.0	0.0 b
3–5	0.0	0.0	0.0	0.0	0.0	0.0 b
5–5	0.0	0.0	0.0	0.0	0.0	0.0 b
14–0[3]	5.7	11.0	8.7	9.0	10.7	9.0 a
Species mean	1.4 ns	2.8 ns	2.2 ns	2.3 ns	2.7 ns	

[1] Mean seedling count (PLS) of 3 replications.
[2] Water sequence means with the same letter are not significantly different ($P<0.05$).
[3] Day 7 was used for the initial plant count of the 14–0 sequence.
[4] Species means with the same letter are not significantly different ($P<0.05$).

There were no significant differences in the Day 14 count among species, water sequences or greenhouse condition ($P<0.05$). In the low humidity greenhouse, soil moisture contents of the seeded zone could not be maintained at adequate levels for sufficient time to induce seed germination and seedling emergence, even with 5 consecutive days of morning water application. The data from the hygrothermograph in the low humidity greenhouse shows that the relative humidity was less than 50% for over one-half of the time (Table 7), similar to field Experiment No. 1.

Table 7. Percentage of time the relative humidity was greater than 30%, 50% and 70%, and air temperature greater than 21° C, 27° C, and 32° C for the greenhouse experiments.

Greenhouse Condition	Experiment Number	Percent of Time					
		Relative Humidity			Air Temperature		
		>30%	>50%	>70%	>21° C	>26° C	>32° C
		(%)	(%)	(%)	(%)	(%)	(%)
Wet	1	100	95	0	100	95	2
	2	—[1]	—	—	—	—	—
	3	100	100	93	100	96	25
Dry	1	48	6	0	100	85	39
	2	91	46	17	100	95	58
	3	79	36	17	98	66	30

[1] Malfunction of hygrothermograph

Conclusions

This study reinforces the conclusions of Frasier et al. (1984). If the wet period is very short, most of the seeds will not have time to germinate and will survive the following dry period as viable seeds. In longer wet periods, many seeds will germinate. There may be a critical length of wet period during which a high percentage of seeds will germinate but the seedlings may not be sufficiently developed to withstand a short drought period. In our studies a 3-day wet period followed by 7 dry days produced fewer seedlings than either 2 or 5 wet days followed by 7 dry days.

The field and previously reported greenhouse studies (Frasier et al. 1985) did show similar seedling establishment characteristics. Most of the final seedlings of the sideoats grama were from plants which emerged from the first wet period and survived the dry period. Final seedlings of the other 4 species were from ungerminated seeds which survived the initial wet-dry period. The number of seedlings which died in the field studies was less than reported for the greenhouse studies. The soil at the field site has a finer texture and a higher water holding capacity than the silica sand used in the greenhouse study. The soil at the field site did not dry out as fast as the silica sand in the greenhouse study.

The study indicates that slight changes in climatic conditions at the time of seeding can be a major factor in achieving successful seedling establishment. High air temperatures and low relative humidities in an early summer experiment resulted in a high potential evaporative demand of soil moisture. With short interval watering periods, it was not possible to maintain soil moisture at levels adequate for seedling establishment. Later in the summer, with the onset of the rainy season, the increased relative humidity reduced the evaporative demand, allowing successful seedling establishment.

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Plant Water Potential for Shrubs in Argentina

DANIEL V. PELÁEZ AND ROBERTO M. BÓO

Abstract

Water relations of *Prosopis flexuosa, P. caldenia, Condalia microphylla, Larrea divaricata,* and *Chuquiraga erinacea,* 5 shrub species of a temperate semiarid region of Argentina were analyzed by periodic measurement of soil water potential, plant water potential, and air humidity. Water potential in all species showed recovery during the night, the values obtained early in the morning being higher (less negative) than those recorded in the afternoon. Plant water potential showed higher correlation with soil water potential than with the other environmental variables considered. Results indicate that these species have the capacity to adjust to summer drought conditions.

Key Words: ***Condalia microphylla, Larrea divaricata, Chuquiraga erinacea, Prosopis* sp., drought tolerance, soil water, plant survival**

Undesirable shrub invasion is one of the main problems of the semiarid phytogeographic region of Argentina known as the Caldén District (Cabrera 1976). This territory extends from southern San Luis through the center of La Pampa to southwest Buenos Aires province. Cow-calf operations are the primary economic activity in this area. Native pastures are the only source of grazing. The high stocking rates practised by traditional management usually tend to deteriorate soil and vegetation (Bóo and Peláez unpublished). One thus finds poorly managed pastures where the proportion of low value grasses and undesirable shrubs is very high (Cano 1975).

The climate diagram of Río Colorado (Río Negro province) 40 km southwest of the study area shows a relative drought period during summer (Fig. 1). Drought may also occur in winter, but with less intensity. These characteristics show that the regional range communities are closely linked to water availability.

Limited water results in stress, thus reducing plant growth either directly or indirectly.

The ecology and physiology of shrubs growing on rangelands are probably influenced more by water relations than by any other group of factors. Periodic water deficits are critical to growth in seasons when other factors such as light and temperature are favorable (Hass and Dodd 1970).

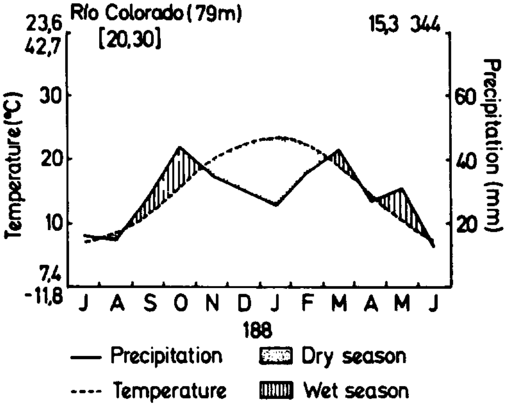

Fig. 1. *Climate diagram of Río Colorado (39° 01'S lat. and 64° 05'W long.), Río Negro province.*

This study was undertaken in order to assess the seasonal plant water potential relationships of 5 of the most conspicuous shrubs of the Caldén District and to relate these measurements to several environmental factors. Water relation values can give some indication of how adaptable these shrubs are to a semiarid environment.

Description of the Study Area

The site where the study was carried out is located in southeast La Pampa province (38° 45'S lat. and 6° 45'W long.). The sampling site is a 20-ha area closed to grazing 12 years ago. The characteristic vegetation of this site is an open shrub stand including jarilla *(Larrea divaricata),* caldén *(Prosopis caldenia),* algarrobo *(P. flexuosa),* and piquillín *(Condalia microphylla).* The most prominent grasses are flechilla negra *(Piptochaetium napostaense)* and flechilla fina *(Stipa tenuis),* both high forage value cool-season grasses. The climax community has totally disappeared and thus valuable species such as pasto de vaca *(Sorghastrum pellitum),* poa *(Poa ligularis),* and flechilla grande *(Stipa clarazii)* are very scarce or nonexistent (INTA et al. 1980).

Yearly average temperature is 15.3° C. The mean temperature of the coldest month (June) is 7° C, with a maximum mean of 13.8° C and a minimum mean of 2° C. The warmest month is January with a mean of 23.6° C, a maximum mean of 32.2° C, and a minimum

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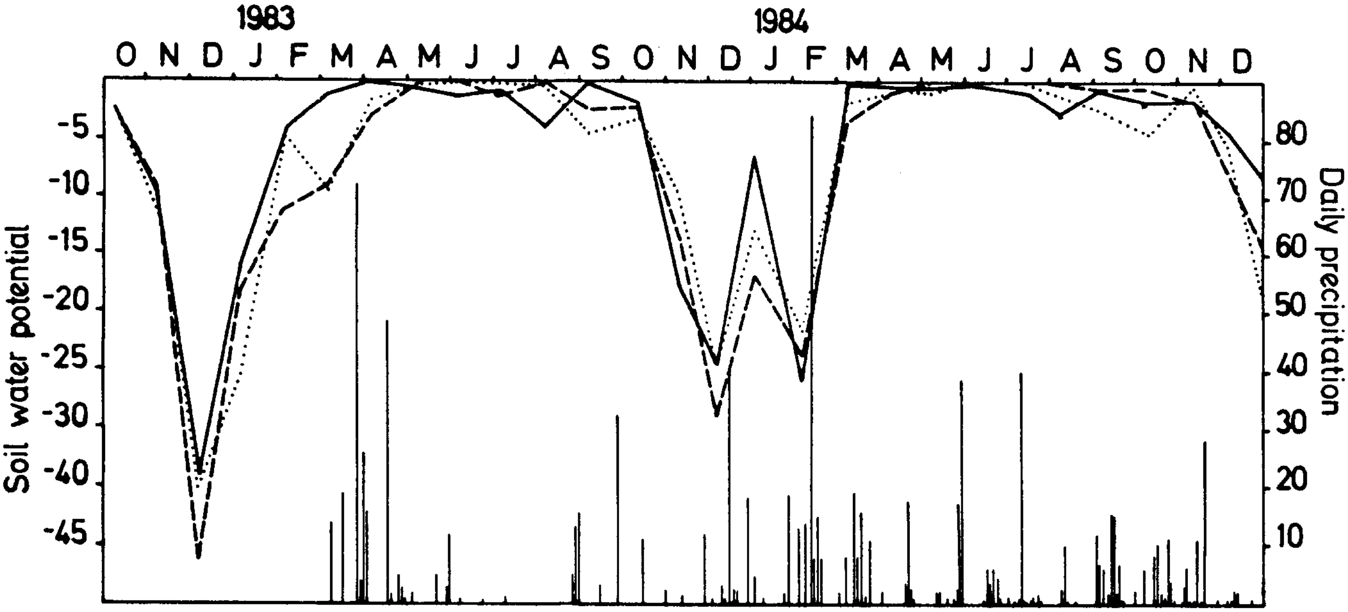

Fig. 2. *Evolution of soil water potential (bars) at 30 (———), 50 (– – –), and 70 cm (·····) depth, and daily distribution of rainfall (mm) during the measurement cycle.*

mean of 14.8° C. For a period between the years 1941 and 1960 the absolute maximum temperature recorded was 42.7° C and the absolute minimum -11.8° C.

The relative mean humidity varied from maximum mean values in winter (June 76%) to minimum mean values in summer (January 47%).

Between the years 1971 and 1982 the average rainfall was 448 mm, concentrated mostly in fall and spring. Average potential evapotranspiration was over 800 mm/year, with a negative water balance all year round.

Soil is a typical Paleorthid, well drained, with a medium to heavy texture and a local slope of 0.5 to 1%. A petrocalcic horizon ("tosca") is found at an average depth of 40-60 cm (Sánchez, personal communication).

Materials and Methods

The hydric state of the soil was characterized by the measurement of water potential at 30, 50, and 70 cm depth. To determine soil water potential, 5 spanner thermocouple psychrometers with ceramic chambers (Dalton and Rawlins 1968, Easter and Sosebee 1974) were located at each depth. Individual calibration of each unit was achieved with sodium chloride (Na Cl) solutions of 0.1, 0.3, 0.5, and 0.8 and 1.0 Molal with known water potential (Wiebe et al. 1971). The microvolt output for each was measured with a microvoltimeter. A regression equation was calculated for each thermocouple psychrometer, allowing conversion of the field recorded microvolt readings into water potential values expressed in bars. Soil temperature was also measured.

The dynamics of plant water potential for jarilla, caldén, algarrobo, piquillín, and chilladora *(Chuquiraga erinacea)* was measured by inserting a young branch of each species into a pressure bomb (Scholander et al. 1965). Measurements were made on 3 plants of each species from 9–10 a.m. and from 3–4 p.m. every 30 days during the growing season (from October until May).

Air temperature and relative humidity were recorded with a hygrometer, and the values were used to calculate vapor pressure deficit.

Precipitation was measured in the same working area with an automatic registering rain gauge.

The minimum water potential of each species, determined on each sampling date, was correlated (Snedecor and Cochran 1971) with the following environmental variables: minimum soil-moisture stress (maximum soil water potential), soil water potential at 30, 50, and 70 cm depth, vapor pressure deficit, and maximum soil and air temperatures.

Results

Precipitation during the study period exceeded the yearly average rainfall of 448 mm (521 mm in 1982, 532 mm in 1983, and 632 mm in 1984).

The evolution of soil water potential (SWP) and daily distribution of rainfall during the measurement cycle are given in Figure 2.

Water availability decreased with increasing depth. This tendency was constant between 30 and 50 cm and between 30 and 70 cm, from October 1982 to April 1983, but became more erratic as of May 1983. Measurements for September and October 1983 and for January and May 1984 then reverted to the former constant trend. The SWP for the 3 levels decreased during spring, reaching its critical value at the end of this season or in the summer. The values of SWP throughout the period oscillated from saturation (0 bar) to a minimum of -41.4 bars recorded at a depth of 50 cm in December 1982.

An important amount of water was stored in the soil due to the high precipitation that occurred January (135 mm), March (130 mm), and April (62 mm) of 1983. As a consequence, high SWP values (greater than -5 bars) were recorded from April to October inclusive. A similar occurrence was observed from April through May 1984.

Plant water potential (plant WP) showed a similar pattern in all species. The afternoon values were lower than those obtained in the morning (Fig. 3 and 4). This was coincident with greater values of temperature and vapor pressure deficit (Fig. 5).

In the first growth cycle studied jarilla exhibited the greatest seasonal fluctuation of morning plant WP, which decreased from -11.2 bars in October to a minimum of -40 bars in December. For the period between 3 p.m. to 4 p.m. the greatest variation was found in algarrobo, whose plant WP oscillated between -35 bars in January and a maximum of -7.3 bars in March. In the 1983-1984 growth cycle, the highest fluctuation was observed in piquillín for the morning determination. Thus, values varied from a minimum of -40 bars in February to a maximum of -8.7 bars in March. With

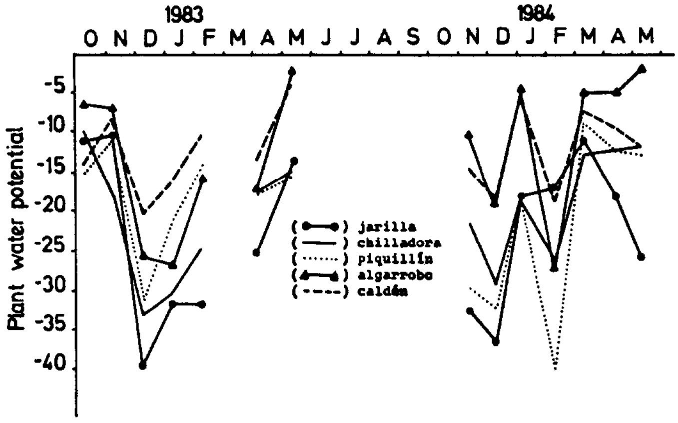

Fig. 3. *Plant water potential (bars) for the period between 9 a.m. to 10 a.m.*

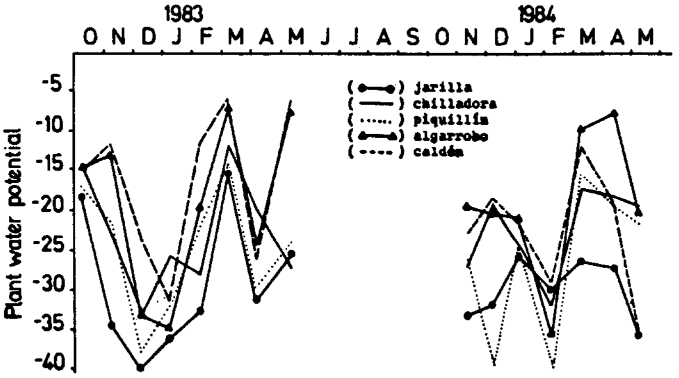

Fig. 4. *Plant water potential (bars) for the period between 3 p.m. to 4 p.m.*

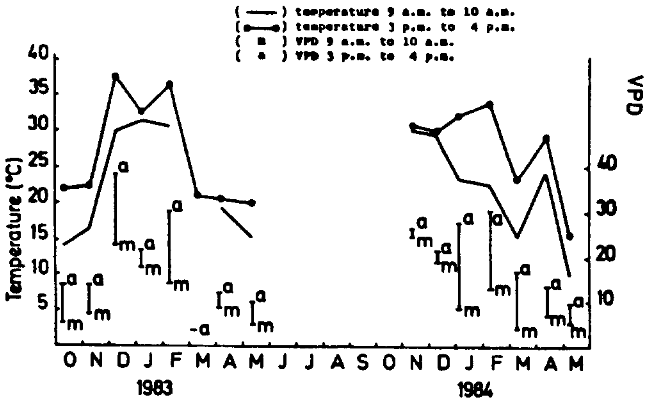

Fig. 5. *Air temperature (° C) and vapor pressure deficit (mm).*

Table 1. Correlation coefficient of plant water potential with 7 measured variables.

Species	Environmental Variables	*r*
Jarilla	minimum soil-moisture stress	.600 *
	vapor pressure deficit	.560 *
	soil water potential at 30 cm	.534*
	soil water potential at 70 cm	.479
	soil water potential at 50 cm	.476
	maximum air temperature	.389
	maximum soil temperature	.212
Chilladora	soil water potential at 70 cm	.806 *
	vapor pressure deficit	.800 *
	minimum soil-moisture stress	.767 *
	maximum air temperature	.673 *
	soil water potential at 30 cm	.665 *
	soil water potential at 50 cm	.584 *
	maximum soil temperature	.344
Piquillín	soil water potential at 30 cm	.870 *
	minimum soil-moisture stress	.847 *
	soil water potential at 50 cm	.792 *
	soil water potential at 70 cm	.771 *
	vapor pressure deficit	.685 *
	maximum air temperature	.575 *
	maximum soil temperature	.423
Algarrobo	soil water potential at 30 cm	.753 *
	soil water potential at 70 cm	.738 *
	minimum soil-moisture stress	.724 *
	vapor pressure deficit	.713 *
	soil water potential at 50 cm	.698 *
	maximum air temperature	.581 *
	maximum soil temperature	.490 *
Caldén	soil water potential at 30 cm	.384
	vapor pressure deficit	.343
	minimum soil-moisture stress	.337
	soil water potential at 70 cm	.330
	soil water potential at 50 cm	.282
	maximum air temperature	.192
	maximum soil temperature	.185

*Significant at 5% level.

recorded values varying from -35.6 bars in February to -7.7 bars in April, algarrobo exhibited the greatest fluctuation for the afternoon determinations.

The highest plant WP morning values were generally found in caldén and algarrobo, and the lowest afternoon values in jarilla. This trend remained constant during the first observation cycle and throughout most of second cycle (Fig. 3 and 4).

Afternoon precipitations occurred during January and December 1983, which affected the 3-4 p.m. determinations, causing increased plant WP values in chilladora and jarilla.

The lowest water potential of each species for each sampling date was correlated with different environmental variables. The simple linear correlation coefficient (*r*) of plant WP with 7 measured variables is shown in Table 1. The plant water potential showed a significant correlation with the analysed soil water potential variations. Even though there was a similar trend for caldén, correlation coefficients were non-significant at $P = 0.05$. For chilladora 2 parameters were closely related with plant WP: the vapor pressure deficit ($r = 0.800$) and SWP at 70 cm depth ($r = 0.806$). The air and soil maximum temperatures were, in general, the worst correlated variables with plant WP ($r \leq 0.673$). The air and soil maximum temperatures are the highest measured on each sampling date for each category.

Discussion

Several authors have demonstrated that plant water potential undergoes daytime variations, exhibiting a maximum peak at dawn and a minimum at midday or in the first hours of the afternoon. In fact, Branson and Shown (1975) recorded the most critical water potential in big sagebrush *(Artemisia tridentata)* at 4 p.m.. Nielsen et al. (1981) found a similar trend in mesquite *(Prosopis glandulosa)* suggesting that this behavior is related to highest stomatal conductance, which occurs in morning hours in arid species.

The lowest plant water potential was better correlated with soil water potential in the present study. A close relationship between plant water potential and moisture stress in soil was demonstrated for *Acacia aneura* (Slatyer 1961) and between the plant moisture stress and soil moisture content for red pine *(Pinus resinosa)* (Sucoff 1972). However, Hass and Dodd (1972) reported the lack of influence of soil moisture upon the minimum and maximum water potential in mesquite. Branson and Shown (1975) found that minimum soil-moisture stress was the highest correlated variable with water stress in big sagebrush. Nevertheless, the same authors emphasized that when soil moisture is readily available for plants, above all in spring, then it is probably factors other than SWP that determine plant WP.

Maximum soil and air temperatures were poorly correlated with plant WP except in the case of chilladora, where maximum air temperature occupied an intermediate plane. Dina et al. (1973) found a highly significant correlation between these 2 variables and the water potential in shrubs belonging to a mountainous area of Utah (U.S.A.).

Vapor pressure deficit was one of the variables best correlated for chilladora. Hass and Dodd (1972) working with mesquite found highly significant correlations between plant water potential and vapor pressure deficit. However, Dina et al. (1973) detected significant correlations between these 2 parameters only in 1 of the 9 species.

The 5 species under study exhibited a plant WP recovery during the night. The values obtained earlier in the morning, were higher (less negative) than those recorded in afternoon hours. According to Sala et al. (1981) such plant behavior can been seen as an indication of plant response flexibility in the face of water stress-inducing changes. A wide range in plant WP between morning and afternoon values would indicate a high degree of flexibility or a high capacity to return daily to relatively high water potentials. On the other hand, a narrow range between values would reveal situations of intensive stress. Two examples which can be used to illustrate the latter are the December 1982 and February 1984 data recordings for jarilla and piquillín. The plant WP values obtained on both dates for these species were of -40 bars in the morning and afternoon hours. The inability of jarilla and piquillín to daily recover their water potential affects the metabolic functions essential to their growth (Kozlowski 1972, Hsiao 1973, Fitter and Hay 1983), implying a higher susceptibility to water stress than the other 3 species studied here.

The water potential range of these shrub species as measured in the morning and afternoon hours suggests a relatively efficient adjustment to the conditions of summer drought. It is hypothesized that such behavior patterns facilitate the elimination of competition from other species, mainly those of the understory, in periods of long or intensive drought. According to Vallentine (1974) drought may be an important cause of undesirable plant invasions on ranges previously weakened by grazing or other factors.

Minimum plant water potential is better correlated with soil water potential for the different forms. Branson and Shown (1975) suggested that the highly significant correlation of internal plant stress with lowest soil-moisture stress indicates that rapid and inexpensive plant-stress measurements might be used to estimate minimum soil-moisture stress.

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Yield and Digestibility of Old World Bluestem Grasses as Affected by Cultivar, Plant Part, and Maturity

S. M. DABO, C. M. TALIAFERRO, S. W. COLEMAN, F. P. HORN, AND P. L. CLAYPOOL

Abstract

Old World bluestems (*Bothriochloa* spp.) have been used in the U.S. for over 60 years but few data are available on effects of management or cultivar differences for forage yield and quality. Field experiments were conducted on a Kirkland silt loam (Uderic Paleustoll) soil for 2 years (1982–83), in order to assess the yield and quality of 4 such cultivars as affected by maturation and plant part. The experimental design was a split-split plot, in a randomized complete block, with 4 replications, 4 cultivars ('Caucasian', 'Ganada', 'Plains', 'WW Spar'), 10 harvest dates, and 3 plant parts (whole plant, stem, and leaf). Cultivars were main plots; harvest dates and plant parts were sub and sub-sub plots, respectively. Response variables were dry matter yield (DMY), in vitro dry matter disappearance (IVDMD), leaf to stem ratio (L/S), and in vitro digestible dry matter yield (IVDDMY). Ganada consistently had the lowest leaf, stem, and whole plant DMY and IVDDMY. Caucasian had higher leaf, stem, and whole plant DMY and IVDDMY than Plains and WW-Spar in 1983, but the DMY and IVDDMY of these cultivars were similar in 1982. Quadratic and linear equations were satisfactorily fit to the DMY and IVDDMY data in 1982 and 1983, respectively. The IVDMD in whole plant samples decreased at average rates of 4.2 and 5.5 g kg ha^{-1} daily in 1982 and 1983, respectively, during harvest week one. Among cultivars, Caucasian had the highest rate of decline and Ganada the lowest. The decline was quadratic in nature and faster in stem fractions. Cultivar IVDMD differences were consistent over plant parts. Ganada and Caucasian had the highest and lowest IVDMD concentrations, respectively. Plains and WW-Spar had IVDMD values of similar magnitude and intermediate to those of Ganada and Caucasian. Cultivar leaf to stem ratios were similar in 1982 but different in 1983 with Plains and Caucasian having higher L/S ratios than Ganada and WW-Spar. For these cultivars leafiness was a poor indicator of digestibility.

Key Words: 'Ganada', 'WW-Spar', 'Plains', 'Caucasian', plant morphology, dry matter yield, IVDMD, IVDDM, leaf to stem ratio

Old World bluestems (*Bothriochloa* spp.) are highly apomictic, perennial, warm-season, bunchgrasses of Eurasian origin (Harlan and Chheda 1963, Harlan et al. 1964, and Taliaferro and Harlan 1973). These grasses are known for their apparent superiority to American forms (*Andropogon* spp.) with respect to production, quality, persistence under grazing, and ability to respond to high fertility levels. They are also potentially important as erosion control and reclamation grasses for millions of hectares of depleted range and marginal farmlands in the southern Great Plains.

Despite extensive use of Old World bluestems (OWB) by livestock producers in the southern Great Plains, few data are available on their yield and quality trends, and on leaf and stem contributions to these parameters throughout the growing season.

Comparative forage yield tests in Oklahoma have shown 'Plains' bluestem [*Bothriochloa ischaemum* (L.) King. var. ischaemum] to be less productive than 'Caucasian' bluestem [*B. caucasica* (Trin.) C.E. Hubbard] but equal in persistence (Taliaferro et al. 1972). Dalrymple et al. (1980) reported preliminary yield test results of commercially available OWB cultivars. The Caucasian and Plains cultivars had the highest yields (about 5,712 kg ha^{-1}) and 'Ganada' [*B. ischaemum* (L.) Keng. var. *ischaemum*] the lowest (about 5,176 kg ha^{-1}).

Taliaferro et al. (1972) found that the in vitro dry matter disappearance (IVDMD) of the Plains cultivar was higher than that of Caucasian (49.3 vs. 45.4%). The IVDMD of both cultivars decreased as the growing season advanced. Horn and Taliaferro (1979), studied seasonal changes in IVDMD values of hay from 5 OWB cultivars including Plains and Caucasian. A downward trend in IVDMD occurred as the season progressed though the total decline was not great. The lowest IVDMD values were reached in August.

The nutritional value of forage may be underestimated by analyzing only whole plant samples because livestock seldom consume whole plants, but rather selectively graze individual parts (Kalmbacher 1983). The parts of a plant (inflorescence, leaf blade, leaf sheath, and culm) differ in quality (Kalmbacher 1983). Generally, the nutritive value of leaves is superior to that of stems (Minson et al. 1960, Minson et al. 1964, Terry and Tilley 1964, and Kalmbacher 1983). In vitro studies by Minson et al. (1960, 1964) with ryegrasses, fescue, timothy and cocksfoot grasses separated into leaf lamina, leaf sheath, stem, inflorescence, and dead material, indicated that digestibility of the leaf lamina fraction decreased 0.10% per day with advancing maturity. Leaf sheaths and stem fractions decreased more rapidly than the lamina with increasing maturity (0.40% and 0.70% per day, respectively). Yet, stem fractions were more digestible than leaf fractions in immature stages of growth. Similar results were reported by Mowat. et al. (1965).

The objectives of this study were to: (a) characterize the forage yield and quality differences of whole plant and component plant parts of 4 OWB cultivars as affected by stage of maturity, and (b) ascertain the relationships between yield patterns and IVDMD.

Materials and Methods

This study was conducted in 1982 and 1983 on the Agronomy Research Station, Stillwater, Okla. The soil type was a Kirkland silt loam (Uderic Paleustoll). The field plot design was a split-split plot, in a randomized complete block design with 4 replications. The 4 OWB cultivars were Plains, Caucasian, Ganada, and "WW-Spar' [*B. ischaemum* (L.) Keng var. *ischaemum*]. Plots were 6 • .6 m, each consisting of 5 rows spaced 15 cm apart. The test was seeded 28 July 1980.

The nursery was prepared for study by cutting the experimental area to a uniform height (staged) of about 1.00 cm, 22 June 1982 and 25 May 1983. The plots were fertilized with 120 kg N ha^{-1} soon after staging. Plots were then divided into ten 0.5 m^2 subplots. During the experiment, the nursery was irrigated regularly to maintain abundant soil moisture. Prior to harvest, plots were trimmed to eliminate border effects. Harvesting was started 3 weeks after staging; and continued at weekly intervals for 10 weeks. Harvest dates (1 through 10) were randomly assigned to subplots. Plants in subplots were clipped at 1.3 cm from ground level. Subplot total green weight was recorded for yield measurements and 2 subsamples were taken. One subsample was oven dried at 65° C for 7 days and used to convert subplot green yield weights to dry

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matter yields (DMY). The second subsample was frozen and later separated into leaf, stem, and head (inflorescence) components. Leaves consisted of blades broken off at the sheath. After separation, the respective plant parts were dried in a forced draft oven at 65° C for 7 days. Dry matter weights of leaves, stems, and inflorescences were used to estimate the percentage of each plant part in the subplot total dry weight. All dried samples were then ground first through a 5-mm screen in a Wiley Mill and through a 1-mm screen in a UDY Cyclone Mill. This resulted in 20 to 30 g of ground forage which was used to determine forage IVDMD. The IVDMD was determined for each dried sample with the exception of inflorescences.

IVDMD was measured by near infrared reflectance (NIRR) spectroscopy using a monochromator. Sixty-four scans of each sample with monochromatic light in the near infrared region, from 1,100 to 2,500 nm, were averaged and stored on a Digital Equipment Corporation mini-computer PDP 11/23. Seven hundred data points at 2.0-nm intervals were recorded for each sample. The monochromator was calibrated with IVDMD data from the laboratory analysis of 480 forage samples (50% of all samples including stems, leaves, and whole plants). The 480 samples were drawn from 2 randomly selected replications. Percent IVDMD for the laboratory analysis was determined in triplicate using a modified Tilley and Terry technique (Monson et al. 1969). Calibration of the monochromator was achieved using the computer software developed at Pennsylvania State University (Shenk et al. 1977). The software combined NIRR reflectance data with the laboratory analyses, performed the necessary mathematical transformations (log 1/R, 1st and 2nd derivatives), and used a modified stepwise linear regression procedure to find the wavelengths most useful for predicting the desired quality parameter. Seven calibration equations resulted and included 1 to 7 wavelengths and their regression coefficients for predicting forage quality characters. On the basis of the R-square, bias, and standard error of prediction statistics, an equation was chosen to predict the IVDMD from the reflectance spectra of the remaining samples.

An overall statistical analysis was first conducted on each response variable using ANOVA procedures for a split-split plot arrangement. Data were analyzed within year and by plant part to assess cultivar differences and effects of harvest dates. The least significant difference test of treatment means backed by significant F-test was used to determine differences among cultivars and maturity stages (Steel and Torrie 1960). Orthogonal polynominals partitioned harvest dates and harvest dates × year sum-of-squares into linear, quadratic, and deviation from quadratic components. Yield results were correlated with whole plant IVDMD values to ascertain the significance of their relationship. The in vitro digestible dry matter yield (IVDDMY) was computed as the product of DMY (kg ha^{-1}) in IVDMD (g hg^{-1}) at each harvest. Leaf to stem ratio (L/S) was calculated and both L/S and IVDDMY data were analyzed by the same statistical procedures as stated above.

Results and Discussion

Because of significant first, second and third order interactions involving cultivars, harvest dates, years, and plant parts for yield and IVDMD, results are reported by year and plant part.

Dry Matter Yields

Differences in whole plant, leaf, and stem DMY due to cultivar and harvest date were highly significant ($P<.01$) each year. The significant ($P<.05$) cultivar × harvest date interactions in 1982 were caused more by differences in magnitude of response, than by changes in cultivar rank. Ganada had the lowest ($P<.05$) DMY of whole plant and component parts both years (Fig. 1). Caucasian consistently had higher ($P<.05$) leaf, stem, and whole plant DMY than Plains and WW—Spar in 1983, but the DMY of these cultivars was similar in 1982. In 1983, the whole plant DMY of Caucasian was about 17% more than Plains. For the same year, the whole plant DMY of Ganada was 16 and 20% lower than that of Plains and WW-Spar, respectively. In 1982, the DMY of Ganada was about 30% lower than the average DMY of Plains, Caucasian, and WW-Spar. These results agree with previous studies (Taliaferro et al. 1972, Dalrymple et al. 1980, and Sims and Dewald 1982) but disagree with others (Dalrymple et al. 1984).

The DMY of all cultivars increased significantly ($P<.01$) with advancing maturity due to accumulated growth (Fig. 1). The data were satisfactorily fit to second order polynomial equations in 1982 and to linear equations in 1983. This inconsistency in DMY trends between years was likely the result of environmental differences on growth.

The linear equations in 1983 revealed weekly mean DMY increases of 393, 41, and 327 kg ha^{-1} for whole plants, leaves, and stems, respectively. In 1982, the derivative of quadratic equations revealed that whole plant DMY increased 700, 440, and 182 kg ha^{-1} weekly prior to harvest dates 2, 5, and 8, respectively. Similarly, weekly mean stem DMY increases were 446, 320 and 195 kg ha^{-1}, respectively. The DMY increases in leaf fractions were less in magnitude as compared to whole plant and stems. Mean leaf DMY increases were 260 and 38 kg ha^{-1} per week prior to harvest dates 2 and 6, respectively, in 1982. Ganada had lower rates of increase than the other cultivars both years. Caucasian had the highest rates of increase in 1983 but not in 1982. The R^2 values obtained for leaves were smaller than those for stems, indicating that maturation contributed more to stem DM yield (data not presented).

In Vitro Dry Matter Disappearance

There were significant differences in the IVDMD of whole plants, leaves, and stems due to cultivar and harvest dates both years. The cultivar × harvest date interactions for the IVDMD of whole plants, leaves, and stems were significant ($P<.01$) in 1982. The same interaction was significant for the stem fraction only in 1983.

Ganada was consistently higher than other cultivars in IVDMD, while Caucasian tended to have the lowest IVDMD (Fig. 2). In 1983, Caucasian stems were higher ($P<.05$) in IVDMD than those of Plains and WW-Spar especially after harvest date 3. The IVDMD values of Plains and WW-Spar were similar both years and intermediate to those of Ganada and Caucasian (Fig. 2). Cultivar differences were more noticeable in leaves than in whole plants or stems (Fig. 2). Differences obtained between Plains and Caucasian agree with previous results (Horn and Taliaferro 1979). The low IVDMD values of Caucasian were probably due in part to

Table 1. In vitro digestible dry matter yield of whole plant, leaf, and stem samples of four old world bluestem cultivars (means of 10 harvest dates).

Cultivar	Whole Plant		Leaf		Stem	
	1982	1983	1982	1983	1982	1983
	kg ha^{-1}					
Plains	1407 a[1]	1294 b	638 a (45)[2]	473 a (37)	766 a(54)	733 b (57)
Caucasian	1277 a	1499 a	468 b (37)	511 ab (34)	722 a (60)	907 a (61)
Ganada	1007 b	1168 b	437 b (43)	325 c (28)	564 b(56)	774 b (66)
WW-Spar	1380 a	1341 ab	566 ab (41)	379 ac (28)	786 a (57)	832 ab (62)

[1] Values within a column followed by the same letter are not significantly different ($P>.05$) as indicated by the L.S.D. test.
[2] Percentage contribution to the whole plant IVDDMY.

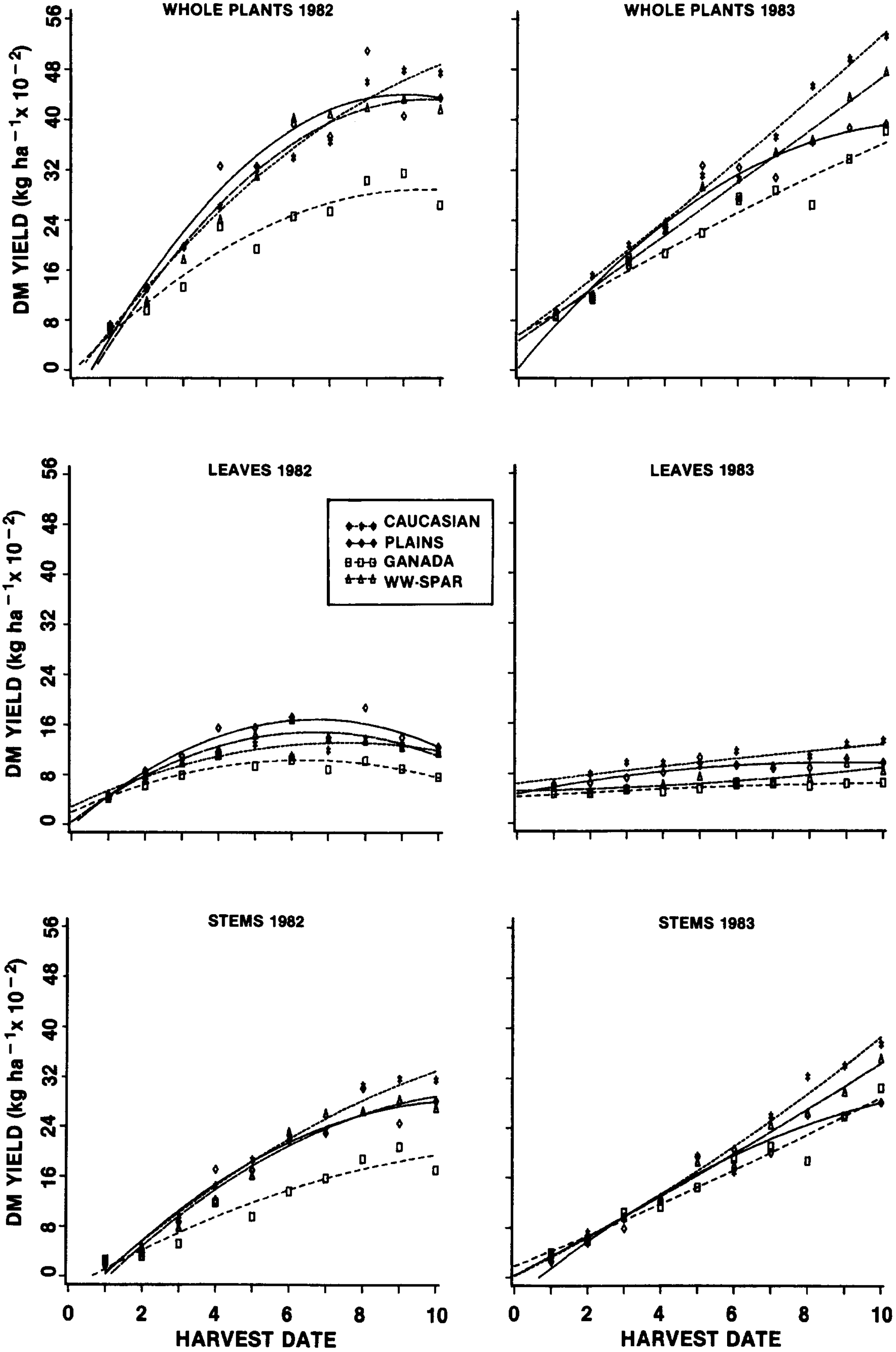

Fig. 1. *Dry matter (DM) yields of whole plants, leaves, and stems of 4 Old World bluestem cultivars at 10 harvest dates.*

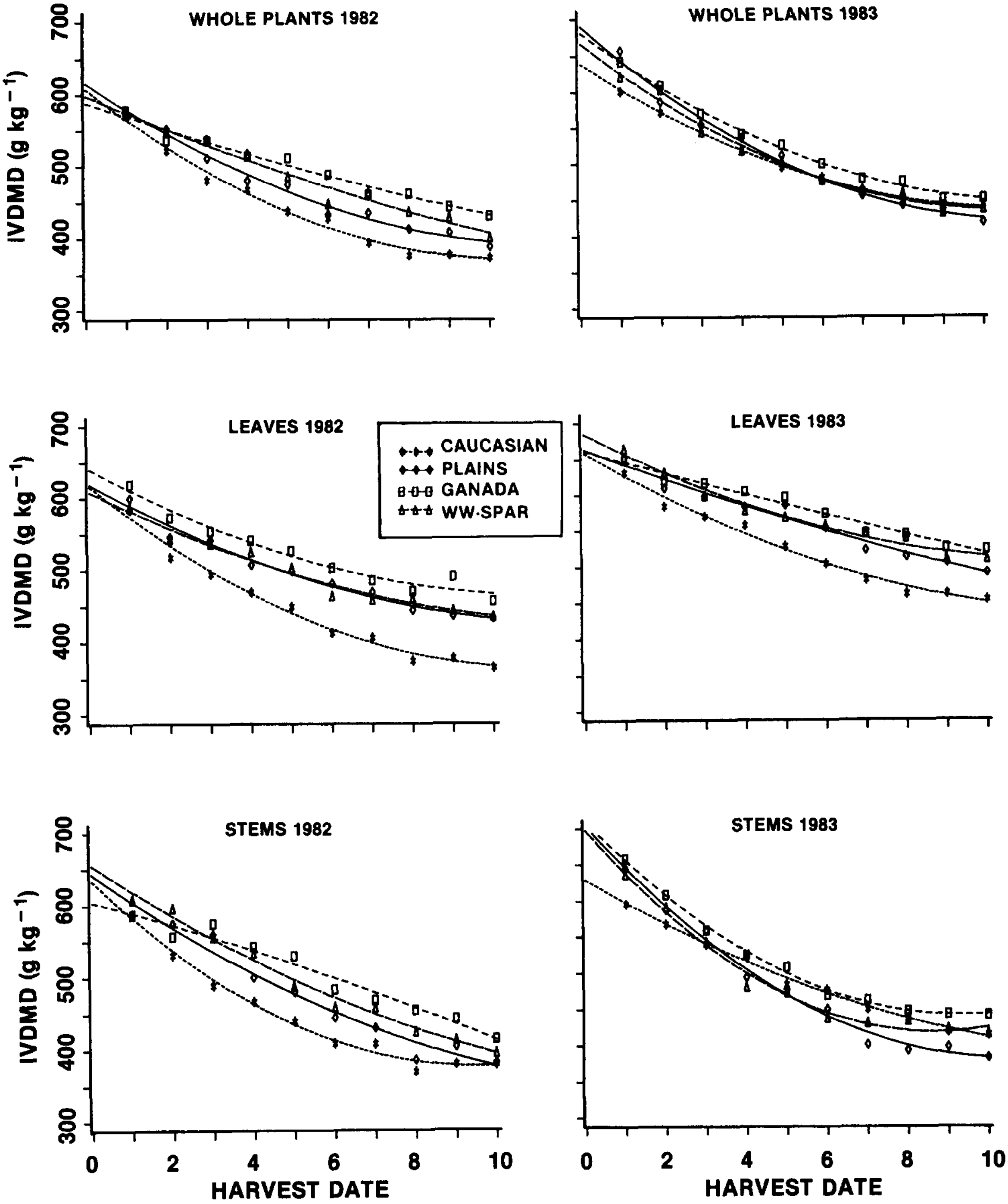

Fig. 2. *In vitro dry matter disappearance (IVDMD) of whole plants, leaves, and stems of 4 Old World bluestem cultivars at 10 harvest dates.*

its rapid growth rate and high DMY as reported by Horn and Jackson (1979).

The mean IVDMD of all cultivars and all plant parts decreased significantly ($P<.01$) with maturation (Fig. 2). Orthogonal polynomials indicated that the data satisfactorily fit quadratic equations but different quadratic equations were required for each year.

The rate of IVDMD decline was generally faster in Caucasian and slower in Ganada, particularly in 1982, with respective rates ranging from 5.8 to 3.2 g kg^{-1} daily in whole plants during harvest week one. For the same period and plant part, the mean IVDMD of all cultivars decreased at rates of 4.2 and 5.5 g kg^{-1} daily in 1982 and 1983, respectively. These rates of decline are comparable to those reported by Pritchard et al. (1963) and Voigt et al. (1981). The IVDMD values of immature stems were similar to corresponding values of leaves (Fig. 2). However, the rate of decline of IVDMD with advancing maturity was greater in stems than in leaves for each cultivar except Ganada in 1982.

Ganada whole plant Mean IVDMD was 8, 5, and 3% higher than of Caucasian, Plains, and WW-Spar (data not presented). This could translate into substantial animal performance differences between cultivars. For example, 'Coastal' bermudagrass [*Cynodon*

Table 2. Simple correlations between dry matter yields and in vitro dry matter disappearance of whole plants, leaves, and stems of four old world bluestem cultivars (data averaged over sampling period and years).

Cultivar	Plant Part Whole plants	 Leaves	 Stems
		r	
Plains	-.82**	-.59**	-.85**
Caucasian	-.76**	-.62**	-.75**
Ganada	-.72**	-.44**	-.71**
WW-Spar	-.83**	-.51**	-.83**

**$P<.01$.

dactylon (L.) Pers], 'Pensacola' bahiagrass (*Paspalum notatum* var. *saurae parodi*) and 'Coastcross-1' bermudagrass were compared for average daily gain (ADG) and IVDMD (Chapman et al. 1972). The ADG over all stocking rates on Coastcross-1 bermudagrass pastures were 50% higher than those for Coastal bermudagrass. The authors concluded that the majority of that difference was due to the greater apparent digestibility (12%) and/or intake of Coastcross-1 bermudagrass.

In Vitro Digestible Dry Matter Yield

Differences in IVDDMY due to harvest date were significant ($P<.01$) but there were no significant ($P>.05$) cultivar × harvest date interactions. Cultivar differences were highly significant ($P<.01$). Over all harvest dates Caucasian consistently had higher ($P<.01$) IVDDMY of whole plant, leaves, and stems than Ganada (Table 1). There was no difference ($P>.05$) in the IVDDMY of Plains, WW-Spar, and Caucasian in 1982 or Plains, WW-Spar and Ganada in 1983. The effect of harvest date on IVDDMY was similar to that discussed above for DM yield. The data satisfactorily fit second and first order polynomial equations in 1982 and 1983, respectively.

Leaf to Stem Ratio

Differences in L/S ratios due to cultivar, and cultivar × harvest date interactions were highly significant in 1983 ($P<.01$) but nonsignificant in 1982 ($P>.05$). Plains and Caucasian had similar ($P>.05$) but higher L/S ratios than Ganada and WW-Spar ($P>.05$) in 1983 (Table 3). Leafiness was a poor indicator of digestibility differences as the less digestible cultivars contained the most leaves. Leaf to stem ratios for the respective cultivars decreased significantly ($P<.01$) with advancing maturity (Table 3) and generally in a quadratic manner.

Significant negative correlations were obtained between IVDMD DMY of whole plant and component parts in all cultivars (Table 2). Among cultivars, Ganada had the lowest correlations for whole plant, leaves, and stems. Plains and WW-Spar had the highest correlations for stems while Caucasian correlations were highest for leaves. Correlations were higher for stems than for leaves. This inverse relationship between DMY accumulation and IVDMD is consistent with reports for many other forage species.

In summary, characteristics such as DMY, IVDMD, and their rates of change dictated the IVDDMY levels of the cultivars at any given harvest date. The cultivars under investigation varied significantly with regard to the above parameters. The cultivar with the highest IVDMD (Ganada) had generally the lowest DMY and IVDDMY. While some yield and quality differences among cultivars were obvious (Caucasian vs. Ganada) others were less conclusive and need to be confirmed. The Plains and WW-Spar cultivars were generally similar for the above parameters. Yields of whole plant and component parts over the 10-week period correlated negatively with IVDMD, suggesting a rapid decline in forage quality with advancing maturity. Leafiness among cultivars was a poor indicator of digestibility differences.

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Table 3. Leaf to stem ratios of four old world bluestem cultivars at ten harvest dates during 2 years.

Harvest date	1982[1] Plains	 Caucasian	 Ganada	 WW-Spar	1983[2] Plains	 Caucasian	 Ganada	 WW-Spar
1	2.37	2.58	1.63	2.09	2.53	1.96	1.23	1.55
2	2.17	1.85	1.94	2.70	1.20	1.11	0.83	0.80
3	1.27	1.05	1.53	1.31	0.93	1.45	0.51	0.57
4	0.92	0.81	1.01	0.99	0.65	0.87	0.47	0.48
5	0.91	0.70	0.98	0.90	0.54	0.79	0.38	0.41
6	0.81	0.51	0.75	0.72	0.45	0.47	0.34	0.34
7	0.61	0.51	0.57	0.54	0.44	0.35	0.30	0.27
8	0.61	0.45	0.56	0.53	0.33	0.33	0.36	0.27
9	0.58	0.40	0.43	0.44	0.39	0.37	0.24	0.33
10	0.45	0.39	0.45	0.43	0.34	0.36	0.21	0.24
$\bar{X}$	1.07	0.92	0.99	1.06	0.78	0.81	0.49	0.53

[1] 5% L.S.D. for harvest date means = 0.12.
[2] 5% L.S.D. for harvest date means = 0.09.

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Grazing Effects on Water Relations of Caucasian Bluestem

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Abstract

Caucasian bluestem [*Bothriochloa caucasica* (Trin.) C.E. Hubb.] is a warm-season grass introduced from Eurasia that is currently used for reseeding rangelands in the southern Great Plains. Although this species is thought to be grazing tolerant, no specific information is available concerning its response to grazing. This study was conducted to evaluate the effect of 2 levels of grazing on xylem water potential (ψ) and total leaf conductance (gT) of Caucasian bluestem. During the grazing period (mid May to mid September) diurnal ψ and gT measurements were made on 3 days in 1983 and 1984, and afternoon measurements were taken at weekly intervals in 1984. Soil moisture at 15, 45, and 75 cm depths was monitored in 1984. Heavily grazed plants exhibited consistently higher (less negative) ψ, and generally higher gT than lightly grazed plants. Averaged over the season, heavy grazing increased mean afternoon ψ and gT by 28 and 76%, respectively, compared to light grazing. Soil moisture was conserved with heavy grazing; treatment differences were greatest during July, which is generally the driest summer month in central Oklahoma. Thus, for Caucasian bluestem, leaves from heavily grazed swards were under less water stress than leaves from lightly grazed swards.

Key Words: *Bothriochloa caucasica*, stomatal conductance, xylem potential, soil moisture

In recent years Old World bluestems (*Bothriochloa* spp.) have gained popularity for use in forage/livestock systems in the Southern Great Plains. These native Eurasian species tend to increase under heavy grazing and other disturbances (Harlan et al. 1958). However, responses of Old World bluestems to defoliation have been studied with clipping (e.g., Anderson and Matches 1983, Coyne and Bradford 1985) rather than grazing. Hodgkinson (1980) and Briske and Stuth (1982) have indicated that grazing patterns are seldom adequately characterized, and such information is necessary if grazing is to be simulated. Because grazing patterns are difficult to reproduce, Hodgkinson (1980) concluded that future studies should examine physiological stress in plants subject to actual grazing and growing in natural communities.

Water stress is critical to plant growth and survival, particularly in regions subject to periodic drought. Leaf expansion is sensitive to even mild water stress, and in many species is completely curtailed with moderate water stress (Hsiao and Acevedo 1974). If leaf area removal by grazing influences water relations, growth would also be affected. The objectives of this study were to determine the effect of continuous heavy and light grazing on xylem pressure potential, total leaf conductance, and soil moisture in swards of Caucasian bluestem (*Bothriochloa caucasica* (Trin.) C.E. Hubb.).

Materials and Methods

The study was conducted during 1983–1984 at the USDA Forage and Livestock Research Laboratory, near El Reno, Okla. Soils at the study site were fine-silty Pachic Haplustolls of the Dale Series. Annual precipitation averaged 76.2 cm from 1977–1984. Precipitation was above average in 1983 (99.0 cm) and slightly below average in 1984 (72.4 cm).

We used a sward of Caucasian bluestem which had been seeded in 1979 and hayed or leniently grazed prior to initiation of this study. Continuous variable (put-and-take) stocking was used to maintain high herbage mass (light grazing) and low herbage mass (heavy grazing) treatments on 1-ha pastures (see Wheeler et al. (1973) for discussion of variable stocking). Steers averaging about 225 kg were put on the pastures mid-May and grazed until late September of both years. Pastures were characterized by measuring herbage mass and sward height twice a month, and leaf area index about monthly (Table 1). Herbage mass was estimated with a pasture meter (Electrical Equipment Limited, Armcliffe, N.S.W., Australia)[1], which was calibrated using double sampling with 8

Table 1. Descriptions of heavily (H) and lightly (L) grazed Caucasian bluestem pastures.

	1983		1984	
	H	L	H	L
Seasonal range in herbage mass (kg/ha)	860–1530	3180–5375	1037–1952	6516–10,100
Sward height (cm)	5–10	20–25	5–10	35–45
Range in number of steers per hectare	3.0–8.00	2.5–4.5	3.0–7.0	2.5–4.2
Leaf area index	0.7–1.0	1.4–3.2	0.4–1.0	1.4–4.5

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[1] Mention of a trade name does not indicate endorsement by USDA.

clipped plots per treatment per sampling date. Sixty measurements per pasture were taken for both herbage mass and sward height at each sampling date. Leaf area index was measured by clipping four 15 × 25-cm quadrats per pasture, separating green leaves and scanning them with a leaf area meter (LI-3000, Li-Cor, Inc., Lincoln, Neb.).

Two teams, each equipped with a pressure chamber (3000 Series, Soilmoisture Equip. Corp., Santa Barbara, Calif.) and porometer (LI-700, Li-Cor, Inc., Lincoln, Neb.) conducted the water relations measurements. Paired samples in the heavily and lightly grazed treatments were taken simultaneously to avoid any affect short-term environmental fluctuations might have on treatment comparisons. Teams were alternated between treatments so that equipment or operator bias also would not affect treatment comparisons. We used fully expanded leaf blades from the upper canopy. Total leaf conductance (gT) was the sum of adaxial and abaxial conductances from the transient porometer. After conductance was measured, the leaf blade was wrapped in moist paper toweling, excised, and xylem water potential (ψ) taken with a pressure chamber. Diurnal trends in ψ and gT were monitored on 3 dates in both 1983 and 1984. On each date, predawn ψ was measured, and during daylight hours ψ and gT were measured 4 times. At about weekly intervals from 14 June to 9 September 1984, ψ and gT were measured between 1300 and 1430 hr. At each sampling time ambient temperature and relative humidity were measured with a sling psychrometer, and photosynthetically active radiation integrated over a 100 s period prior to sampling with a quantum sensor (LI-183, Li-Cor, Lincoln, Neb.).

Sample leaves were selected at random from paired (parallel) 5 × 5-m macroplots located along the fenceline separating the pastures. There were 4 sets of macroplots (thus 4 per treatment) located at about 20-m intervals. At each sampling time 1 sample per macroplot was measured for ψ and gT. Soil moisture was monitored at about 10-day intervals during 1984 with gypsum blocks (5200 Series Soilmoisture Equip. Corp., Santa Barbara, Calif.) buried at 15, 45, and 75 cm within each macroplot.

Data for gT and ψ were analyzed using analysis of variance with grazing treatment and time of day or date as main effects. Predawn ψ was analyzed separately from daytime ψ values using paired-*t* tests. Treatment differences in soil moisture were analyzed with pair-*t* tests for each date and depth within date.

Results and Discussion

Leaves sampled during the day from the heavily grazed pasture were generally under less water stress (less negative ψ) and had higher gT than leaves from the lightly grazed pastures (Figs. 1, 2 and 3). Predawn ψ measurements showed no treatment effects except on 27 September 1983, when values were less negative on the heavily grazed pasture. Presumably roots in the lightly grazed pasture extracted enough water to rehydrate leaf tissue at night, but could not provide enough moisture for transpiration demand during the day. Wolf and Parrish (1982) found that clipping tall fescue *(Festuca arundinacea)* leaves improved ψ in remaining plant parts and thereby accelerated cell expansion. They stated that removal of transpiring leaf area overcame growth limitations imposed by an inadequate root system and/or low soil moisture. Jackson (1974) studied swards of perennial ryegrass *(Lolium perenne)* and found that cutting reduced water stress and increased stomatal conductance under nonirrigated conditions. In contrast, Nowak and Caldwell (1984) found no improvement ψ of similarly aged foliage elements on clipped and unclipped bunchgrasses.

Plant water status is important in that leaf expansion and thus vegetative growth are severely inhibited by moderate water stress (Kramer 1983). Leaf expansion tends to be more sensitive to water stress than is CO_2 assimilation; thus dry matter may be reduced by water deficits that are not severe enough to limit stomatal opening and photosynthesis (Hsiao and Acevedo 1974). In many cases a decrease in ψ of 0.3 to 0.4 MPa relative to well-watered conditions

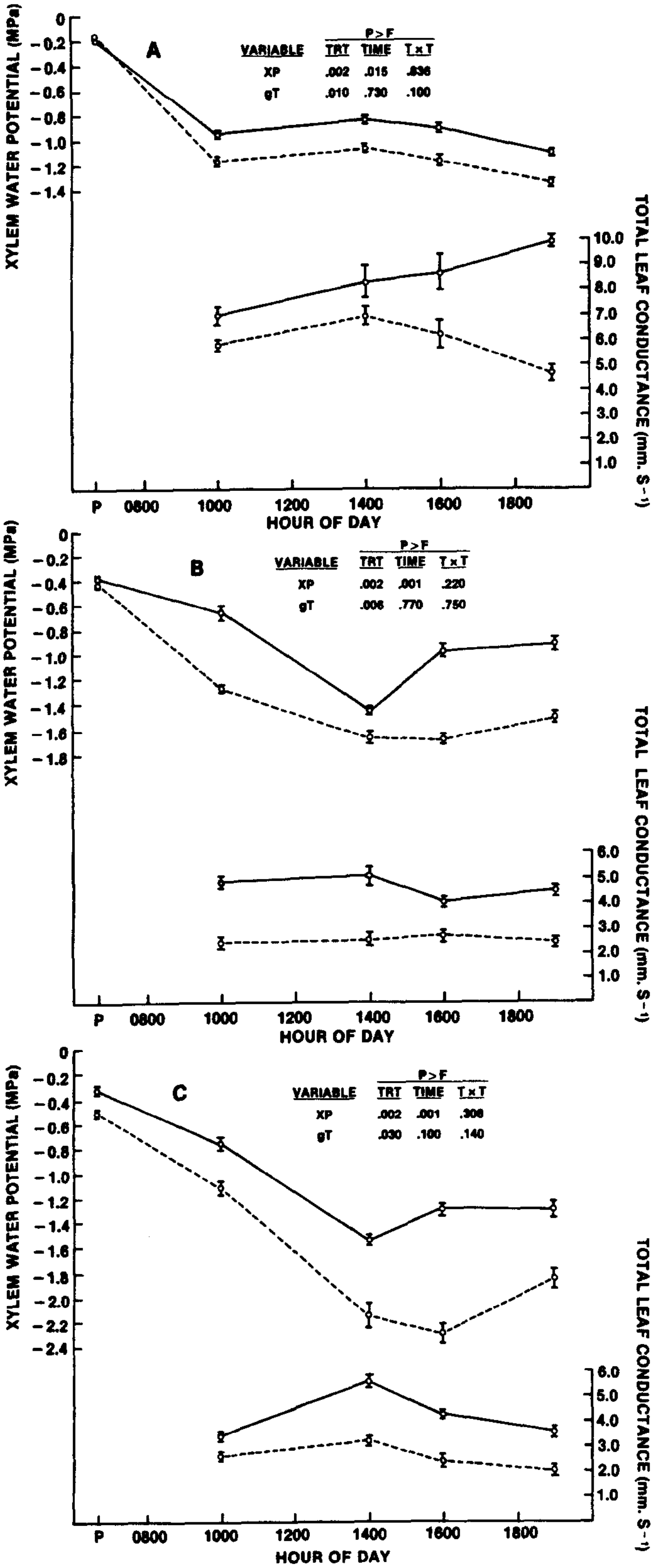

Fig. 1. *Diurnal trends in xylem water potential (XP) and total leaf conductance (gT) for heavily (solid lines) and lightly (dashed lines) grazed Caucasian bluestem in 1983. Dates are as follows: A = July 6, B = July 25, and C = September 27. Probability statements of treatment and time effects and their interaction appear at the top of each graph (predawn (P) values are not included in the analysis). Vertical lines represent 1 standard error of the mean (n = 4).*

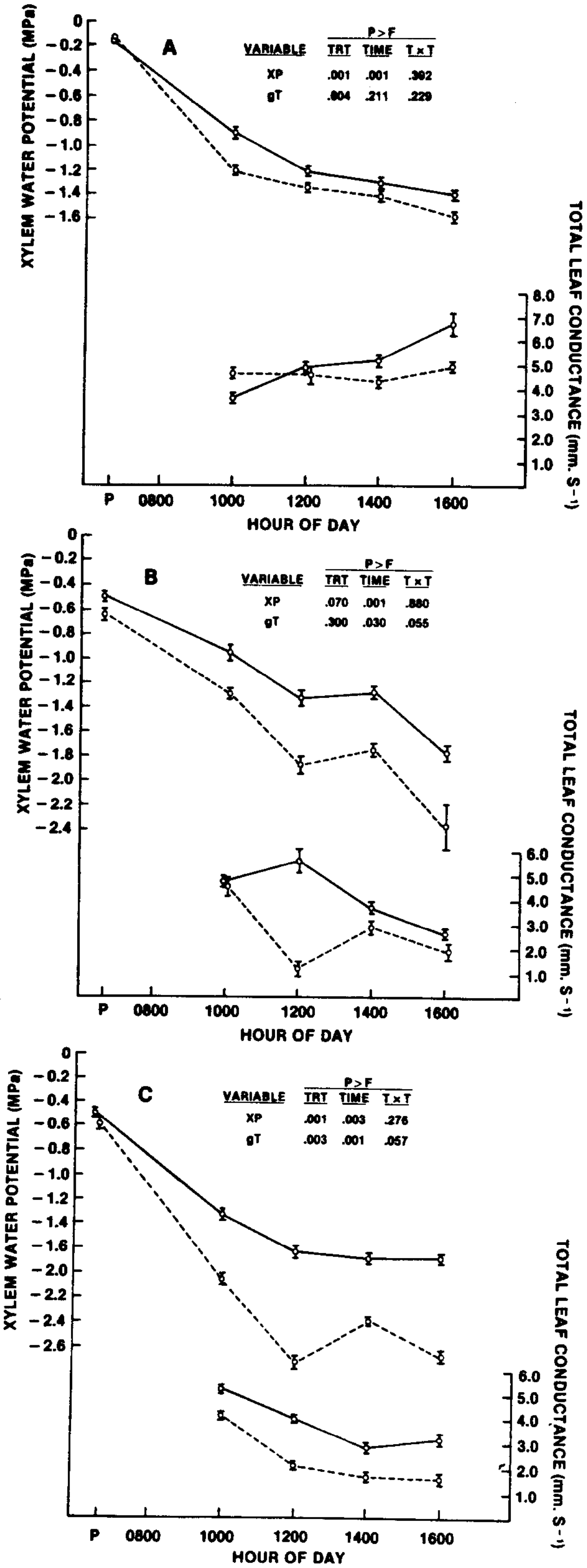

Fig. 2. *Diurnal trends in xylem water potential (XP) and total leaf conductance (gT) for heavily (solid lines) and lightly (dashed lines) grazed Caucasian bluestem in 1984. Dates are as follows: A = June 16, B = July 17, and C = August 16. Probability statements for treatment and time effects and their interaction appear at the top of each graph (predawn (P) values are not included in the analysis). Vertical lines represent 1 standard error of the mean (n = 4).*

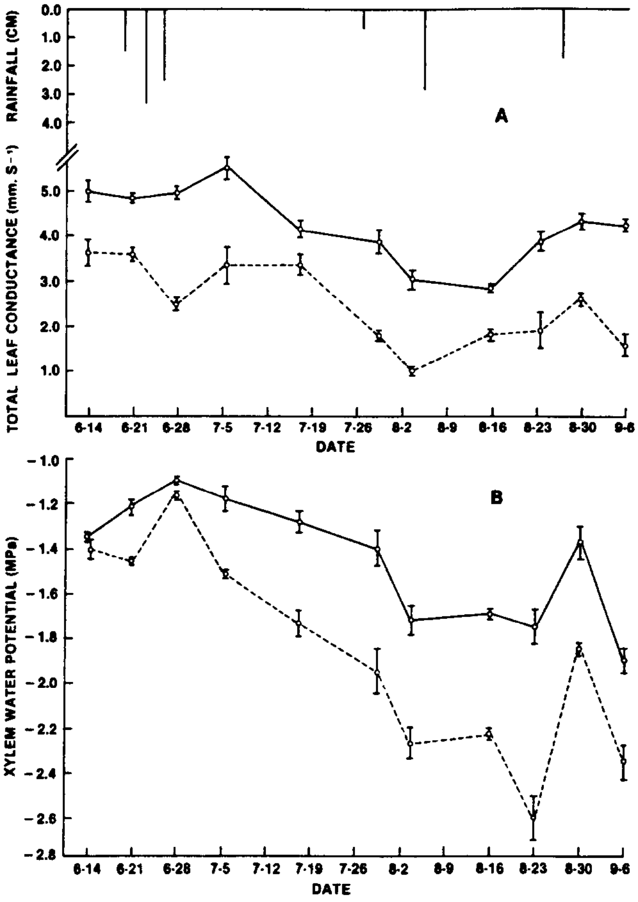

Fig. 3. *Seasonal trends in total leaf conductance (A) and xylem water potential (B) for heavily (solid lines) and lightly (dashed lines) grazed Caucasian bluestem. Measurements were taken between 1300 and 1430 hrs on each measurement date. During sampling, ambient temperature ranged from 34–39° C, relative humidity from 40–55% and photosynthetically active radiation from 1,800–2,000 µmoles m^{-2} S^{-1}. Rainfall events are presented at the top. Veritical lines around each point are 1 standard error of the mean (n = 4).*

is sufficient to stop cell enlargement entirely (Hsiao et al. 1976). In this study, level of herbage removal had a major impact on water stress. During July and August of 1984, afternoon ψ was 0.3 to 0.9 MPa less negative in the heavily grazed than in the lightly grazed pasture (Fig. 3), and similar differences were noted in the diurnal measurements (Figs. 1 and 2).

In addition to reduced water stress on the heavily grazed pasture, there was an increase in stomatal conductance relative to the lightly grazed pasture. This is consistent with the results of several defoliation studies (Gifford and Marshall 1973, Deinum 1976, Detling and Painter 1983, Heichel and Turner 1983). The importance of gT in regulating photosynthesis will depend on the relative contribution of stomatal and mesophyll resistances to total CO_2 flux resistance. In warm-season grasses, stomatal resistance tends to dominate the total resistance to CO_2 flux (Boyer 1970, Ludlow and Wilson 1971, McPherson and Slayter 1973, Gifford 1974), especially at the higher temperatures that are optimum for this group of grasses (e.g., Coyne et al. 1982). At full sunlight and 35° C ambient temperature, Coyne and Bradford (1984) found that stomatal resistance of Caucasian bluestem accounted for 70% of the total resistance to CO_2 flux. In our study, the overall mean gT for the 1984 afternoon measurements (Fig. 3) was 2.52 mm s^{-1} and 4.44 mm s^{-1} for lightly and heavily grazed plants, respectively. A 76% increase in gT would likely result in increased photosynthetic rate per unit leaf area. However, the increase in gT was less than the

Table 2. Soil moisture tension (MPa) on heavily (H) and lightly (L) grazed Caucasian bluestem pastures during 1984[1].

		Date								
Grazing Trt	Depth (cm)	6/15	6/26	7/9	7/18	7/30	8/7	8/23	8/30	9/11
H	15	–0.02	–0.02	–0.13	–1.5	–1.5	–0.08*	–1.5	–0.5	–1.5
	45	–0.02	–0.02	–0.02	–0.04*	–0.25	–0.5	–1.5	–1.5	–1.5
	75	–0.02	–0.02	–0.02	–0.02*	–0.04*	–0.07	–0.3	–0.6	–1.5
L	15	–0.02	–0.02	–0.18	–1.5	–1.5	–1.3	–1.5	–1.5	–1.5
	45	–0.02	–0.03	–0.04	–0.25	–1.5	–1.5	–1.5	–1.5	–1.5
	75	–0.03	–0.03	–0.04	–0.14	–0.9	–1.5	–1.5	–1.5	–1.5
Rainfall Received During each Interval (cm)			7.34	0.08	0.00	0.64	2.95	0.41	1.73	0.20

[1] An asterick indicates that treatments were significantly different ($P<0.05$) at that particular date and depth.

reduction in leaf area attributable to heavy grazing (Table 1). Thus on a whole canopy basis CO_2 uptake was probably greater on the lightly grazed pasture.

In general, our results support McNaughton's (1983) contention that herbivory can improve water relations of leaf tissue. He suggests that the improved water relations result from a greater ratio of absorbing root surface to transpiring leaf area. In addition, the reduction in transpiring leaf surface may conserve soil water, thus sustaining plant growth over a longer period (McNaughton 1983). Indeed we did find that soil moisture declined more slowly on the heavily grazed pasture than on the lightly grazed pasture (Table 2). The difference between treatments was most obvious during July, which is typically the driest summer month in central Oklahoma. Thus, in the case of Caucasian bluestem, there were several potentially beneficial effects of heavy grazing: (1) water stress was reduced; (2) stomatal conductance was increased; and (3) soil moisture was conserved.

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Adaptive Strategies of Desert Grasses in Saudi Arabia

U.G. BOKHARI, FAISAL ALYAEESH AND MAHMUD AL-NORI

Abstract

Adaptive strategies of dominant grasses in terms of stomatal resistance, rate of transpiration and photosynthesis, water potential of plants, and soil and water-use-efficiency were studied at 3 locations in the Kingdom. The locations chosen represented 3 different contrasting soil and climatic conditions of the regions. Results indicated that the desert plants have developed strategies to adjust stomatal behavior, rate of transpiration and water potential to cope with the harsh environment of the desert. The strategies involved appear to ensure survival of the species rather than high productivity.

Key Words: transpiration, photosynthesis, stomatal resistance, water potential, water-use-efficiency, protein, carbohydrates, drought tolerance

In Saudi Arabia, more than 70% of the land is considered rangelands covered with sand in one form or another. These rangelands have been the main sources of nutrition for different types of livestock.

The so-called desert ecosystem contains a multitude of plant species of grasses, forages, and shrubs which are under constant pressure by pastoral grazing and the environmental stresses. These plants have developed strategies both morphological and physiological to cope with the harsh environment of the desert (Mulrey and Rundel 1977, Noy-Meir 1973). Examples of morphological adaptation include leaf structure and orientation of leaves, leaf abscission, dormancy under adverse condition, and root-shoot ratio. Many desert plants operate on the C_4 photosynthetic pathway, which imparts drought resistance, efficient utilization of water and high light intensity under high temperatures. The physiological processes involved in the drought resistance or drought avoiding mechanisms usually include stomatal regulation, leaf water potential, transpiration, and photosynthesis adjustment. To what extent these processes are involved in adjusting to the harsh environment of the desert in Saudi Arabia have not been completely studied.

This study was undertaken to evaluate some of the physiological and nutritive characteristics of dominant grass species in 3 locations in the Kingdom.

Major objectives were (1) To evaluate the physiological performance of dominant desert grasses in terms of stomatal conductance, transpiration, water potential, and photosynthesis; (2) To determine the nutritional characteristics of these grasses; and (3) To use the information obtained through objectives 1 and 2 for seeking other species with similar characteristics for introduction and development in the Kingdom for livestock consumption.

Materials and Methods

Three locations representing contrasting soil and climatic conditions of the Kingdom were chosen in the central, eastern, and southwestern regions. Certain soil and climatic characteristics of the above regions are given in Figure 1 and in Tables 1 to 3 which indicate that the southwestern region is generally characterized by mild temperatures, low humidity, high precipitation and low salinity as compared to the central and eastern region. The eastern region with high summer temperatures is accompanied by high relative humidity, high salinity, and high water tables near the coastal areas. Study sites within each region were selected on the basis of visual observation of the diversity of plant species. Dominant species within each site were again determined by visual observation of the community and the population of each species within the community.

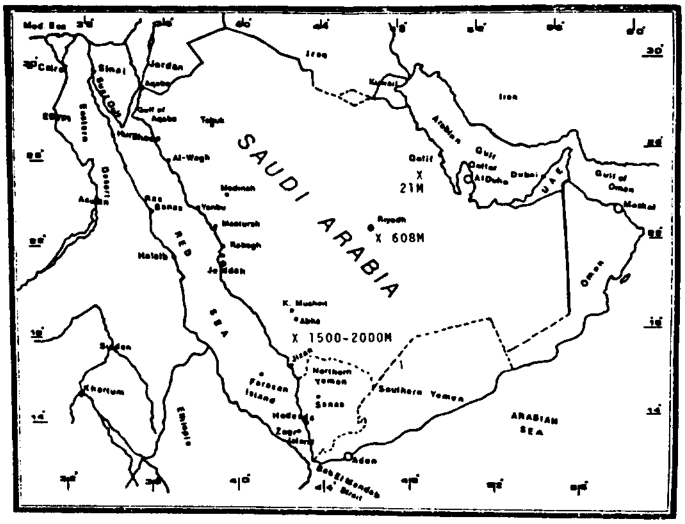

Fig. 1. Map of the Kingdom of Saudi Arabia. X shows study sites.

Table 1. Soil characteristics of study sites.

Region	EC	P	K	Organic Matter	Na	Ca	SO_4
	micromhos/ cm	ppm	ppm	%	———	meq/1	———
Central	5.40	5.7	87	0.42	22	32.3	34.1
Eastern	5.25	5.1	75	0.53	13	11.2	13.1
South Western	2.2	4.5	214	0.77	23	30.2	41.3

Dominant species chosen for this study within each study site are shown in each table. Thermocouple psychrometers were installed near the root zone of at least 3 plants of each species to keep track of soil water potentials. Detailed data collections were started at different times at the 3 locations depending upon the occurrence of first event of rainfall at each site. Data were collected during the vegetative and flowering stage. Vegetative stage was defined as when tillers and leaves had fully developed; flowering stage was defined as when flowers were visible and anthesis and pollination had already taken place. Stomatal resistance of several leaves of the same plants was measured with a steady state porometer and averaged over all the plants of the same species. Similarly, rate of transpiration was measured on the same leaves used for stomatal resistance measurement using steady state porometers.

Water potential of several branches of the same plant was measured using a pressure bomb technique. At the same time, soil water tension was measured with a microvoltmeter and the thermocouple psychrometers. Photosynthesis of a few species was measured with a differential Beckman infrared gas analyzer, Model 865, using ambient CO_2 concentrations. Power to the

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Table 2. Average mean monthly and annual temperature of different regions of Saudia Arabia (10 years averages).

Region	Met. Station	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Annual Average
									C°					
Southwestern	Taif Khamis-	14.8	16.2	19.4	21.9	24.9	28.3	27.9	28.1	27.1	22.5	18.5	15.3	22.0
	Mushait	13.7	15.2	17.0	18.9	21.3	24.2	23.2	23.2	22.5	18.9	16.2	13.6	17.8
	Abha	12.6	14.1	15.9	16.8	20.2	23.0	22.6	22.4	21.3	17.7	15.0	12.4	16.8
Central	Riyadh	13.8	16.2	20.3	25.2	31.0	34.5	34.7	34.8	32.1	26.6	20.5	14.9	24.1
	Qassim	12.2	14.8	19.5	23.6	29.2	32.9	33.9	33.7	31.6	25.7	19.5	14.1	21.5
Eastern	Dhahran	15.8	17.0	20.8	27.5	31.3	34.5	36.0	35.7	33.2	29.0	23.4	17.8	26.7

Table 3. Average mean monthly and annual rainfall of different regions of Saudi Arabia (10 years averages).

Region	Met. Station	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Annual Average
									MM					
Southwestern	Taif Khamis-	9.3	5.7	19.8	29.8	34.8	4.5	1.5	6.3	5.2	6.0	26.8	6.5	156.2
	Mushait	8.1	16.8	52.9	34.2	34.7	7.3	23.0	18.1	7.5	0.4	18.1	21.6	242.0
	Abha	119.3	3.4	15.6	48.0	147.5	19.9	32.6	168.7	36.5	44.4	18.4	0.9	655.2
Central	Riyadh	18.9	4.5	29.4	36.3	16.5	0	1.0	0.1	0	0	3.9	7.7	119.3
	Qassim	19.4	8.7	21.7	25.1	8.5	0	0	0	0	1.0	21.1	18.6	125.0
Eastern	Dhahran	15.5	10.9	10.7	8.9	1.8	0	0	0	0	0	9.1	14.5	71.4

IRGA was supplied through a portable generator and a stabilizer.

Protein was determined by Kjeldahl N × 6.25. Kjeldahl N was determined on the aboveground parts of plants at vegetative and flowering stages. Similarly, total nonstructural carbohydrates (TNC) were determined on aboveground parts of plants according to the method described by Smith (1969).

Results and Discussion

Table 4 shows the water potentials of soil and different species from the 3 sites. In southwestern region 2 species namely *Eragrostis braunii* and *Hyperrhenia hirta* maintained higher water potential than the other species from the same site. *Panicum turgidum* and *Astenatherum fragilis* from the eastern region and *Panicum turgidum* from the central region maintained high water potentials (less negative) during the vegetative stage. Soil water potentials in the southwestern region were higher than in the central or the eastern region, but in all the locations it was beyond the sensitivity level of the thermocouple psychrometer. The water potentials of all the species at the 3 locations were lower (more negative) during the flowering stage than the vegetative stage. The same species that maintained high water potentials during vegetative stage also maintained high water potentials during flowering stage.

The decline in water potentials of aboveground parts of plants during flowering stage could be attributed to the depletion of soil water potentials as well as to the increased demand by the developing inflorescence. Most of these species, especially in the central and eastern regions, have a very short growing season. The vegetative stage is usually completed within 1 or 2 months following the event of rainfall. The flowering stage once initiated under favorable soil moisture conditions continues through a number of dry months. During this period most of the grain-bearing tillers slow down their vegetative growth and the developing inflorescence become the major sink for water and mineral resources.

The stomatal resistance and rate of transpiration of various grass species are given in Table 5. *Andropogon distachyus* and *Chrysopogon plumullosus* in the southwestern region, *Astenatherum fragilis* in the eastern and *Panicum turgidum* in the central region encountered higher stomatal resistance and correspondingly lower transpirational losses than the remaining species. Maintenance of high water potentials during periods of prolonged

Table 4. Water potentials of dominant grasses at vegetative and flowering stages.

Location	Species	Water Potential		Soil Water Tension	
		Vegetative	Flowering	Vegetative	Flowering
		bars		bars	
Southwestern	*Andropogon distachyus*	−20	−25		
	Chrysopogon plumulosus	−18	−20	>−30	>−30
	Eragrostis braunii	−15	−20		
	Themeda triandra	−23	−25		
	Hyperrhenia hirta	−14	−16		
Eastern	*Panicum turgidum*	−16	−18		
	Astenatherum fragilis	−14	−17	>−50	>−50
	Stipagrostis plumosa	−32	−27		
Central	*Panicum turgidum*	−15	−17	>−50	>−50

Table 5. Stomatal resistance and transpiration of dominant grasses at vegetative and flowering stages.

Location	Species	Stomatal resistance Vegetative	 Flowering	Transpiration Vegetative	 Flowering
		S/CM		mg/dm²/h	
Southwestern	*Andropogon distachyus*	10.5	18.7	2.4	0.8
	Chrysopogon plumulosus	8.7	15.8	3.5	1.2
	Eragrostis braunii	7.5	12.7	4.7	1.5
	Themeda triandra	6.5	10.7	5.8	1.7
	Hyperrhenia hirta	5.7	12.5	5.3	1.4
Eastern	*Panicum turgidum*	5.6	11.8	6.2	0.9
	Astenatherum fragilis	7.2	12.5	4.2	1.2
	Stipagrostis plumosa	5.3	11.3	4.8	1.8
Central	*Panicum turgidum*	8.3	15.8	2.8	1.1

dry season is one of the strategies developed by drought-avoiding plants to economize on the available water (Hsiao and Acevedo 1974, Bamberg et al. 1975, Stocker 1960, Teare et al. 1973).

Stomatal resistance of all the species was considerably greater during flowering stage than during vegetative stage and correspondingly the rate of transpiration was also lower than the vegetative stage. Plants adapted to the extreme environmental stresses adjust their stomatal conductance and water potential during rainless period to conserve water for the developng inflorescence. It was mentioned earlier that due to the prolonged seed development period, these plants utilize the water already present in the root-shoot system more efficiently. There is also the possibility of atmospheric moisture becoming available to these plants as a result of condensates at night when temperature are considerably lower than in the day time.

It is not clear from this study how stomatal adjustment is maintained to counteract the increasing atmospheric evaporative demand during the hotter parts of the day. Whether stomata close completely or partially and the degree of density of stomata have not been studied in these plants. However, a number of studies have shown stomatal regulation under drought or under high temperature and water stress conditions (Cowan 1977; Evenari et al. 1975; Frank and Barker 1976; Schulze et al. 1972, 1973).

Rate of photosynthesis of a few species studied (Table 6) was higher during vegetative stage than during flowering stage. At the same time, the water-use-efficiency was higher during flowering stage than the vegetative stage (Table 7). The higher photosynthetic rates could be attributed to the presence of more photosynthetic surface and more availability during the vegetative stage. Since the vegetative stage lasts for a few weeks, these plants, therefore, take advantage of the available water by increasing the rate of photosynthesis. At flowering stage, the higher water-use-efficiency again indicates the adaptive strategy of these plants economizing on the available water. Generally, these rates of photosynthesis are lower than those of other desert plant species (Bamberg et al. 1975, Ludlow and Wilson 1972, Berry 1975, Fischer and Turner 1978, Bjorkman et al. 1972). In fact, many desert plant species are there not for the purpose of increased productivity but merely for survival and these rates are adequate enough to maintain the perpetual survival and existence of their progenies.

Table 6. Photosynthesis of dominant grasses during vegetative and flowering stages.

Location	Species	Photosynthesis Vegetative	 Flowering
		$mgCO_2/dm^2/h$	
Eastern	*Panicum turgidum*	10.5	7.3
	Astenatherum fragilis	8.2	5.8
	Stipagrostis plumosa	7.8	4.5
Central	*Panicum turgidum*	11.8	8.7

Table 7. Ratio of transpiration/photosynthesis at vegetative and flowering stages.

Location	Species	Transpiration / Photosynthesis Vegetative	 Flowering
Eastern	*Panicum turgidum*	590	123
	Astenatherum fragilis	512	206
	Stipagrostis plumosa	615	400
Central	*Panicum turgidum*	237	126

In Table 8 are given the protein and carbohydrate contents of the aboveground parts of plants (flowers not included) during the vegetative and flowering stages. All the species were higher in both protein and carbohydrates during the vegetative and flowering stages. All the species were higher in both protein and carbohydrates during the vegetative stage than the flowering stage. *Panicum turgidum, Andropogon distachyus* and *Hyperrhenia hirta* exhibited higher protein content than the other species. The amounts of protein in these species is considerably higher than many desert grass species.

The decline in both protein and carbohydrates of leaves and stems during the flowering stage could be due to the translocation of these energy rich sources to the developing inflorescence. Total nonstructual carbohydrates at any time during the growth of these plants appear to be very low as compared to other species of the same taxonomic group.

TNC is a readily available source of energy and it appears that these are being used constantly by the plants and do not accumulate in any appreciable amounts in the aboveground parts or are translocated as reserves to the below-ground parts for use during stress or during regrowth. Data on the contents of below-ground parts are not available at the time of writing of this article.

These preliminary data on the physiological adaptation of desert grasses clearly indicate that these plants have developed strategies to cope with the adverse climatic conditions. Adjustment to the harsh environment is brought about by a particular parameter at different stages of development. The adaptive strategies such as stomatal regulation, leaf water potential, rate of photosynthesis etc., are adjusted according to the stress involved and the stage of maturity of the plants. How these changes are brought about and what are triggering mechanisms for signaling these changes are not known.

It is too soon to draw any definite conclusion about the real adaptive mechanisms of these plants. This preliminary data especially in the extreme arid environment are not enough to develop hypotheses describing the relationships between the state and the driving variables. However, study of this nature has not been

Table 8. Protein and carbohydrates of dominant grasses during vegetative and flowering stages.

		Protein		Carbohydrates	
Location	Species	Vegetative	Flowering	Vegetative	Flowering
		%		%	
Southwestern	*Andropogon distachyus*	7.8	5.7	6.5	4.8
	Chrysopogon plumulosus	6.5	4.8	5.8	4.2
	Eragrostis braunii	5.2	4.2	4.5	3.2
	Themeda triandra	4.8	3.2	6.7	4.7
	Hyperrhenia hirta	8.5	6.3	7.2	5.8
Eastern	*Panicum turgidum*	10.5	8.2	7.5	6.2
	Astenatherum fragilis	8.2	7.2	6.7	5.2
	Stipagrostis plumosa	6.8	5.5	5.2	4.3
Central	*Panicum turgidum*	9.7	7.2	7.3	5.8

reported anywhere on the desert grasses in Saudi Arabia. Thus it is considered important to indicate the trends in magnitude of the physiological parameters undergoing adjustment during the phenological stages under the harsh environment of the Kingdom.

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SRM Election Results

The Elections Committee Acting Chairman, Thane Johnson, along with several other Colorado Section members, counted the ballots for new officers on Monday, December 8, 1986, at the Society for Range Management headquarters. Elected officers are:

Second Vice-President—**Thomas E. Bedell**

Directors (1987-1989)—**Marilyn J. Samuel** and **Kenneth D. Sanders**

Directors Samuel and Sanders will replace retiring Directors Hunter and Whetzell in February 1987.

Ballots and tally sheets are retained in the Denver office for one year for review. Approximately 30% of the membership voted.

Relationship of Saltbush Species to Soil Chemical Properties

HARMON S. HODGKINSON

Abstract

The relationship of pure stands of 6 saltbush species to sodium adsorption ratio, electrical conductivity, and alkalinity are documented. The data gathered were obtained while correlating soils to range sites for National Cooperative Soil Surveys. Soil scientists gathered detailed soil information and obtained lab data. Range conservationists correlated the saltbush species to specific soils and by using lab data made a direct relationship to pure saltbush stands. Species ranked from highest to lowest adaptability to SAR, EC, and pH are: mat saltbush *(Atriplex corrugata* S. Wats.), mound saltbush *(A. obovata* Moq.), Castle Valley clover *(A. cuneata* A. Nels.), sickle saltbush *(A. falcata* (M.E. Jones) Standl.), shadscale *(A. confertifolia* (Torr. & Frem.) S. Wats.) and fourwing saltbush *(A. canescens* (Pursh) Nutt.). By knowing the SAR, EC, and pH tolerances of these 6 species, interpretations for inventorying, rating plant community potentials, and applying range improvements will be achieved with greater success.

Key Words: ***Atriplex communities, soil analysis (chemical), saltbush adaptability, soil-plant relationships***

Salt-desert shrub communities of the Intermountain West cover some 16 million ha of rangeland within the Great Basin Desert (Holmgren and Hutchings 1972). Studies have been conducted for more than 70 years on the description and ecology of salt-desert shrub communities (Billings 1945, 1949; Blaisdell and Holmgren 1984; Blauer et al. 1976; Fautin 1946; Hutchings and Stewart 1953; Kearney et al. 1914; Shantz and Piemeisel 1940; Singh 1967; Stewart et al. 1940; Tiedemann et al. 1984; Vest 1962; Wagner and Aldon 1978; West and Ibrahim 1968; and Wood 1966). Many of these salt-desert plant communities are in pure stands of single species while others occur as a mixture of species.

There are many factors that develop the often distinct boundaries of salt-desert plant communities. West (1982) attributes this to the fact that the salinity and aridity tolerance levels of various species cause a sorting effect along a moisture and salinity gradient. Branson et al. (1967) observed soil-moisture relationship and soil salts as the primary cause of different plant communities. In western Utah, Gates et al. (1956) established differences between soils and salt-desert plants, but concluded that no specific soil factor limited each species range as there was an overlap of the soil factors measured. However, there were different amounts of salt and sodium between the soils of each species. Billings (1949) found salt-desert shrub soils to have carbonates accumulating just below the surface and the presence of salts in the subsoil.

Saltbush species have been studied along with other salt-desert plants in relation to soluble salts, sodium, pH, and other soil characteristics (Blauer et al. 1976; Hansen 1962; Naphan 1966; Welch 1978; and West and Ibrahim 1968). However, correlation of species directly to sodium adsorption ratio (SAR), electrical conductivity (EC), and alkalinity (pH) is lacking. The purpose of this study was to document the relationship of 6 saltbush species to SAR, EC, and pH on the soils where they occurred as the dominant shrub in pure stands.

Study Area and Methods

The study was conducted while correlating soils to range sites in cooperation with National Cooperative Soil Surveys. The sample sites within the soil surveys are located in northeastern Arizona and northwestern New Mexico as shown in Figure 1.

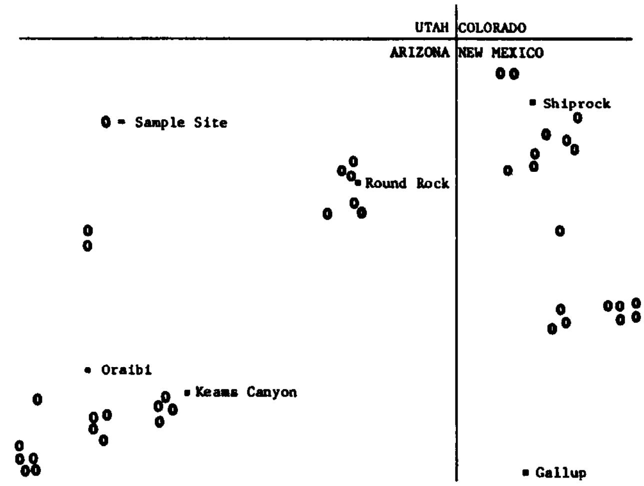

Fig. 1. *General location of sites sampled in northeastern Arizona and northwestern New Mexico.*

The climate is arid and semiarid. Average annual precipitation ranges from 13 to 25 cm with a great variation from year to year. About 55% of the moisture occurs during the fall-winter-spring months. Forty-five percent occurs as summer thundershowers from moist tropical air from the Gulf of Mexico. Winds occur in the spring and usually precede the summer storm fronts. Elevations range from 1,463 to 1,859 m.

During the soil mapping process, soil scientists gathered detailed soil profile descriptions and soil samples for analyzing chemical properties and assisting in classifying the soil. The samples were sent to the Bureau of Indian Affairs soils lab in Gallup, N. Mex., or the Soil Conservation Service National Soil Survey Laboratory, Lincoln, Neb., for analysis. From the lab reports, the SAR, EC, and pH were obtained.

At each soil sampling location, the saltbush species present were recorded. The 6 species identified in the study area were fourwing saltbush (*Atriplex canescens* (Pursh) Nutt.), sickle saltbush (*Atriplex falcata* (M.E. Jones) Standl.), Castle Valley clover (*Atriplex cuneata* A. Nels.), mat saltbush (*Atriplex corrugata* S. Wats.), mound saltbush (*Atriplex obovata* Moq.), and shadscale (*Atriplex confertifolia* (Torr. & Frem.) S. Wats.). Soils having similar characteristics and a corresponding plant community were grouped together. Using the lab data, the SAR, EC, and pH values were compared and correlated to each saltbush species. In a sodic soil, the SAR indicates the sodium amounts that affect soil properties and may interfere with plant growth. A high EC in a saline soil contains soluble salts that may interfere with plant growth. A pH value of 7.4 or more indicates an alkaline soil.

Results and Discussion

During soil surveys, soil scientists and range conservationists work together in correlating and grouping soils to range sites. A main purpose for this correlation of surveys on rangeland is to aid in interpretations of the soil capabilities and vegetation potentials for use and management. It was during this correlation process

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that it became apparent that pure stands of saltbush with associated species occurred on soils each having distinct chemical characteristics.

Naphan (1966) reported the most important soils occurring in the salt-desert shrub ecosystem were of the Aridisols and Entisols orders within the National System of Soil Classification. The soils sampled in the study area are of the Aridisols and Entisols orders. All species of saltbush occurred in both orders and sometimes occurred in the same family and subgroups. However, there was a distinct difference in the SAR, EC, and pH of the soils that corresponded to the pure stands of each saltbush species (Table 1).

A summary of each saltbush species depth, position on the landscape, and associated plants; and the soils sodicity, salinity, and alkalinity (Fig. 2) follows:

Mat saltbush occurred on moderately deep and deep soils on hillslopes, ridges, footslopes, knolls, and toeslopes of undulating plateaus. It was always the dominant plant species. Other plants present in minor amounts were alkali sacaton (*Sporobolus airoides* (Torr.) Torr.), Indian ricegrass (*Oryzopsis hymenoides* (Roem. & J.A. Schultes) Ricker Ex Piper), and bottlebrush squirreltail (*Sitanion hystrix* (Nutt.) J.G. Smith). The soils were moderately to strongly sodic; slightly to strongly saline; and moderately to strongly alkaline.

Mound saltbush occurred on deep soils on alluvial fans, stream terraces, and fan terraces. The major plants associated with mound saltbush in order of dominance were: alkali sacaton, galleta (*Hilaria jamesii* (Torr.) Benth.), bottlebrush squirreltail, and western wheatgrass (*Agropyron smithii* Rybd.). Black greasewood (*Sarcobatus vermiculatus* (Hook.) Torr.) and ribscale (*Atriplex powellii* S. Wats.) were sometimes present. The soils were moderately to strongly sodic; very slightly to moderately saline; and moderately alkaline.

Castle Valley clover occurred on moderately deep and deep soils on toeslopes below mesas and cuestas, and small benches of undulating plateaus. Associated plants in order of dominance were Indian ricegrass, alkali sacaton, galleta, and sand dropseed (*Sporobolus cryptandrus* (Torr.) Gray). The soils were slightly to moderately sodic; very slightly to moderately saline; and moderately to mildly alkaline.

Sickle saltbush occurred on shallow soils on knolls and footslopes below cuestas and low mesas. Associated plants in order of dominance were alkali sacaton, Indian ricegrass, galleta and minor amounts of hairy coldenia (*Coldenia hispidissima* (Torr. & Gray) Gray). The soils were slightly sodic; slightly saline; and moderately to mildly alkaline.

Shadscale occurred on very shallow, shallow, moderately deep, and deep soils on fan terraces, hillslopes, and undulating plateaus and structural benches. Galleta was the dominant associated plant. Others were alkali sacaton, Indian ricegrass, and bottlebrush squirreltail. The soils were slightly to moderately sodic; non-saline to slightly saline; and moderately alkaline.

Fourwing saltbush occurred on deep soils on alluvial fans and stream terraces. Associated plants in order of dominance were Indian ricegrass, galleta, bottlebrush squirreltail, western wheatgrass, and Greene rabbitbrush (*Chrysothamnus greenei* (Gray) Greene). The soils were slightly sodic; non-saline to very slightly saline; and mildly alkaline.

Conclusions

Each saltbush species has adapted to certain soil chemical properties. During the soil mapping-plant community correlation process, management units can be established which will identify those species most adapted to each unit.

By knowing the SAR, EC, and pH tolerances for the 6 species, interpretations can be made as to suitability of sites for a particular species.

By matching the saltbush to its adapted SAR, EC, and pH, a higher quality of management can be expected. Range management techniques will be achieved with greater success, whether it be a grazing system, seeding or other range improvement project.

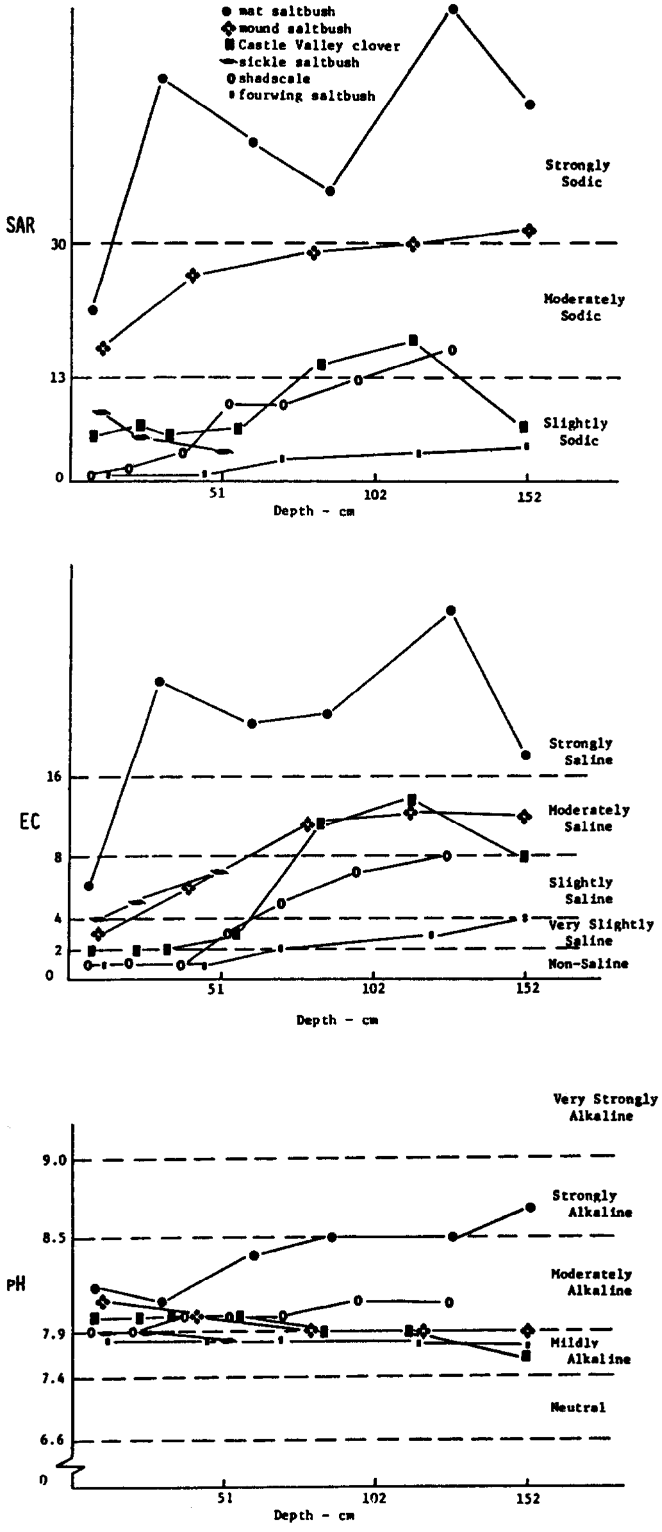

Fig. 2. *The relationship of 6 saltbush species to SAR, EC, and pH.*

Specific data on SAR, EC and pH tolerances should be very useful in reclaiming disturbed areas where the values of these factors are believed to be high enough to influence normal plant establishment and growth. Data on tolerance values should be

Table 1. Composite of soil samples taken for each species.

No. of Samples	Species	Soil Family and Subgroup	Depth cm	SAR avg	EX×10^3 avg	pH avg
5	Mat Saltbush	fine, mixed (calcareous), mesic Typic Torriorthents	0–8	22	6	8.2
			8–30	62	28	8.1
			30–61	46	23	8.4
		fine-silty, mixed (calcareous), mesic Typic Torriorthents	61–86	37	24	8.5
			86–127	83	37	8.5
			127–152	57	19	8.7
32	Mound Saltbush	fine, montmorillontic, mesic Typic Natrargids	0–10	17	3	8.1
			10–41	26	6	8.0
		fine-loamy, mixed (calcareous), mesic Typic Torrifluvents	41–81	29	10	7.9
			81–114	30	12	7.9
			114–152	32	11	7.9
		fine-loamy, mixed mesic, Typic Camborthids				
		fine-loamy, mixed, mesic, Typic Natrargids				
		fine, mixed, mesic Typic Camborthids				
10	Castle Valley Clover	fine-silty, mixed (calcareous), mesic Typic Torriorthents	0–8	6	2	8.0
			8–23	7	2	8.0
			23–33	6	2	8.0
		coarse-silty, mixed (calcareous) mesic Typic Torriorthents	33–56	7	3	8.0
			56–84	15	10	7.9
		coarse-silty, mixed, mesic Typic Camborthids	84–114	18	13	7.9
			114–152	7	8	7.6
		fine-silty, mixed, mesic Typic Camborthids				
7	Sickle Saltbush	loamy, mixed (calcareous), mesic, shallow Typic Torriorthents	0–10	9	4	7.9
			10–23	6	5	7.9
			23–51	4	7	7.8
18	Shadscale	fine-loamy, mixed, mesic Typic Haplargid	0–8	1	1	7.9
			8–20	2	1	7.9
		fine, mixed, mesic Ustollic Haplargid	20–38	4	1	8.0
			38–53	10	3	8.0
		fine-loamy, mixed, mesic Haplic Natrargids	53–71	10	5	8.0
			71–97	13	7	8.1
		coarse-loamy, mixed, mesic Calcic Gypsiorthids	97–127	17	8	8.1
		fine-silty, mixed mesic Typic Camborthids				

Table 1. Continued

No. of Samples	Species	Soil Family and Subgroup	Depth cm	SAR avg	EX×10^3 avg	pH avg
15	Fourwing Saltbush	coarse-loamy, mixed (calcareous) mesic Typic Torriorthents sandy over loamy, mixed (calcareous) mesic Typic Torriorthents fine-loamy, mixed, mesic Ustollic Camborthids fine-loamy, mixed, mesic Typic Camborthids coarse-loamy, mixed mesic Typic Calciorthids	0–13	1	1	7.8
			13–46	1	1	7.8
			46–71	3	2	7.8
			71–117	4	3	7.8
			117–152	5	4	7.7

especially valuable to those involved in mine reclamation efforts.

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C_3/C_4 Production Shift on Seasonal Burns—Northern Mixed Prairie

ALLEN A. STEUTER

Abstract

This study investigates the potential of fire to manipulate the balance of C_3 (cool-season) and C_4 (warm-season) herbage in 2 northern Mixed Prairie communities. The xeric high prairie community and mesic low prairie community were chosen to represent regional moisture extremes. Treatments included dormant spring burn, mid-summer burn, dormant fall burn, and untreated. The high prairie community appears to be a C_3-dominant type. All 3 burn treatments increased the C_3 herbage fraction relative to untreated sites. Total production, however, was unaffected by treatment. The C_3/C_4 ratio of high prairie communities appears to be the result of long-term adaptation rather than short-term adjustments to fire or weather effects. Spring burning shifted low prairie communities towards C_4 herbage relative to other treatments. This was due to an increase in C_4 herbage (and total) rather than to a decrease in C_3 herbage. The C_3/C_4 ratio of low prairie communities did appear to respond to short-term adjustments in moisture, temperature, and light caused by the spring burn. The response of low prairie C_3/C_4 ratios to mid-summer and dormant fall burns appeared to be related to phenological and indirect weather effects rather than to changes in site microclimate caused by the fires.

Key Words: fire effects, herbage accumulation, δ ^{13}C ratio

Native rangelands of the northern Mixed Prairie region have the potential to provide wild and domestic herbivores with diverse, high quality forage throughout the growing season. Northern Mixed Prairie is characterized by a complex of native mid-height and shortgrass species with C_3 (cool-season) and C_4 (warm-season) photosynthetic pathways (Dix and Smeins 1967, Ode et al. 1980, Singh et al. 1983). C_3 species dominate region-wide. Tallgrass (C_4) species can be locally important on sites remaining moist during the short warm season (Barnes et al. 1983). The eastern ranges of the northern Mixed Prairie can shift strongly towards exotic C_3 species under repeated rest, overgrazing, or summer haying. Maintaining herbage production from 2 temporal guilds with distinct seasonal growth curves should increase nutrient availability for herbivores, while minimizing production declines from seasonal drought.

Several authors (Ehleringer 1978, Teeri and Stowe 1976, Tiezen et al. 1979) have documented predictable relationships in the field between microclimate, latitude, and elevation and C_3 and C_4 plant distribution. In general, C_4 species appear better adapted to the warmer and drier sites with high light intensities and lower leaf CO_2 concentrations. However, Baskin and Baskin (1985) suggest that photosynthetic pathway is only one of a suite of factors determining success or failure of a plant taxon in a particular environment.

In addition to climate, grazing and fire were major factors influencing community structure and function in the pre-settlement northern Mixed Prairie (Hanson 1984, Higgins 1984, Moore 1972). The season and intensity of fire and grazing events were probably interdependent (Steuter 1986). Herbage removal by either event would modify site microclimate (Redmann 1978, Savage and Vermeulen 1983, Owensby and Anderson 1967), and thus growth conditions for C_3 and C_4 species. Ode et al. (1980) and Singh et al. (1983) suggest that grazing will shift northern Mixed Prairie towards C_4 species. Fire suppression may result in accumulation of dead material and self-shading favoring C_3 species (Ode et al. 1980). Spring burning reduces the herbage density of northern Mixed Prairie (Huber and Steuter 1984) allowing more light into the foliage during the growing season. Although not as well documented as in the southern Mixed Prairie, the role of fire in manipulating species composition appears to have useful management implications depending on objectives and burn prescription (Dix 1960, Engle and Bultsma 1984, Gartner et al. 1978, White and Currie 1983).

Native communities with appropriate C_3/C_4 herbage production should meet the diversity and forage quality objectives of natural area and range livestock managers, respectively. The objective of this study was to determine the influence of fire on the production dynamics of C_3 and C_4 plant guilds within 2 communities of the northern Mixed Prairie.

Study Area and Methods

The study was conducted on the Samuel H. Ordway, Jr. Memorial Prairie. This north-central South Dakota (45° 43′ N, 99° 06′W) preserve is a 3,076-ha native grassland owned and managed by The Nature Conservancy. Vegetation has been characterized as northern mixed-grass (Weaver and Albertson 1956). The preserve lies just west of the narrow Tallgrass Transition zone of Küchler (1964). Geology of the glaciated prairie pothole landscape has been described by Christensen (1977). The area has a continental climate of hot summers and cold winters with about 80% of the mean annual precipitation occurring during the April through September growing season. Precipitation during the 2-year study period was below the long-term average (Table 1). The September 1983 through August 1984 period was 18% below, and the September 1984 through August 1985 period was 35% below average precipitation. Spring 1985 was well above average in temperature.

Table 1. Actual cool season (9/1 to 5/31) and warm season (6/1 to 8/31) precipitation (cm) during the study period, and deviation (cm) from the long-term average.

	9/1/83 to 5/31/84	6/1/84 to 8/31/84	9/1/84 to 5/31/85	6/1/85 to 8/31/85	Total
Study Period[1]	24.9	15.7	20.8	11.6	73.0
Deviation from long-term-average[2]	−3.7	−5.2	−7.9	−9.2	−26.0

[1]Recorded at gauge 0.75 km from study plots.
[2]Recorded at U.S. Weather Station (18 yr) Leola, SD-16 km east of site.

The study site consisted of a 0.4-ha, 22° south-facing slope within a 97-ha pasture. The pasture had been ungrazed since May 1982, lightly grazed (0.12 to 0.18 AUM/ha) by bison during October through May from 1980 to 1982, and moderately grazed (0.25 to 0.32 AUM/ha) by cattle during May through October prior to 1980. Plant communities on the study site ranged from a high prairie community on the 5° to 10° south-facing ridge crest through a mid prairie community (30° slope), to a low prairie community near the base of the slope (2° to 5°). This study is restricted to an evaluation of seasonal fire effects on the high

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Table 2. Description of fire treatments applied to two replications each within the study site—untreated not included. Values within the table are treatment means for n = 20 fuel load and % moisture, n = 2 ROS, and n = 4 FL.

Treatment	Date	Community	Fuel Load (g/m^2)	% Moisture[1] Dry Wt. Basis	Ros[2] (m/min)	FL[3] (m)
Summer Burn	8/3/83	High Prairie	339	70	0.4	0.3
		Low Prairie	612	134	0.2	0.2
Fall Burn	10/17/83	High Prairie	480	34	18.8	1.1
		Low Prairie	841	41	14.2	1.4
Spring Burn	4/19/84	High Prairie	433	27	24.0	1.2
		Low Prairie	753	34	21.4	1.8

[1] % moisture derived from composite fuel samples dried for 48 hr at 105° C.
[2] ROS = Rate of fire spread visually timed between two points.
[3] FL = Flame length visually estimated by two observers.

prairie and low prairie communities. Barnes et al. (1983) provide a detailed description of these plant communities on Ordway Prairie with nomenclature following Van Bruggen (1976).

The high prairie community occurred on Vida/Williams loams (silty range site). Vida/Williams loams are fine-loamy, mixed Typic Argiborolls. Major C_4 species are the gramas (*Bouteloua gracilis* (H.B.K.) Griffiths and *B. curtipendula* (Michx.) Torr.), little bluestem (*Andropogon scoparius* Michx.), and plains muhly (*Muhlenbergia cuspidata* (Torr.) Rydb.). Major C_3 species are needlegrasses (*Stipa comata* Trin. & Rupr. and *S. viridula* Trin.) sedges (*Carex filifolia* Nutt. and *C. eleocharis* Bailey), and western wheatgrass (*Agropyron smithii* Rydb.). Untreated high prairie sites had a mean of 302 g/m^2 of pre-1984 litter and standing dead on 28 May 1984 and 169 g/m^2 on 14 Sept. 1984. Pre-1984 litter and standing dead on burned treatments averaged 76 g/m^2 and 21 g/m^2 on the same dates, respectively.

The low prairie community is on a Bowbells loam (overflow range site). Bowbells soils are fine-loamy, mixed Pachic Argiborolls. Major C_3 species are big bluestem (*A. gerardi* Vit.) and switchgrass (*Panicum virgatum* L.). Major C_3 species are slender and western wheatgrass (*A. caninum* (L.) Beauv.), porcupine grass (*S. spartea* Trin.), and bluegrass (*Poa* sp. L.). Untreated low prairie sites had a mean of 907 g/m^2 of pre-1984 litter and standing dead on 28 May 1984 and 761 g/m^2 on 14 Sept. 1984. Pre-1984 litter and standing dead on burned treatments averaged 132 g/m^2 and 86 g/m^2 on the same dates, respectively.

The study site was divided into eight, 15-m by 40-m experimental units, each with a high and low prairie community. Experimental units were randomly assigned to 1 of 2 replications of 4 treatments. Treatments were dormant spring burn, mid-summer burn, dormant fall burn, and untreated (Table 2). Burn dates were designed to approximate peak seasonal fire probabilities based on fuel conditions and ignition sources (Higgins 1984, Moore 1972, Steuter 1986).

Herbage was clipped monthly from May to September in 1984, and at peak cool season (7 June—based on green needlegrass flowering) and warm season (31 July—based on big bluestem flowering) standing crop in 1985. Five sample points were systematically located in each community of each experimental unit. At each sample date a 0.10-m^2 quadrat was clipped radially from around each of the points. Care was taken to maximize the distance between clipped quadrats. The 5 clipped samples of each community/replication combination were air-dried and weighed, then composited and quartered. These reduced samples were sorted into green, current year dead, and past year dead components, then re-weighed. The green component was ground through a 40-mesh screen and stored in plastic canisters pending $\delta^{13}C$ analysis.

The relative contribution of C_3 and C_4 plants to seasonal green herbage was determined from $\delta^{13}C$ values obtained through mass spectrometer analysis (Tieszen et al. 1979, Troughton and Card 1975). Known C_3 and C_4 plants were analyzed to obtain mean $\delta^{13}C$ values (C_3 = −27.1%., C_4 = −11.4%.) of dominant species in the 2 communities sampled. These mean values were used to estimate the percent composition (C_3 vs C_4) of green herbage by treatment, community, and sample date. Data were analyzed using analysis of variance with Duncan's multiple range mean separation. Significant differences were identified at the 95% confidence level unless otherwise indicated.

Results

High Prairie Community

The percentage of C_3 herbage in the green component was highest during May and September and lowest during July and August for all treatments (Fig. 1). However, during mid-summer the untreated sites had the highest percentage of C_4 herbage in the green component (ca. 60%). The 3 seasonal burn treatments maintained greater than 50% C_3 herbage in the green component throughout the season. During the second season following the burn treatments there was no difference in the green C_3/C_4 percentages. The C_3 fraction on all treatments remained above 50% throughout the peak warm season growth period during the second dry year (Fig. 1).

Green herbage peaked during July of the first season, and June of the second season following burning of high prairie communities (Fig. 2). Total current year herbage (and green) was significantly reduced only on spring and fall burns at the first sample date (Table 3). This reduction was due almost exclusively to a lower C_3 contribution early in the first season following fall or spring burning. However, green C_3 herbage tended to be highest on the fall burns late in the first season. Total current year herbage on fall

Table 3. High Prairie—Total (green and dead) current year herbage (g/m^2) for treatments ($\bar{X}$) by sample date.

Treatment	Sampling Date						
	5/28/84	6/20/84	7/21/84	8/13/84	9/14/84——	6/7/85	7/31/85
Summer Burn 1983	75b[1]	127	215	200	167[2]	113	116
Fall Burn 1983	33a	109	223	234	181	107	88
Spring Burn 1984	36a	106	247	237	197	109	95
Untreated	71b	135	238	243	218	125	106

[1] Means within a column followed by the same letter, or no letter, are not significantly different ($P>0.05$).
[2] Summer Burn treatment less than Spring Burn and Untreated ($P<0.10$).

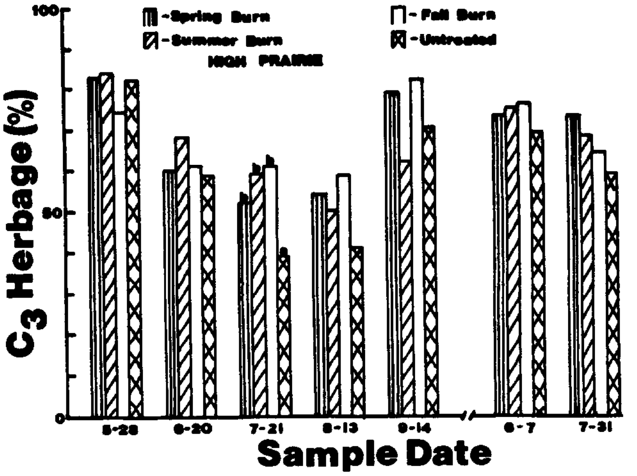

Fig. 1. *High Prairie—Seasonal progression of* C_3 composition for green herbage. The same or no letter atop bars within a sample date (1984–85) indicates treatment means are not different (P>*0.05).*

burned and untreated sites peaked in August of the first season, while the peak on spring and summer burned sites occurred in July (Table 3). Total current year herbage was lowest on summer burned treatments ($P<0.10$) at the end of the first growing season.

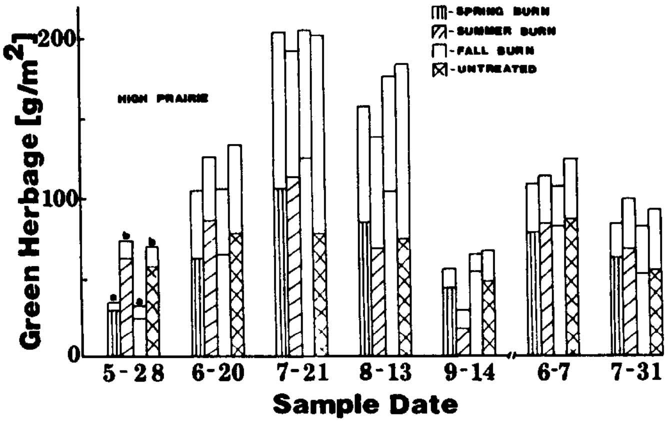

Fig. 2. *High Prairie—Seasonal progression of green herbage. The lower lined, slashed, open, and cross-hatched portion of bars represents the* C_3 *contribution, while the open upper portion represents* C_4 *contribution to green herbage. The same or no letter atop bars within a sampling date (1984–85) indicates treatment means are not different* (P>*0.05).*

Low Prairie Community

The C_3/C_4 ratio and herbage accumulation in low prairie communities were quite responsive to fire treatments (Fig. 3 and 4, Table 4). Again, May and September sample dates had the highest percentage of green C_3 herbage on all treatments (Fig. 3). The spring burn treatment had the highest percentage of green C_4 herbage (ca. 75%) throughout the warm-season growth period. By July the untreated sites had a C_4 herbage fraction similar to the spring burns (Fig. 3). During the September cool-season growth period, the summer burn and the untreated sites had the lowest percentage of green C_3 herbage. All treatments except the summer burn had a less than 50% green C_3 fraction during August of the first year following treatment. The spring burn continued to have the highest green C_4 percentage during the second year following treatment. Rapid growth of the C_4 guild contributed to the green herbage fraction at an earlier date than in the first year following spring burns (Fig. 3).

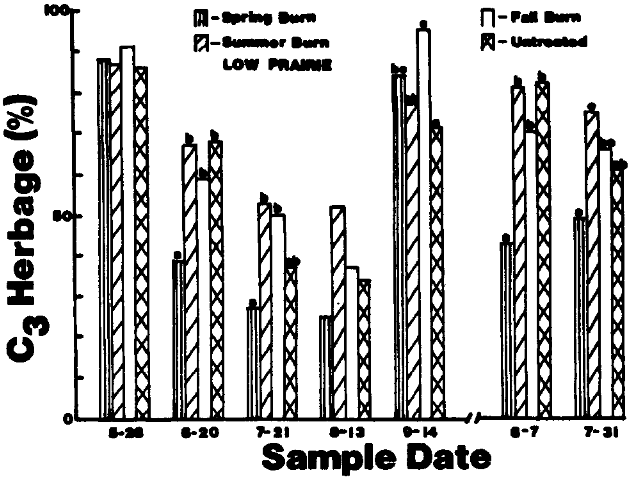

Fig. 3. *Low Prairie-Seasonal progression of* C_3 *composition for green herbage. The same or no letter atop bars within a sampling date (1984–85) indicates treatment means are not different* (P>*0.05).*

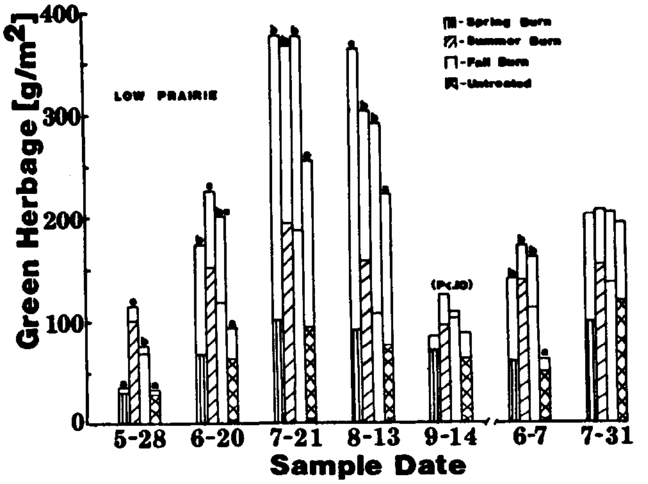

Fig. 4. *Low Prairie—Seasonal progression of green herbage. The lower lined, slashed, open, and cross-hatched portion of bars represents the* C_3 *contribution, while the open upper portion represents* C_4 *contribution to green herbage. The same or no letter atop bars within a sampling date (1984–85) indicates treatment means are not different* (P>*0.05).*

Table 4. Low Prairie—Total (green and dead) current year herbage (g/m²) for treatments ($\bar{X}$) by sample date.

	Sampling Date						
Treatment	5/28/84	6/20/84	7/21/84	8/13/84	9/14/84——	6/7/85	7/31/85
Summer Burn 1983	115c[1]	240c	426b	470b	373b	173b	221
Fall Burn 1983	76b	203b	425b	464b	414bc	162b	225
Spring Burn 1984	36a	178b	416b	497b	444c	141b	215
Untreated	33a	95a	288a	368a	294a	62a	215

[1] Means within a column followed by the same letter, or no letter, are not significantly different ($P>0.05$).

Spring burn and untreated sites had a slower herbage accumulation rate during the May and June period (Fig. 4). This was due primarily to lower C_3 herbage relative to summer and fall burns. High rates of C_4 accumulation during July and August resulted in equivalent, or higher, green and total herbage on spring burns relative to summer and fall burn treatments (Table 4). Growth rates on the untreated sites were substantially less than on burned treatments through August. On these low prairie sites, the summer and fall burn treatments maintained the nearest to a 50:50 ratio between C_3 and C_4 herbage during July and August. Total current year herbage on summer and fall burns was intermediate to the spring burn (highest) and untreated (lowest) sites at the end of the first season. However, spring burned and untreated sites had similar C_3 herbage throughout the season even though current herbage on the spring burns was 135% that of untreated sites during the August peak (Table 4).

Low prairie growth was reduced on all treatments during the second dry year (Table 4). The untreated sites had considerably less current herbage than any of the burn treatments during the cool-season growth period (Table 4). Green C_3 herbage was highest on summer burns, followed by fall and spring burns at the cool-season sampling date (Fig. 4). Untreated sites had the lowest C_3 green herbage, and proportionately much less C_4 herbage at the same date in the second season following treatment. Total current and green herbage was similar across treatments by the middle of the warm-season growth period in this second dry year. Summer burns had the highest C_3 green herbage at that time (Fig. 3).

Discussion

The changes in C_3/C_4 herbage following burning were not always explained by the expected treatment effects on site moisture, temperature, and light status. The C_3/C_4 ratio of high prairie during the cool-season growth period was generally unaffected by burning. Unlike the silty range sites studied by Engle and Bultsma (1984), Kentucky bluegrass *(Poa pratensis* L.) was a minor component of the high prairie community of this study. The large reduction in this exotic C_3 species reported by these authors following late spring burning may have affected the C_3/C_4 ratio. The increase in C_3 herbage on all 3 burn treatments (current study) relative to untreated sites during the warm-season growth period was unexpected. These results are contrary to the hypothesis of Ode et al. (1980) that reduced fire frequencies would favor C_3 species due to increased self-shading and cooler soil temperatures. I interpret the current results as being indicative of a native C_3 guild well adapted to the primary pre-settlement fire seasons. The C_4 species present in high prairie communities appear to be less well adapted to fire disturbance on these dry northern sites. The over-riding influence of a northern continental climate and general dominance of the C_3 pathway produce fire effects quite dissimilar to those from even the extreme northern range of the southern Mixed Prairie (Schacht and Stubbendieck 1985).

The shift to C_3 herbage resulting from burning high prairie appears short lived. The trend towards an increasing C_3 fraction on all treatments during the second dry year emphasizes the dominance of the native C_3 guild. The C_4 guild within high prairie communities appears unable to respond positively to short-term site warming, drying, or increased light whether resulting from fire or weather. The use of fire alone to improve the C_4 herbage component of high prairie communities does not appear feasible. Selective use of C_3 species by herbivores following a fire may improve the competitive position of the C_4 guild above that realized from fire alone (Ode et al. 1980).

Unlike high prairie communities, the species in the C_4 guild of low prairie communities dominate with the increased light and warmer site conditions produced by dormant spring fires. Similar results have been reported following spring burning in a drought year by Engle and Bultsma (1984). Whether this effect continues past the second year is unknown since mulch build-up is rapid in the absence of grazing. The negative phenological impact of the mid-summer burn treatment on the C_4 guild completely over-rode the benefits of higher irradiance and a warmer, drier site. The result of these summer burns was a C_3 dominated low prairie community through the second dry season. The large C_3 fraction on summer burns is especially impressive when compared to the much lower C_3 herbage on the heavily mulched untreated sites.

Why low prairie communities treated with dormant fall burns did not respond more similarly to dormant spring burns is not readily apparent. An obvious difference in the C_3 component of summer versus fall burn treatments was the near absence of Kentucky bluegrass in the fall burns, while summer burns were heavily infested. Yet, fall burned treatments had a C_3 fraction more similar to the summer burns than to the spring burns. This suggests that fall burned treatments had a stronger native C_3 component than summer burns. The fall burn treatments should have been phenologically neutral relative to C_3 and C_4 guilds—similar to the spring burns. Fall burning was as effective as spring burning in removing mulch. Thus light intensity and soil temperatures should have been similar. December 1983 was one of the coldest on record and lack of insulating mulch on the fall burns may have resulted in winter kill of C_4 tallgrasses, and exotic C_3 species. More information is needed on the role of fall burning since this was a peak pre-settlement fire season for much of the northern Mixed Prairie (Moore 1972, Steuter 1986).

The topographic position of low prairie communities (Barnes et al. 1983) insures that they are subirrigated throughout all but the driest growing seasons (e.g., year two of this study). High and mid prairie communities occur on sites characterized by limited soil moisture following the spring rainy season (Dix and Smeins 1967). Unpublished data for Ordway Prairie indicate that optimum soil temperatures for C_4 species growth may be restricted to the July and August period. The co-occurrence of reliable soil moisture and warm soil temperatures results in the potential for the C_4 guild to dominate low prairie communities managed with dormant spring burning even though the region is C_3 dominated. C_4 herbage on spring burns was nearly twice that of untreated sites with 2 years mulch accumulation. The enhancement of the C_4 guild was dramatized by its rapid early growth during the second dry growing season. The summer and fall burned treatments suggest that if the C_4 guild is suppressed or poorly represented, burning will just as effectively enhance C_3 growth relative to untreated sites with heavy mulch loads.

Low prairie communities are more restricted in size and distribution than high and mid prairie communities. However, when present, their productivity is double that of most other northern mixed grass types. Increasing the C_4 (warm-season) herbage from this community with the judicious use of spring burning will provide a more balanced forage resource on C_3 (cool-season) dominated northern Mixed Prairie ranges. As with high prairie communities, the interactive effects of grazing following burning may enhance or negate the simple effects of burning.

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Influence of Clipping Frequency on Herbage Yield and Nutrient Content of Tall Wheatgrass

D. J. UNDERSANDER AND C. H. NAYLOR

Abstract

Grazing or cutting frequency has been shown to affect yield and quality of many grasses, but similar data are lacking for tall wheatgrass [*Agropyron elongatum* (Host) Beauv. 'Jose']. The objective of the research was to determine the effect of frequency of clipping on tall wheatgrass. The study was conducted at the Texas Agricultural Experiment Station at Bushland, Texas, in 1979, 1980, 1981, and 1984 on a Pullman clay loam soil. Plots were irrigated as needed from February to the end of the growing season and fertilized with 112 kg N/ha every 2 months for maximum yield and clipped either every week, 2 weeks, of 4 weeks at a 5-cm stubble height. Herbage yield was highest from spring harvests and declined over summer as is typical of cool-season grasses. The plots that were clipped every 4 weeks produced greater herbage yields than plots that were clipped 1 or 2 weeks, suggesting that rotational grazing would increase productivity. The nutrient content of the herbage was highest during summer when herbage yield was lowest. Plants clipped less frequently had the highest concentrations of phosphorus and potassium and the lowest concentrations of calcium and magnesium. The greatest differences in nutrient content occurred among years, which emphasizes the importance of continual herbage analysis to optimize mineral supplementation of grazing cattle.

Key Words: *Agropyron elongatum*, nitrogen, phosphorus, potassium, calcium, magnesium

The dry winter and wet summer precipitation pattern of the Southern Plains favors warm-season grasses. Cattle are grazed on wheat (*Triticum aestivum* L.) pasture during the early November to mid-March period prior to the time when warm-season grasses are available for grazing. This void in available pasture has increased interest in cool-season grasses, particularly where supplemental irrigation is available. In recent years, tall wheatgrass [*Agropyron elongatum* (Host) Beauv.] has been grown on many hectares in the Southern Plains. This cool-season grass begins growth early in March most years and provides pasture near the time cattle are taken off wheat pasture. Little information is available on the management of this grass in the Southern Plains. Schuster and Garcia (1973) reported tall wheatgrass to be the easiest to establish of several cool-season species evaluated in the Texas Panhandle. They further reported that tall wheatgrass would be available for grazing in late September through November until wheat was available for grazing and that it could be grazed in the spring beginning in April when the cattle are removed from wheat pasture. They found that tall wheatgrass survived under dryland conditions when other cool-season grasses, that yielded more under full irrigation, did not survive.

Clipping has been shown to increase herbage yields of some species, (Drawe et al. 1972, Eck et al. 1975, Svejcar and Rittenhouse 1982) while clipping too frequently reduced yields and reduced plant survival of crested wheatgrass (Carter and Law 1948) and of rough fescue (McLean and Wikeem 1985). Pitman and Holt (1983), when evaluating 2-, 4-, and 8-week harvest frequencies of kleingrass (*Panicum coloratum* L.), green sprangletop

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(*Leptochloa dubia* (H.P.K.) Nees), and plains bristlegrass (*Setaria macrostachya* H.P.K.), found that the 8-week clipping frequency generally increased dry matter production of the grasses, and also found that the 4-week harvest frequency produced optimum yields of highly digestible, leafy herbage.

Similar information on the effects of clipping frequency is not available for tall wheatgrass. Further, there is little information on seasonal changes or effects of frequency of clipping or grazing on nutrient content. Such information may be useful for suggesting supplementation regimes for cattle grazing tall wheatgrass.

The objectives of this research were to evaluate the effect of frequency of clipping on yield and nutrient content of tall wheatgrass over the growing season.

Materials and Methods

Tall wheatgrass cv. 'Jose' was established in pure stands in level bordered field plots during the fall of 1978 and 1983. The soil was a Pullman clay loam (fine, mixed, thermic Torrertic Paleustoll). Plots were fertilized with 112 kg N/ha as ammonium nitrate, at the end of February, April, June, and August of 1979–1984. Plots were irrigated from the beginning of February until mid-October whenever visual symptoms of stress occurred. Approximately 5 m water per week was applied to the plots during peak water use periods, less during spring and fall.

Treatments consisted of 3 frequencies of clipping: every 1, 2, or 4 weeks. Treatments, in 1.2 × 3-m plots, were arranged in a randomized complete block design with 3 replications. Once randomized, plot areas were not changed during 1979 to 1981. No observable stand changes occurred that could be attributed to clipping frequency. Data from 1984 were from a new seeding made in September 1983. Entire plots were clipped with a lawn mower at 5-cm stubble height and accumulated at dates shown in Table 1 when 4-week clippings occurred. Individual harvest samples were oven dried at 60° C for 72 hours and weighed. Yields were totaled for each replicate of each treatment for each 4-week period.

Table 1. Four-week harvest dates and dates at which yields were collected and nutrient contents determined for Jose Tall Wheatgrass at Bushland, Texas.

Harvest	Year 1979	1980	1981	1984
1	8 May	2 June	8 June	16 May
2	8 June	25 June	6 July	27 June
3	16 July	29 July	3 Aug.	25 July
4	16 Aug.	21 Aug.	3 Sep.	22 Aug.
5	21 Sep.	25 Sep.	29 Sep.	20 Sep.
6	17 Oct.	24 Oct.	29 Oct.	18 Oct.

Nutrient analyses were determined only on samples collected when all 3 frequencies of clipping were harvested on the same day. Oven-dried samples were ground through a 1-mm screen in a Wiley mill[1] prior to analysis. Nitrogen determinations were made by the micro-kjeldahl method using a Tecator digestor and distiller. Other nutrients were determined on ground samples ashed in a muffle furnace at 450° C for 6 hours. The ash was then dissolved in 5 ml of 4N hydrochloric acid and brought to 25 ml final volume. Phosphorus content of the digest was determined by the vanadomolybdophosphoric acid-yellow procedure (Assoc. Off. Anal. Chem., 1980) while potassium, calcium, and magnesium were determined by atomic absorption on a Perkin Elmer 4000 spectrophotometer. Calcium and magnesium determinations were made in 0.18 M lanthanum oxide/hydrochloric acid solution.

Yields, totaled for 4-week periods, and compositional data were analyzed by analysis of variance using the Statistical Analysis System. Harvests were considered to be nested within years. Where a significant *F* value occurred, Student-Newman-Keuls' multiple range test was used to separate means.

Results and Discussion

Annual herbage yields ranged between 8,690 and 15,980 kg/ha during 1979 to 1981 (Table 2) while yields were in a considerably lower range during 1984. The 1984 data were collected from a different planting than the first 3 years of the study; however, stand density was sufficient for considerably greater yields and other management practices were similar to those of previous years. The daily low temperatures were lower later into the spring in 1984 (Fig. 1) than in other years of the study. This cool weather undoubtedly reduced forage growth for the first harvest and resulted in the considerable reduction in total herbage production for the year.

Table 2. Forage production of Jose tall wheatgrass totaled over 6-four week intervals for each clipping frequency during each year at Bushland, TX.

Clipping frequency	Year 1979	1980	1981	1984	Mean
	———————	———	kg/ha	———	———————
Weekly	8690 b[1]	15980 ns	10690 b	4060 b	9855 b
2 weeks	9120 b	14290	10960 b	3790 b	9540 b
4 weeks	11760 a	15050	12970 a	5430 a	11303 a
Standard error	162	414	312	322	225

Standard error = 302

[1]Means within a column followed by the same letter are not significantly different, Student Newman-Keuls' ($P<0.05$ for individual years and $P<0.01$ for mean).

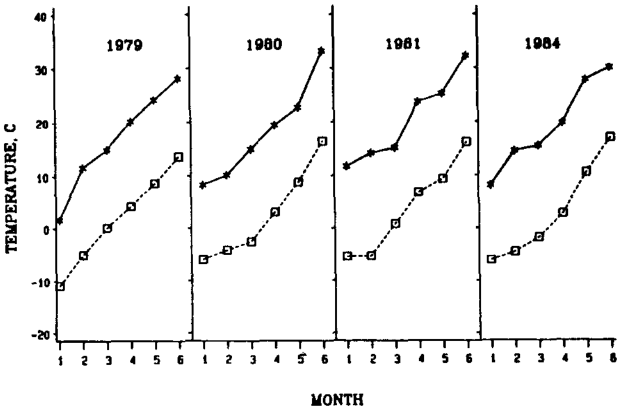

Fig. 1. *Mean monthly maximum and minimum temperatures at Bushland, Texas, during January to June.*

No significant difference in yield occurred among plots clipped weekly or biweekly. The plots that were clipped monthly yielded 12 and 18% more than those clipped weekly or bi-weekly, respectively. The data are basically in agreement with data of previous researchers (Drawe et al. 1972, Eck et al. 1975, Pittman and Holt 1983, Mutz and Drawe 1983), which indicate some clipping during the growing season can increase herbage yield, but clipping too frequently can decrease herbage yields. Moore et al. (1981) reported that there was no difference under irrigation in yield or quality of Jose tall wheatgrass when clipped at either 5-cm or 12.7-cm or 21 day intervals. Frequent clipping, particularly at a low stubble height, may reduce photosynthetic area to the extent that photosynthate is not available for regrowth after clipping. This would suggest, that under intensive management, pastures should be rested periodically to maximize herbage yields.

Herbage yields of the 3 clipping frequencies for each 4-week harvest period are presented in Figure 2. The yield difference among the treatments occurred in 1979 at the second harvest where

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[1]Mention of a trademark is for informational purposes only and does not constitute endorsement of the product by the Texas Agricultural Experiment Station.

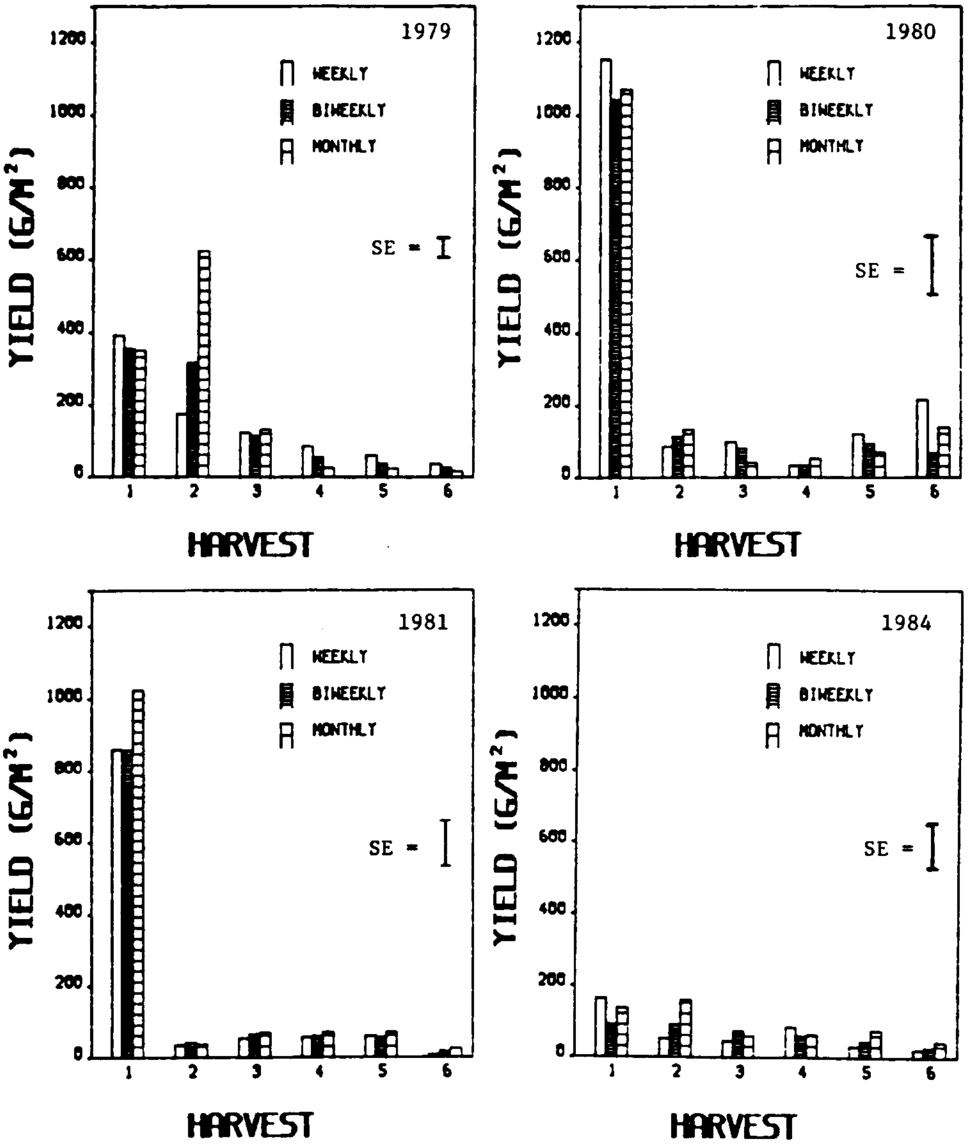

Fig. 2. *Herbage yield of tall wheatgrass at 6 harvest periods for 3 clipping frequencies during 1979, 1980, 1981 and 1984.*

less frequently clipped plots yielded more. Harvest 1 occurred between the middle of May and the first week of June each year while harvest 2 occurred during the last week of June or the first week of July. Less frequent clipping may have allowed the higher rate of spring growth to continue for a longer period. In 1981 and 1984, the higher total annual yield of the plots clipped every 4 weeks resulted from nonsignificant trends in higher yield of this treatment throughout the growing season.

The nitrogen content of herbage was not affected by the 3 clipping frequencies (Table 3). The results are somewhat surprising because, generally as herbage matures, the nitrogen content declines (Van Soest 1983). Tall wheatgrass is considered to be a late maturing cool-season grass, which may mean that the normally observed trend would have occurred in older material than 4 weeks. The herbage remained in vegetative stages during all samplings. Therefore, maturity may not have been an important factor in determining nitrogen content. Further, nitrogen content of the tall wheatgrass remained at higher levels than reported for other grass species (Mutz and Drawe 1983, Koshi et al. 1982, Eck et al. 1981). This may have occurred because the plots were heavily fertilized and irrigated, which may have resulted in higher nitrogen content than under other conditions. However, the experience of this author has been that tall wheatgrass tends to maintain higher nitrogen content than other species grown in the region, even at low levels of fertilization.

Potassium and phosphorus contents were lower in herbage from the more frequently clipped plots while calcium and magnesium were higher. Potassium decreased from 2.22% in the plots clipped every 4 weeks to 2.03% in the weekly clipped plots. While differences among treatments were not always significant within years, trends were fairly consistent. All levels were above the minimum requirement of animals (National Research Council 1976) and thus the changes in levels of this nutrient may be of little consequence in grazing systems. Phosphorus declined from 0.19% to 0.17% in the respective treatments but differences were generally not significant within years. Calcium and magnesium contents were not affected by clipping frequency in some years but the overall effect was for calcium to increase from 0.37 to 0.43% and magnesium to increase from 0.16 to 0.18% as clipping frequency increased.

The most striking observation from the nutrient analysis of tall wheatgrass herbage was that the highest content of each nutrient occurred in harvest 3 or 4 during the mid-summer period (Table 4). Speculatively, this may arise from the lack of water stress during the summer period when growth is restricted by high temperatures.

Table 3. Nitrogen, potassium, phosphorus, calcium, and magnesium content of Jose tall wheatgrass averaged over 6-four week intervals for 3 clipping frequencies in 4 years at Bushland, TX.

Year	Clipping Frequency	Nutrient Nitrogen	Potassium	Phosphorus	Calcium	Magnesium
		%				
1979	Weekly	2.30 ns	2.19 a[1]	0.14 ns	0.46 ns	0.16 ns
	2 weeks	2.14	1.73 b	0.14	0.46	0.15
	4 weeks	2.48	2.50 a	0.15	0.45	0.16
1980	Weekly	2.53 ns	2.07 ns	0.17 ns	0.51 ns	0.20 ns
	2 weeks	2.90	2.24	0.18	0.59	0.23
	4 weeks	2.71	2.25	0.17	0.49	0.18
1981	Weekly	3.43 ns	1.62 ns	0.14 b	0.43 ns	0.20 a
	2 weeks	3.60	1.72	0.19 a	0.37	0.18 a
	4 weeks	3.10	1.94	0.19 a	0.29	0.14 b
1984	Weekly	3.51 ns	2.25 ns	0.22 ns	0.30 ns	0.16 ns
	2 weeks	3.44	2.20	0.22	0.31	0.15
	4 weeks	3.44	2.28	0.20	0.31	0.16
Standard Error		0.26	0.20	0.01	0.05	0.02
Mean	Weekly	2.94 ns	2.03 b	0.17 b	0.43 a	0.18 a
	2 weeks	3.02	2.05 b	0.19 a	0.44 a	0.18 a
	4 weeks	2.93	2.22 a	0.19 a	0.37 b	0.16 b

[1] Means within a column for each year followed by the same letter are not significantly different, Student Newman-Keuls ($P<0.01$).

Transpiration, and therefore water uptake from the soil, continued because water was not limiting due to the irrigation procedure. Thus, mineral uptake was continuing and, since growth was decreased (Fig. 1) by the elevated temperatures, the concentration of nutrients in the herbage was increased.

Table 4. Four year average nitrogen, potassium, phosphorus, calcium, and magnesium content of Jose tall wheatgrass for 6 harvest periods at Bushland, TX.

Harvest Period	Nutrient Nitrogen	Potassium	Phosphorus	Calcium	Magnesium
	%				
1	2.7 c[1]	2.18 b	0.18 b	0.32 d	0.12 c
2	3.1 ab	2.07 b	0.18 b	0.47 b	0.21 b
3	3.3 a	2.33 a	0.21 a	0.35 cd	0.18 c
4	3.3 a	2.47 a	0.18 b	0.52 a	0.24 a
5	3.1 ab	2.09 b	0.18 b	0.40 c	0.18 c
6	2.9 bc	1.62 c	0.17 b	0.39c	0.15 d
Standard Error	0.075	0.057	0.004	0.017	0.006

[1] Means within a column followed by the same letter are not significantly different, Student Newman-Keul's ($P<0.01$).

Table 5. Average nitrogen, potassium, phosphorus, calcium, and magnesium content of Jose tall wheatgrass during 1979, 1980, 1981, and 1984 at Bushland, Texas.

Harvest Period	Nutrient Nitrogen	Potassium	Phosphorus	Calcium	Magnesium
	%				
1979	2.3 c[1]	2.11 b	0.14 b	0.50 a	0.17 b
1980	2.7 b	2.19 b	0.17 b	0.53 a	0.20 a
1981	3.4 a	1.76 c	0.17 b	0.36 b	0.17 b
1984	3.5 a	2.50 a	0.21 a	0.31 c	0.16 b
Standard Error	0.06	0.042	0.01	0.013	0.004

[1] Means within a column followed by the same letter are not significantly different, Student Newman-Keuls', ($P<0.01$).

While significant differences occurred between clipping frequencies and during the growing season, the largest changes in nutrient content were among years of the study (Table 5). The concentrations of nutrients in the herbage other than magnesium varied by 50% or more among the years of the study. Calcium was highest the first 2 years of the study (0.50% and 0.53%) when nitrogen concentration was lowest and lower the last 2 years of the study (0.36% and 0.31%) when nitrogen concentration was highest. Magnesium was significantly ($P<0.01$) higher in the samples collected in 1980 than in the samples collected during the other years of the study. With the exception of nitrogen and potassium, the nutrients ranged from deficiency to sufficiency for livestock during the years of the study. This points to the need for sampling and analyzing herbage cattle are grazing to determine the appropriate mineral supplementation.

In summary, when Jose tall wheatgrass was produced under irrigation with nitrogen fertilization and clipped at 3 frequencies (every week, 2 weeks, and 4 weeks), less frequent (every 4 weeks) clipping produced the highest yields. While nutrient differences among treatments were frequently not significant, over the 4 years of the study, less frequently clipped plants had the highest concentration of phosphorus and potassium and the lowest concentration of calcium and magnesium. This would indicate that rotational grazing would tend to result in higher herbage production than continuous grazing and may require different mineral supplementation to optimize animal production. Herbage harvested during mid-summer contained the highest concentration of nutrients. The greatest, however, variation in nutrient content was among years.

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The Woody Vegetation of Eastern Senegal

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Abstract

The woody component of the vegetation of eastern Senegal was sampled using the point-centered quarter method. Data were evaluated using cluster, principal component, and multiple discriminant analysis (MDA) techniques. Sites were grouped into 8 ecologically significant groups. Six of these groups were considered woodland lateritic sites, and 2 drainage sediment sites. Species of the genus *Combretum* dominated all sites. The effect of livestock grazing on the botanical composition was inferred through the use of 4 environmental variables as discriminant factors in MDA. A floristic record of species composition and guidelines for management are embodied in the results of the analyses.

Key Words: Sahel, *Combretum*, vegetational analysis

Many ecologists are concerned that livestock water developments in the Sahel have negative consequences because they allow numbers of animals to increase (Sandford 1983). Without control of grazing, livestock water developments may simply allow additional areas to be degraded. In the Sahel such exploitation is critical because of the fragile nature of the ecosystem involved.[1] Much of the rural population in this area depend directly on livestock for survival. Problems of survival in the Sahel are intensified by reoccurring severe drought. The 1968–74 drought resulted in high mortality of livestock and starvation among the human population.

The objective of this study was to describe and classify the woody vegetation in an area in eastern Senegal. Baseline data were needed to measure changes resulting from livestock water point developments and periodic drought. Emphasis was confined to the relatively stable woody component of the vegetation. Time did not permit an evaluation of the highly variable understory of annual grasses and forbs.

Description of the Study Area

The study area was a 1,000 km^2 area in eastern Senegal, between 14° and 15° N latitude and between 12° and 13° W longitude, about 30 km southwest of Bakel. Bakel is near the Senegal River, about 500 km inland from the West African coast (Fig. 1). Twelve Peulh villages are within the area. The villagers are sedentary agro/pastoralists who live in the area yearlong.

The terrain consists of a flat, lateritic plateau dissected by shallow drainage channels and occasionally interrupted by shallow rock depressions. Surface runoff seasonally accumulates in depressions on the lateritic high ground and in catchments in the drainage channels. A few of the natural catchments store water for several months after the rains and provide an important source of water for livestock and wild animals. Perennial water is only available in association with villages where hand dug wells are constructed.

Rainfall generally falls during a 60-day period between 1 June and 30 September. Average yearly rainfall for 1975 through 1980 was 450 mm. Information concerning the vegetation of Senegal is very general and some applies more directly to less forested areas (Naegele 1971, ORSTOM 1975). Vegetation of the study area consisted of a savanna with a herbaceous understory of annual grasses.

Methods

To insure complete coverage during the time available, subdivision of plant community types was made only to the level of the 2 major soil types, i.e., the lateritic and drainage sediment soils. Sample sites were selected using the "subjective-without-preconceived-

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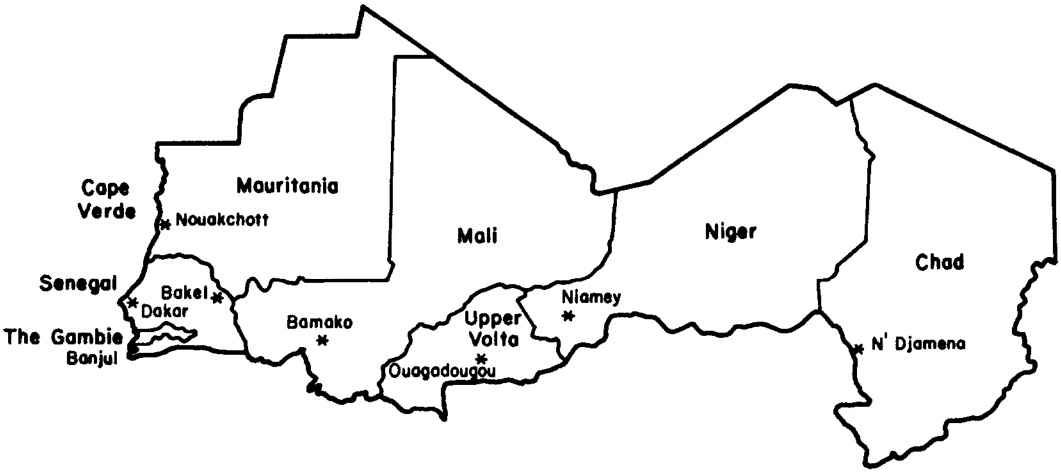

Fig. 1. *Map of the Sahel region of western Africa showing study location.*

bias" approach (Mueller-Dombois and Ellenberg 1974). With this approach the investigator is expected to discriminate wherever common sense and experience make a distinction obligatory. Within the 2 edaphically defined entities, sample units were located subjectively on the basis of perceived livestock utilization patterns.

The point-centered quarter method was used to obtain detailed information about the population of woody plants (Dix 1961). In addition to point-centered quarter sampling, a relève tally sheet (Mueller-Dombois and Ellenberg 1974) was completed for each sample unit. The cover/abundance scale of Braun-Blanquet (1932) was used to assign values to each species.

Relative density, relative frequency, relative dominance, and importance values were calculated. Importance values were calculated as the sum of relative density, relative frequency, and relative dominance (Mueller-Dombois and Ellenberg 1974). Importance values were summed and averaged for each species over all sample units. Those species with importance values ≥2.0 were separated from the total species group. Analysis of vegetation data was limited to the more prevalent species.

Point-centered quarter data as summarized above were subjected to cluster analysis. The polythetic, agglomerative, hierarchical procedures that were employed followed the general theory of clustering strategies presented by Lance and Williams (1967) and Orloci (1978). The procedure is based on a distance measure comparing all possible pairs of sample units. Average standard euclidean distance grouped sample units in a way that described the ecological relationships in the field as they were understood by the investigators. The average standard euclidean option calculates the distance between 2 points in euclidean space and tends to emphasize the larger differences in abundance of the species not in common between 2 sample units being compared.

The selected clustering strategy, or actual method of grouping sample units, was the flexible strategy. Briefly, a matrix D was constructed showing all possible pair combinations of sample

Table 1. Multiple discriminant analysis, cluster group member sample units, and mean values of environmental variables.

		Environmental variable $\overline{X}$							
		Distance							
Group	S.U. Members	Permanent H_2O		Temporary H_2O		N/Baseline		Soil Code[1]	
		Km	SE[2]	Km	SE	Km	SE		SE
I	76, 83, 6, 15, 28, 60 79, 31, 59, 40, 61, 49 73, 77, 1, 53, 43, 34, 45, 38, 17, 70, 72, 44	6	2.8	1.4	1.8	19.4	7	1.1	.4
II	5, 42, 39, 20, 16, 23, 11, 38	3.4	1.6	2.8	2.1	14.4	7.9	1.0	0
III	2, 46, 54, 3, 30, 65, 52, 55	4	1.5	1.9	1.5	25.3	4.7	1.5	.8
IV	10, 51, 19, 58, 36, 41, 47	7.7	3.7	3.3	1.7	15.3	10.1	2	0
V	4, 14, 25, 37, 50, 27, 29, 63, 74	3.7	3.7	3.2	2.1	15.2	8.1	1.4	.7
VI	18, 62, 33, 78, 80, 79, 82, 81	3.7	2.5	3.4	.9	13.3	5.7	2.0	0
VII	8, 32, 35, 75, 26, 64	4.5	3.5	3.3	1.5	18.3	5.6	2.2	.4
VIII	56, 66, 67, 68, 69	1.4	1.5	.7	.6	15.6	7.9	1.4	.6

[1] Soil Code 1 = Laterite
2 = Drainage Sediment
3 = Other

[2] SE = Standard error

Table 2. Mean importance value of species with constancy value > 55% for eight groups differentiated by cluster analysis. Groups I, III, II, V, VII, and VIII are representative of the woodland laterite site. Groups IV and VI represent the drainage sediment woodland site.

	Woodland															
	Combretum gl. Grewia bi.		Sterculia se. Combretum gl.		-Combretum ni.		Combretum lg. Combretum mi. Guiera se.		-Combretum ni. -Grewia bi.		Anogeissus le. Combretum gl. Combretum ml.		-Combretum ge.			
Species	$\bar{X}$I.V.	%C	$\bar{X}$I.V.	%C	$\bar{X}$I.V.	%C	$\bar{X}$I.V.	%C	$\bar{X}$I.V.	%C	$\bar{X}$I.V.	%C	$\bar{X}$I.V.	%C	$\bar{X}$I.V.	%C
Sterculia setigera (Stse) T[1]					70	88										
Grewia tenax (Grte) S											33	80				
Ziziphus mucronata (Zimu) S											18	60				
Acacia ataxacantha (Acat) S			10	100							22	60				
Combretum nigricans (Coni) T	84	88	52	88	79	100	42	100	90	83			39	100		
Grewia bicolor (Grbi) S	45	100	88	100	37	88	29	89	42	100	39	100	44	86		
Pterocarpus lucens (Ptlu) T			21	100			37	89	57	67	27	100				
Bombax costatum (Boco) T	25	68			23	88	18	67	43	83			23	100		
Cassia sieberiana (Casi) T	19	60	11	63	8	88	18	67					19	86		
Boscia senegalensis (Bose) S	13	56	15	88							41	60	14	78		
Pterocarpus erinaceus (Pter) T					12	63									21	75
Combretum glutinosum (Cogl) T	157	100	103	100	124	100	128	100	60	100	53	100	73	100	95	100
Combretum micranthum (Comi) S	18	88	38	100	21	88	23	100	37	67	119	100	57	100	18	88
Guiera senegalensis (Guse) S	25	92	52	100	37	75	98	100	88	100	93	100	34	100	48	100
Combretum geitonophyllum (Coge) T	23	80	10	61	13	63					20	60	22	71	55	100
Acacia macrostachya(Acma) S	47	76	44	100					22	83			62	100	37	88
Feretia apodanthera (Feap) T	8	56			10	75			13	67	8	80	15	86	15	100
Acacia seyal (Acse) T											18	60	17	86	20	88
Anogeissus leiocarpum (Anle) T													45	86	23	88
Dichrostachys cinerea (Dici) T															18	75
Entada africana (Enaf) T													10	86		
Combretum aculeatum (Coac) T															10	63
Ostryoderris stuhlmanni (Osst) T															14	63
Piliostigma reticulatum (Pire) T															22	88
Sclerocarya birrea (Scbi) T															17	88
Strychnos spinosus (Stsp) T													11	71		
Terminalia macroptera (Tema) T															38	81

[1] T indicates a tree; S a shrub.

units. The matrix was reduced by calculating the distance of newly formed groups of joined sample units with all other sample units. The following linear model was used:

$D_{jk,1}$ = Alpha j × d_{jl} + Alpha k × d_{kl} + Beta S d_{jk} where the distance between a group formed from sample units and/or groups j and k, and a third sample unit and/or group can be calculated from the known distances d_{jk}, d_{jl}, and d_{kl} and the parameters Alpha and Beta. Beta is flexible with the constraint that Alpha j + Alpha k + Beta = 1, and that Alpha j = Alpha k. Beta = −.25 has been found appropriate for most purposes, and was used in this analysis. The values Alpha j = .625, Alpha k = .625, and Beta = −.25 were used. With the parameters = 1, then successive hierarchial joinings are monotonic and reversals do not occur[2].

Principal component analysis (PCA) was used to arrange sample units and species in a coordinate system such that species distances are an accurate reflection of their ecological similarity. The method used follows the scheme and terminology of Orloci (1966, 1967).

Multiple discriminant analysis (MDA) was used in a multivariate community comparison test. The procedure employed follows the method first used by Fisher (1936) and Mahalanobis (1936) and described recently by Lindeman et al. (1980). Groups identified from the cluster analysis and verified by the principal component analysis were compared in a pair-wise fashion with a D^2 statistic calculated as a measure of the multivariate distance between pairs of communities. An F ratio associated with the D^2 statistic was used to test the statistical significance of each D^2 distance. Four environmental variables were evaluated by the MDA program. For each sample unit, values were entered for (1) distance to the nearest village with permanent water supply, (2) distance to the nearest natural seasonal water hole, (3) distance north of a baseline drawn on the horizontal axis at the southernmost point of the project area, and (4) soil type. Distances were measured in a straight line on a 1:50,000 scale map. Soil type was simplified to the 3 types, laterite, drainage sediment, and other.

Results

Vegetation Inventory

A total of 70 woody species were identified on the sample units (S.U.) in the analysis. Of the 70 species, 52 were identified by their scientific names. The remaining species were extremely rare in the study area. Twenty-nine of the species had mean importance values (I.V.) >2.0.

Vegetation Classification

Cluster analysis differentiated 8 groups considered ecologically significant (Table 1). The groups were designated for the dominant woody species which occurred there.

Principal component analysis produced component scores for the ordination of sample units and species in coordinate systems. Figure 2 shows all 79 S.U.s arranged in 2-dimensional space, such that intersample unit distances are an accurate reflection of their ecological resemblance. S.U. ordination groups are labeled by Roman numerals to show agreement with cluster analysis groups. S.U.s of group VIII were widely dispersed by PCA analysis. No attempt was made to force the S.U.s to group in euclidean space. Otherwise, outlying S.U.'s affiliations for various PCA groups (as suggested by cluster analysis) are shown by directional arrows.

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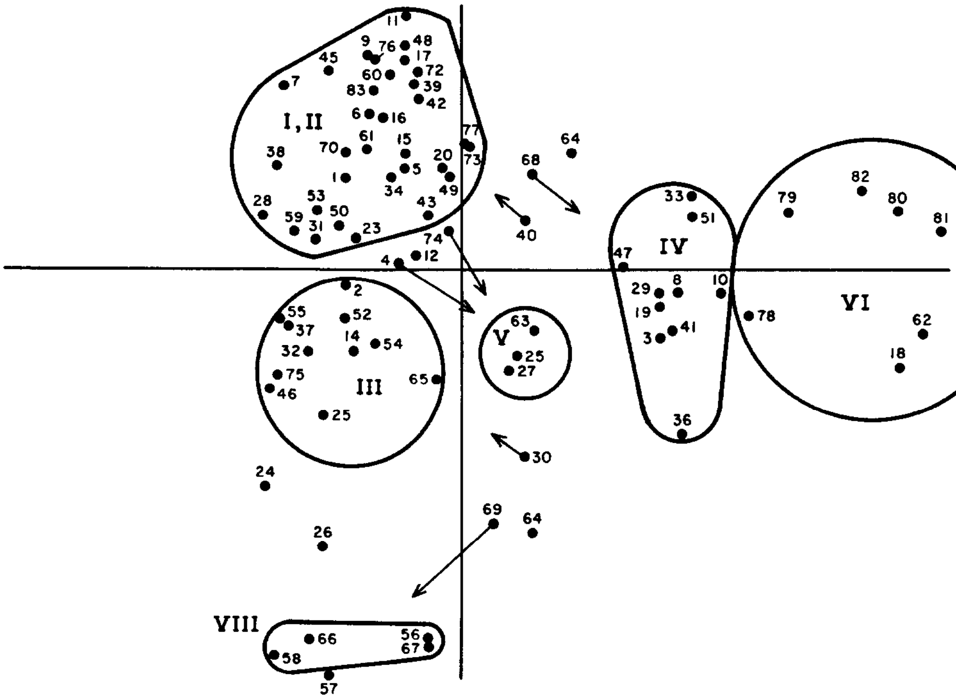

Fig. 2. *Principal component analysis and sample unit ordination.*

Table 2 lists the sample unit members for each of the 8 cluster groups as they were used in multiple discriminant analysis. S.U.'s 71, 57, and 24 were eliminated before subjecting the data to MDA. It was decided, subjectively, that their presence would confound interpretation, as they are not representative of a group and would detract from intra-group homogeneity.

Intra-group similarities of sample units and distinctions indicated by inter-group comparisons led to the construction of Table 2. Constancy values (percentage of sample units in which the species occurred) were calculated within each group. The table lists the mean importance values of species with constancy values >55% for the 8 groups differentiated by cluster analysis. The table is designed to facilitate intra- and inter-group comparison of species importance values and percent constancy.

As shown in Table 3, groups I, II, III, V, VII and VIII are similar. Five of these 6 groups are variants of the community type that is common for the lateritic site in the study area. For the sake of this discussion, group I will be considered the core representative of the lateritic community. The unique characteristics of groups II, III, V, VII, and VIII are highlighted by comparing them to group I.

Groups IV and VI are representative of the more productive drainage sediment site. The 2 groups are presented as a separate community type following the discussion pertaining to the lateritic site.

Combretum Laterite Woodland

The 24 sample units of group I represent the identification, distance and basal area measurements of 2,500 trees. All sample units of the group but 1 occurred on a lateritic soil (Table 1). The mean distance to the nearest village with permanent water was 6 km while the mean distance to temporary water was 1.4 km. Variable 3, mean distance north of the southern baseline was 19.4 km, where 35 km is the maximum possible. Group I therefore appears representative of the area outside zones of constant use around permanent settlements. Proximity to temporary water holes indicates concentrated seasonal use during the rainy season and in the early-to-mid dry season. The sample units that form group I occur in the more xeric, northern half of the study area.

The species composition and values given for mean importance and percent constancy in group I of Table 2 are typical of the vegetation community found on the dry lateritic soils subjected to moderate use. Four species of the genus *Combretum* have constancy values ≥80%. *Combretum glutinosum*, the dominant overstory species, had a mean importance value of 157 and was 100%

Table 3. Multiple discriminant analysis: calculated statistical values for group pairs.

	Group 1 to Groups						
	II	III	IV	V	VI	VII	VIII
D^2	1.67	2.41	7.42	2.38	9.57	6.98	4.02
Sign. by F	2.28	3.29*[1]	9.13**[2]	3.57*	13.10**	7.56**	3.73*
R^2	0.25	0.32	0.58	0.33	0.65	0.54	0.37
Disc. Fun. F. values for Environmental variable							
1. Dist. to perm H_2O	17.39**	25.51**	0.72	5.69*	1.69	0.42	74.81**
2. Dist. to temp H_2O	5.50*	0.0	8.41**	30.83**	8.40**	3.73	2.74
3. Dist. north of Base line	4.14	23.34**	2.32	1.78	3.69*	0.03	0.0
4. Soil type	0.20	6.86*	76.67**	9.08**	61.99**	108.96**	2.83

[1] *indicates significance at .05 level.
[2] **indicates significance at .01 level.

constant among sample units of the group.

These data suggest that the genus *Combretum* has a strong influence on the group I vegetation type, thus group I may be generally referred to as a *Combretum* woodland community. *Acacia macrostachy, Combretum micranthum, Grewia bicolor* and *Guiera senegalensis* typified the understory shrub layer. The community typified by group I is representative of about 60% of the vegetation in the study area.

Group II contained 8 sample units (Table 1). All sample units occurred on the lateritic soil type. The mean distance to permanent water was 3.4 km; the mean distance to temporary water was 2.8 km, and the mean distance north placed the sample unit group in the mid-to-southern portion of the study area. There were 11 species in both group II and group I; mean importance value and percent constancy were almost identical for *Combretum geitonophyllum, C. glutinosum, C. micranthum,* and *C. nigricans.* The difference between the groups is that *Acacia macrostachya* and *Boscia senegalensis* of group I are replaced by *Pterocarpus erinaceus* and *Sterculia setigera* in group II. *Acacia macrostachya* and *Boscia senegalensis* are shrubby species that do well under dry conditions. Both *Petercarpus erinaceus* and *Sterculia setigera* are large (>10 m) trees. Although *Sterculia* trees occurred throughout the study area, their greatest concentrations were in the more moist, southern portion. Group II is representative of the *Sterculia-Combretum* woodland type that covered most of the mid-to-southern portion of the study area. As a variant of the group I *Combretum* woodland lateritic community, group II covered approximately 40% of the estimated 60% for group I.

In the typical *Sterculia-Combretum* woodland community, *Sterculia* trees stand 4 to 8 m above the canopy layer formed by *Combretum* spp. The understory shrub layer, as in group I, was typified by *Combretum micranthum, Grewia bicolor* and *Guiera senegalensis.*

An ecological association between *Sterculia setigera* and *Adansonia digitata* was noted in the field and is indicated by the species ordination (Fig. 3) (species abbreviations are shown in Table 2). The 2 species are circled and labeled B for reader identification. *Adansonia digitata,* more commonly known as "Baobab," had a 50% constancy value among the sample units of group II.

Mahalanobis D^2 value for the group I–group II comparison was nonsignificant ($\alpha \leq .05$) (Table 3). A low, nonsignificant value was expected since group II is a relatively simple variant of the group I type. The discriminant function F value for the mean distance to permanent water was significant ($\alpha \leq .01$) (Table 3). The highly significant value resulted from the fact that the sample unit members of group I were in the northern-to-mid latitudes and were relatively far from permanent settlements. Group II sample units were in the southern half of the study area where people and permanent water supplies are more concentrated.

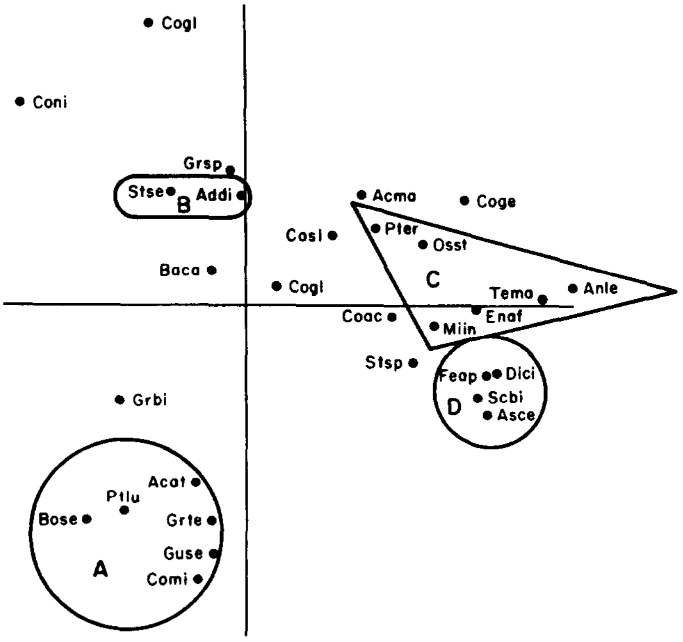

Fig. 3. *Principal component analysis and species ordination.*

The sample unit members of group III were at moderate distances from permanent and temporary water in the northern third of the study area (Table 1). Group III, like group I, had an overstory layer dominated by *Combretum* spp. (Table 2). As a variant of the group I type, it is interesting because it includes sample units 3, 30, and 65 (Table 1). These 3 sample units are on drainage sediment soils in areas that are heavily utilized by livestock. Importance values for the dominant shrub species *Combretum micranthum, Grewia bicolor,* and *Guiera senegalensis* were higher in group III than in group I. The importance values of the 2 dominant overstory species, *Combretum glutinosum* and *Combretum geitonaphyllum,* are comparatively low. This kind of change in community structure is to be expected on the lateritic site, where moisture conditions are more favorable with light-to-moderate use, or on the drainage sediment site where heavy use creates more xeric conditions. Intergroup comparison with group I revealed a significant D^2 value ($\alpha \leq .05$) (Table 3).

The sample unit members of group V were not close to permanent or temporary water; they had a mean distance of 15.2 km north of the baseline and were on either the laterite or drainage sediment sites (Table 1). The 2 sample units (27 and 74) of the group that were on drainage sediment soils were in heavily utilized areas. Species composition of these 2 sample units had been modified through heavy use. The importance value of understory shrubs was higher, and the importance values of the 2 dominant overstory species were reduced compared to those of group I. The D^2 value calculated for the group I to group V comparison was significant ($\alpha \leq .05$). Discriminant function coefficient F values were significant for the first, second, and fourth environmental variables (Table 3).

The sample units in group VII were grouped due to their dissimilarity with characteristics of the other drainage woodland groups. Group VII consisted of a mixture of sample units that represented a seral community type. All the sample units appeared to be highly disturbed. The group is probably representative of the drainage woodland community under stress. Heavy utilization pressure has altered species composition so that the drainage woodland community resembled the more xeric lateritic group I type. In comparison with the S.U.s of the woodland type (groups IV and VI), S.U.s in group VII have less diversity (Table 3), lower tree densities, and a smaller average tree diameters (Table 4).

Table 4. Group average values for number of trees per 100 square meters, total basal area per 100 trees and individual tree diameters.

	Average Values Per Group					
Group	Trees per 100 sq. M	Standard Error	Total Basal Area/ 100 Trees	Standard Error	Mean Diameter (cm)	Standard Error
I	2.8	0.9	28505	15607	17	12.5
II	2.6	0.7	45664	21872	21	14.8
III	4.2	2.5	23642	6430	15	8.0
IV	2.9	0.9	40390	20791	20	14.4
V	3.6	1.6	25490	12840	16	11.3
VI	3.8	1.1	48436	24132	22	15.5
VII	2.8	1.8	34082	17139	19	13.0
VIII	3.3	1.4	28030	17272	17	13.0

The D^2 values for the group I–group VII comparison was significant ($\alpha \leq .01$) (Table 3).

The sample unit members of group VIII were all close to permanent and temporary water and were on the laterite or drainage sediment soils (Table 1). The mean distance to permanent water for group VIII was only 1.4 km. Table 2 shows that species composition is altered from the group I, typical community, in favor of shrubby species. All of the species typified by group VIII are highly resistant to grazing pressure. *Acacia ataxacantha* and *Ziziphus mucronata* are thorny shrubs that resist grazing pressure even by goats.

Acacia ataxacantha is in the species association of Figure 3 that is marked A for reader identification. The species of this association appear to be persistent under grazing pressure. They all have a wide range ecological adaptability and were found on both laterite and drainage sediment sites. *Ziziphus mucronata* had a low overall importance value of <2.0 and was therefore not among the 29 species used in the computer-assisted analysis.

For the group I–VIII comparison, the D^2 value was significant ($\alpha \leq .05$). The discriminant function coefficient F value calculated for the distance to permanent water was significant ($\alpha \leq .01$) for the pair (Table 3). The sample unit associations of groups VII and VIII suggest that the plant communities around permanent settlements and in areas of heavy grazing were severely disturbed.

Anogeissus-Combretum Drainage Woodland

Groups IV and VI represented sample units at moderate-to-great distances from permanent water and were relatively far from temporary water. The mean distance of these groups was 14 km above the baseline and all were on drainage sediment soil (Table 1). The species composition and values given for mean importance and percent constancy for these 2 groups (Table 2) were typical of the vegetation community found on the more productive drainage sediment site under moderate use. The large trees *Anogeissus leiocarpum, Combretum glutinosum* and *Acacia seyal* dominated and typified the drainage sediment site. Also typical, though less abundant, were the trees *Entada africana, Pterocarpus erinaceus, Ostryoderris stuhlmanni* and *Sclerocarya bierrea.* Understory vegetation was dominated by *Combretum* spp., *Grewia* spp., and others.

The triangle marked C in the species ordination of Figure 3 includes most of the large trees which dominated the drainage sediment site. The encircled species marked D occurred in association with one another in the deeper drainage channels of the mid-to-southern portion of the study area. *Sclerocarya birrea* and *Acacia seyal* occurred only on the more productive soils. *Acacia seyal* was most often found at the edge of drainage channels, whereas *Sclerocarya birrea* tended to occur near the center of a drainage, where its base may be intermittently submerged in water for short periods of time. *Acacia seyal* may be shade intolerant and have a tap root which can reach the water it needs. *Feretia apodanthera* appeared to be a species with wide latitude of adaptability. It was common on both laterite and drainage sediment soils.

When they were paired with group I, groups IV and VI produced significant D^2 values ($\alpha \leq .01$). Values for the coefficient of determination (R^2) were high for both pairs (Table 3).

Interpretations for Management

The results of these analyses indicate that significant changes in botanical composition occurred in the study area before new seasonal water points were introduced. The groupings of woody species in the preceding section suggest that the community composition of woody species surrounding a water point can be significantly affected by distance to the nearest village. This may be inferred from the results of multiple discriminant analysis where the first discriminating variable was distance to permanent water (a village). Specific botanical changes associated with overuse are illustrated in the group comparisons. For example, overuse of an area by livestock can shift botanical composition to reflect more xeric conditions. As stated, group VII's botanical composition (Table 2) indicates similarity to the drier lateritic community type, while the sample units of group VII were all on soils of the drainage woodland community type. When perennial overstory cover is diminished, soil degradation through heating, compaction and erosion follows. Loss of preferred forage species such as *Combretum aculeatum* and *Maerua angolensis* will quickly result in lower livestock productivity. When dominant overstory species such as *Ostryoderris stuhlmanni* and *Cassia sieberiana* disappear from the community (Table 3) a trend toward degradation may be indicated. Since woody species provide most of the perennial cover, and therefore the only long-term site protection, it is difficult to imagine that removal of any woody species can be justified for the sake of "increased livestock production". We suggest that care should be taken to avoid the loss of species diversity. Although "proper" stocking rates are not known, it would be prudent to reduce grazing pressure on drainage woodland community sites. Moderate grazing is especially important in proximity to permanent water where livestock must concentrate in the dry season. Protection and rational use of woody species should be encouraged. Management and future research should look for ways to insure regeneration of preferred perennial vegetation (in this case, trees and shrubs) and site stability.

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An Evaluation of Range Condition on One Range Site in the Andes of Central Peru

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Abstract

Little published information is available on the vegetation or its response to grazing in the high elevation (3,900–4,800m) grasslands of the Andes, known as the puna. The objective of this study was to evaluate grazing-induced vegetation changes on a major range site in the puna. Basal cover and diversity were compared on (1) rangelands managed by a cooperative of land holders (moderate grazing); (2) communal grazing land (heavy grazing); and (3) sacrifice or holding pastures (very heavy grazing). Basal cover was determined using point transects. With increased grazing pressure standing height of the vegetation was greatly reduced as was vegetation basal cover. Total cover of grasses was reduced while forb cover increased. Ability of a species to grow close to the soil surface probably enabled it to tolerate very heavy grazing. Species diversity as determined by Simpson's D, Shannon-Weaver's H′, and species richness was highest on the community lands.

Key Words: plant succession, grazing effects, puna

Livestock grazing can have a profound impact on range vegetation (Stoddart et al. 1975). The general pattern of grazing-induced vegetation change is well documented in the U.S. and much of North America. It is known that less palatable plants increase at the expense of the more palatable species. Community structure is vastly altered when improper grazing continues for long periods (Daubenmire 1968). Adams (1975) and Ellison (1960) presented reviews of the abundant literature available on the effects of grazing management on North American rangelands. Much less is known about South American rangelands, particularly the high elevation grassland of the Andes, known as the puna (Fig. 1).

These high elevation grasslands are important grazing lands for the Andean countries. The puna extends over many hundred thousands square kilometers from latitutes 8° S to 27° S. The puna is associated with a series of high plateaus and intermontane basins beginning with the Pampa de Junin in central Peru. The altiplano, a tableland in southern Peru and Bolivia, is the most familiar of these plateaus. Elevation of the puna varies from about 3,900 to 4,800 m. Troll (1968) divided the puna into 3 provinces: the moist puna, the dry puna, and the desert puna. The moist puna begins in northern Peru at about latitude 8° S where it blends in with another high elevation grassland typical of the northern Andes, the paramo, and lies adjacent to the eastern cordillera of the Andes as far south as Bolivia. The dry puna beings in southern Peru and extends into the altiplano of Boliva, while the desert puna occurs in southern Boliva and Chile adjacent to the Atacama Desert.

Precipitation in the puna is concentrated in a single wet season, between October and April, of variable length, and ranges from 150 mm in the desert puna to 1,200 mm per annum in the moist puna belt (Molina and Little 1981). Annual rainfall decreases to the south and west. There is also a steady increase in concentration of the rainfall period as one moves south (Johnson 1976). The mean annual temperatures are less than 10° C and nocturnal frosts are common, especially during the dry season (Troll 1968). Frost

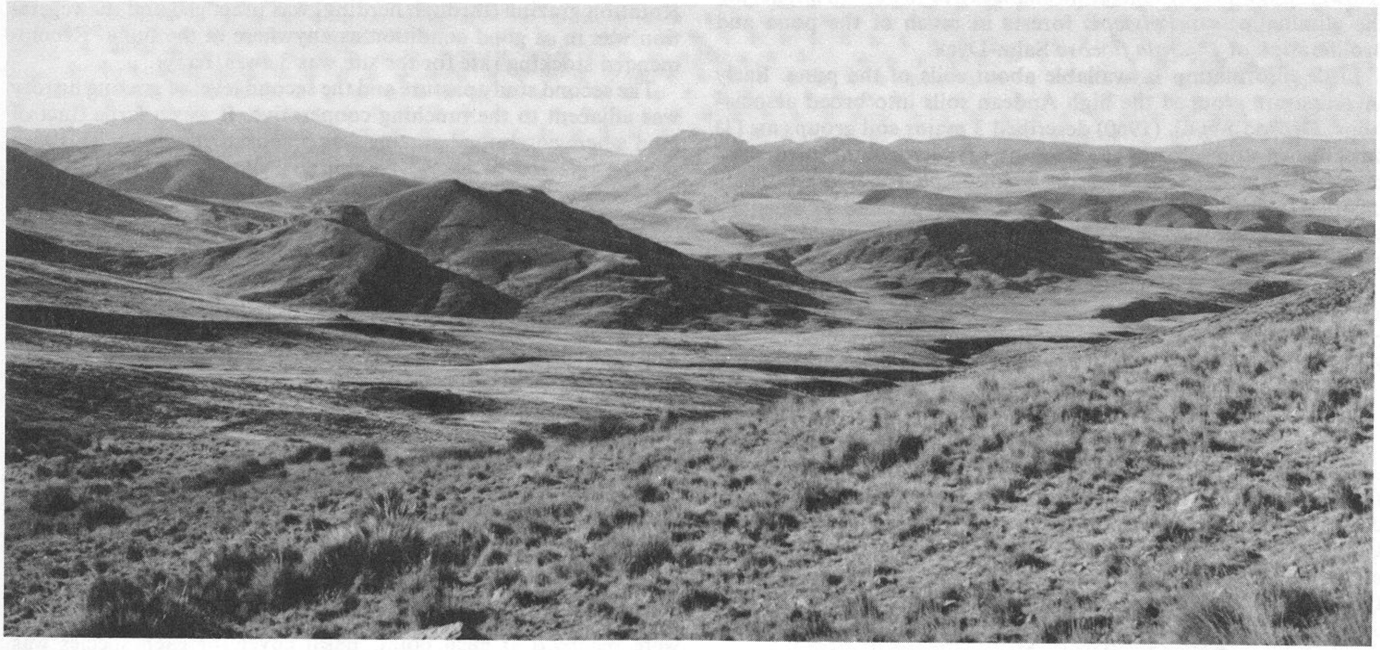

Fig. 1. *The puna in the central Andes of Peru has a rugged topography and is dominated by cool-season grasses and forbs. Shrubs and trees are uncommon.*

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occurs nightly at 4,100 m. The diurnal season fluctuations can be as much as 20° C in the moist puna and even greater in the desert puna. The paramo grasslands are distinguished from the puna by the lack of seasonal differences in precipitation and temperature, and also by a higher relative humidity.

The puna vegetation has evolved under harsh environmental conditions, such as a lengthy dry season, frequent frosts, low temperatures, pronounced diurnal variation, high solar radiation, and low oxygen (Thomas and Winterhalder 1976). Plants have adapted to these environmental stresses in various ways (Cabrera 1968). Perennial forbs typically have well-developed root systems, many times larger than the aboveground portions of plants, and grow very close to the ground surface. Leaves are often reduced, felty, and lightly pubescent, or have a thick cuticle layer. Succulents such as *Opuntia* are also common. Many grasses have rolled leaves. Stems are often reduced or are below ground with only the leaves protruding above the surface.

Weberbauer (1936) distinguished 4 major vegetation formations in the moist puna: (1) puna mat, (2) bunchgrass, (3) *Distichia* moor, and (4) the vegetation of rocks and stone fields. The puna mat is composed predominantly of dwarf herbaceous forbs and cushion plants growing in areas of moderate water content. Tall grasses, erect shrubs, mosses, and lichens are of minor importance. The bunchgrass formation is the most extensive and composed chiefly of perennial grasses such as *Festuca, Poa, Stipa* and *Calamogrostis* species. Many of the forbs found in the puna mat also are present in the bunchgrass formation. The *Distichia* moor remains moist yearlong and *Distichia muscoides* Nees et Mey. is the characteristic plant. Vegetation of the rock and stone fields is distinctive in that lichens, mosses, ferns, erect shrubs, and tall-stalked herbs occur more abundantly. Tufted grasses also are an important component. The radiated heat provided by the rocks allows his formation to extend up to 5,000 m, while the other formations disappear around 4,600 m. Weberbauer (1936) described this formation as a heat oasis, allowing certain plants to thrive which otherwise would not grow in the puna. He also noted scattered *Polylepis* groves, sometimes extending for several kilometers and growing up to the snowline.

Floristically the moist and dry puna are closely related. Evergreen shrubs are more common in the dry puna (Molina and Little 1981). In the desert puna shrubs predominate and vegetation cover is lower. Examples of vegetation changes due to human impact are the elimination of *Polylepis* forests in much of the puna and proliferation of *Opuntia flocosa* Salm-Dyck.

Little information is available about soils of the puna. Early investigators grouped the high Andean soils into broad associations. Drosdoff et al. (1960) described 3 major soil groups as: (1) dark brown stoney loams to silt loams, (2) deep well-drained, dark brown to black loams and silt loams, and (3) hydromorphic medium to fine texture soils. Beek and Bramao (1968) included the soils of the central Andes as Paramo soils, and described them as being derived from heavy clays of glacial origin.

The vegetation in the central Andes is poorly understood (Glaser and Celecia 1981) especially as regards responses to grazing. The objective of this study was to investigate the vegetation of a major range site in the moist puna belt under 3 different grazing regimes.

Study Area and Methods

The study area of approximately 17,700 ha was located on and adjacent to an agricultural cooperative, Sociadad Agricola de Interes Social (S.A.I.S.) Pachacutec, headquartered at Corpacancha in the Department of Junin, Peru (11°25'S, 76°15'W) (Fig. 2). Corpacancha is about 42 km ENE of La Oroya, Peru. Rangeland of the cooperative has historically received better management than most of the puna, much of which is severely overgrazed. The elevation ranges from 4,150 m to 4,700 m. Topography is both gently rolling glaciated and rugged mountainous terrain.

Corpacancha is in the moist puna belt as classified by Troll (1968). Vallejos and Quillatupa (1975) reported that in Corpacancha, the average yearly precipitation from 1965 to 1972 was 865 mm, and varied from 672 mm to 1,033 mm. Snow makes up a small percentage of this precipitation and does not accumulate below the permanent snow line (Troll 1968), which begins at about 5,150 m (Thomas and Winterhalder 1976).

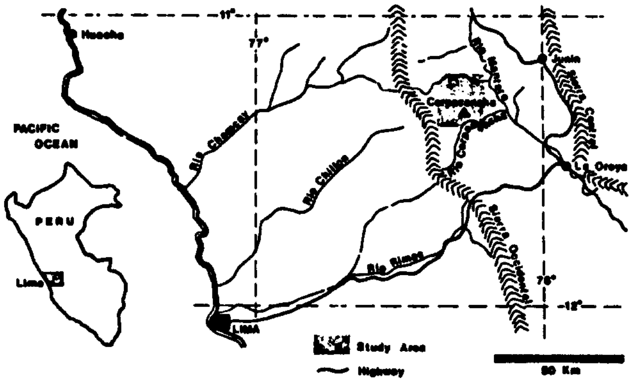

Fig. 2. *Map of the study area in the central Andes of Peru.*

Wilcox (1982) delineated 8 range sites on the study area. All of them are dominated by cool-season mid to tall grasses. Common genera include *Calamagrostis, Festuca, Poa, Stipa,* and *Muhlenbergia.* Low growing forbs are also common. Trees are absent and shrubs are rare.

The range site selected for this research made up 50% of the study area and occurs on the glaciated mountain valley slopes (Fig. 3). Soils developed on glacial till and are moderately deep (B horizon extends from 40–100 cm). They also commonly exhibit umbric epipedons and argillic horizons. Organic carbon is around 6% in the upper sola and pH is between 4.5 and 6.0. Textures are loam in the A horizon and clay loam to gravelly clay loam in the B horizon. Often the soil is mantled by a thin organic horizon. Soils were classified as Mollic Cryoboralfs (Wilcox 1982).

Study pastures were representative of 3 levels of past grazing history. The first level occurred on the ranching cooperative at Corpacancha. Agricultural cooperatives are common in Peru. Workers have an active voice in the management of the cooperatives, but trained agriculturalists are employed as managers. Sheep and alpaca were the principal grazing animals on the cooperative. Rotation grazing (through herding) was practiced and the vegetation was in as good condition as anywhere in the puna. Recommended stocking rate for the site was 3 ewes/ha/yr.

The second study pasture and the second level of grazing history was adjacent to the ranching cooperative. It was a large tract of land where communal grazing was practiced year long. This area will be referred to as the community site. Based on a year of observation, it appeared to be more heavily grazed than the cooperative. Standing biomass was less as was standing height of the vegetation. Sheep and llama grazed the community site. Stocking rate information was not readily available.

A third level of grazing pressure occurred on the holding pasture of the cooperative. The pastures were sacrifice areas and were the most heavily grazed. Stocking was difficult to estimate because of the put-and-take nature of its use.

These different grazing intensities on the same range site provided an excellent opportunity for studying grazing-induced vegetation changes in the puna. The puna has been grazed by humankind's domestic livestock for over 10,000 years (Engel 1976). No part of it has been left undisturbed. Thus, no true relict areas were available for comparison.

Basal cover was estimated with the point sampling method (Goodall 1952). Point samples were recorded along 25-m transects at 0.5-m intervals. Species name, bare-ground, rock, litter, or moss were recorded at each point. Basal cover for each species was calculated as the percentage of direct hits per transect.

The number of transects on the ranching cooperative, commun-

Fig. 3. *The range site selected for study (foreground) was the most common range site in the study area.*

ity site, and the holding pasture were 46, 9, 11, respectively. The ranching cooperative was more heavily sampled because of associated vegetation inventory studies there (Wilcox 1982). The sampling intensity on the community lands and in the holding pasture was adequate to characterize basal cover. Wilcox (1982) used reciprocal averaging ordination to classify plant-community groups in the ranching cooperative. All 46 transects were closely grouped by reciprocal averaging analysis, and thus judged to be in the same plant community. Soil parent material, soil types, slope, and topographic position were similar on all sites sampled.

Shannon-Weaver's H′ and Simpson's D diversity indices (Greig-Smith 1964) were calculated for each grazing treatment. Simpson's D is most strongly influenced by abundance of dominant species. Rare species have little influence on it (Whittaker 1972). The Shannon-Weaver index is more strongly affected by the occurrence of intermediate and rare species (Whittaker 1972, Peet 1974). Both indices are independent of sample size if the sample size is adequate to represent the community (Whittaker 1972). Species richness values were calculated as the number of species occurring in each transect averaged across treatment.

Nomenclature of plant species follows that of McBride (1936), and Tovar (1960, 1965, 1972). Species identification was confirmed at San Marcos University in Lima.

Results and Discussion

The dominant species on the ranching cooperative site was *Festuca dolichophylla* Presl, a common bunchgrass of the puna (Table 1). Typical height was about 60 cm. Basal cover of *F. dolichophylla* was estimated to be 3 times that of the next most important species *Calamagrostis vicunarum* (Wedd.) Pilger, also a bunchgrass. *C. vicunarum* has much finer leaves and it is not as tall as *F. dolichophylla.* Other important species were *Carex ecuadorica* Kunth and *Festuca rigescens* Kunth. Both of the *Festuca* species are coarse grasses and have similar growth forms but *F. dolichophylla* grows taller. Forbs on the ranching cooperative made up less than 2% of the basal cover. Wilcox (1982) noted that generally forbs were less common as sites become more mesic. *Alchemilla pinnata* R. & P. was the most abundant forb. Like many puna forbs this plant grows very close to the ground and has well developed roots.

Table 1. Basal cover (%) and associated standard errors for the ranching cooperative, community lands, and holding pasture.

	Ranching Cooperative	Community Land	Holding Pasture
Grasses			
Aciachne pulvinata	1.4 (0.4)	2.9 (1.3)	0 (0)
Agrostis breviculumis	0.6 (0.2)	3.3 (0.8)	2.4 (0.8)
Bromus lanatus	1.0 (0.2)	0.2 (0.2)	0.4 (0.4)
Calamagrostis vicunarum	4.4 (0.6)	4.2 (0.9)	1.8 (0.6)
Dissanthelium calycinum	0.1 (0.3)	0.7 (0.3)	0.4 (0.2)
Festuca dolichophylla	14.9 (1.1)	1.6 (0.7)	0 (0)
Festuca rigescens	2.2 (0.5)	5.8 (1.0)	6.9 (1.5)
Hordeum muticum	0.1 (0.1)	0.2 (0.2)	0 (0.)
Muhlenbergia ligularis	0.2 (0.1)	0.4 (0.3)	0.8 (0.6)
Poa candomoana	0.4 (0.2)	0 (0)	0.6 (0.3)
Stipa brachyphylla	0.4 (0.1)	1.6 (0.6)	0.6 (0.5)
Total grasses	26.0 (1.0)	20.9 (1.2)	13.9 (2.3)
Forbs			
Alchemilla pinnata	0.4 (0.1)	0.8 (0.5)	1.8 (0.7
Baccharis alpina	0.4 (0.3)	1.8 (0.7)	0.2 (0.2)
Geranium sessiliflorum	0.1 (0.1)	0.4 (0.3)	0.4 (0.2)
Paronychia andina	0.5 (0.2)	1.4 (0.7)	0.6 (0.5)
Total forbs	1.8 (0.5)	5.3 (1.1)	6.0 (1.6)
Sedges			
Carex ecuadorica	2.6 (0.4)	2.2 (0.7)	1.6 (0.7)
Scirpus rigidus	1.0 (0.3)	0 (0)	0 (0)
Total sedges	3.6 (0.5)	2.2 (0.3)	1.8 (0.7)
Litter	57.5 (1.7)	60.2 (1.6)	38.4 (4.6)
Bareground	7.5 (1.0)	9.8 (1.4)	36.2 (6.3)
Moss	3.3 (0.7)	1.1 (1.8)	3.7 (1.2)
Rock	0.3 (0.1)	0.5 (0.4)	0

Several vegetation differences were evident on the community site. The most obvious difference was the lower basal cover of *F. dolichophylla.* It was reduced from the dominant species to a common one. Basal cover was only 2% on this site while it was 15% on the ranching cooperative. No other species was so affected. *C. vicunarum* and *C. ecuadorica* remained about the same. Several species had higher basal cover estimates, most notably *F. rigescens*. Others were *Aciachne pulvinata* Benth, *Stipa brachyphylla* Hitchc., and *Agrostis breviculmis* Hitchc. *A. pulvinata* is a low growing grass species which grows in isolated clumps. It appeared to be coarse and quite unpalatable. Estimated total basal cover of grasses and sedges were lower on this site than on the cooperative. Forb basal cover was significantly higher. Cover of *Bacharis alpina* H.B.K. and *Paronychia andina* A. Gray increased the most. *B. alpina* is a spreading prostrate semishrub whose stems grow just under the soil surface, leaving only its small leaves exposed. *P. andina* is also a spreading species which grows close to the ground.

The vegetation in the holding pasture was only a few centimeters above the ground and in general was of low vigor (Fig. 4). Also much more ground was exposed than in the other 2 areas. One cannot be absolutely certain that *F. dolichophylla* was eliminated from the holding pasture or that *F. rigescens* increased slightly. These species are difficult to separate from one another in the field if they are in a stunted condition, as they were, induced by the extreme grazing. No grass species with the possible exception of *F. rigescens* increased in basal cover from the community site. Florez et al. (1985) reported that *F. rigescens* greened up about 2 weeks later and had lower protein content than other common cool season grasses in the Pampas Galeras Vicuna Reserve, also in the puna. These characteristics perhaps made it less palatable and allowed it to increase under the heavy grazing of the holding pasture. *S. brachyphylla* and *Muhlenbergia ligularis* (Hack) Hitchc. had an estimated basal cover in the holding pasture slightly higher than on the ranching cooperative. Florez et al. (1985) found that these 2 species had the highest crude protein contents and in vitro digestibility of any grasses evaluated in their study. *C. vicunarum* and *C. ecuadorica* were reported by Farfan and Bryant (1984) to be favored by alpaca during the dry season. These data suggest that survival of these species under heavy grazing is not due to inherent low palatability. Rather, it may be due to their ability to grow very close to the soil surface, providing protection to the apical meristem. Forb basal cover was about the same on the holding pasture as on the community site; however, there was a shifting of cover among the forb species. *A. pinnata* increased with cover while the other forb species decreased. Ability of forbs to tolerate heavy grazing pressure is also probably a result of their decumbent growth form rather than low palatability. In the altiplano, to the south, *A. pinnata* was a highly selected forage species during the dry season (Farfan and Bryant 1984).

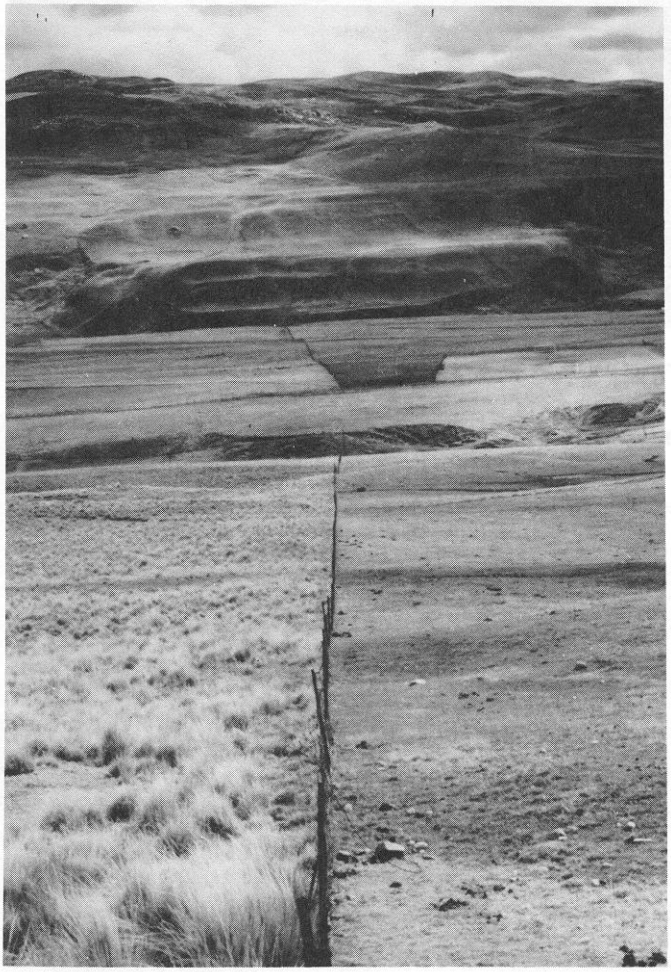

Fig. 4. *Heavy grazing in the puna reduces the bunchgrass vegetation to decumbant grasses and forbs.*

Species diversity was higher on the community site than either the ranching cooperative or the holding pasture (Table 2). This was substantiated both by estimates of species diversity and species richness. The observed pattern of species diversity does not adhere to the classical view stating that diversity should increase with advancing succession (Bazzaz 1975, Whittaker 1972). Accordingly, species diversity should have decreased with grazing pressure. Whittaker (1972) did note, however, that climax communities sometimes have lower species diversity than immediately lower seral communities. Others have also observed a varied pattern of species diversity with succession (Denslow 1980, Drury and Nizbit 1973). The pattern observed here more closely follows Huston's (1979) dynamic equilibrium model for species diversity, which states that diversity is controlled by the rate of competitive displacement among species and forces that prevent equilibrium (any disturbance which reduces population size). Huston (1979) stated that the frequency of population reductions has a major effect on species diversity. His model predicts that for communities with low or intermediate growth rates (such as those of the puna), diversity will be reduced at high frequencies of disturbance (holding pasture) by the reduction or extinction of populations unable to recover from the disturbances. Also, at low frequencies of disturbance (ranching cooperative) diversity will be lower because of competitive displacement. Diversity is highest at intermediate frequency of disturbance (community site). Thus if one assumes that frequency and severity of grazing disturbance were low on the ranching cooperative, intermediate on the community site, and high on the holding pasture, then the dynamic equilibrium model for species diversity explains the pattern of diversity observed.

Table 2. Simpsons D, Shannon-Weavers H', and species richness as indicators of species diversity for the cooperative, community site and holding pasture.

grasses	Ranching cooperative	Community site	Holding pasture
D	0.84	0.92	0.87
H′	2.48	2.72	2.50
Species richness	10.9	13.5	10.5

Conclusions

Reductions in standing height and biomass of the vegetation were the most obvious differences between the 3 compared areas. *F. dolichophylla* was most severely affected by grazing pressure. Generally basal cover of the other grass species were little affected by grazing pressures. *F. rigescens* increased with grazing pressure as did forbs. Ability of species to survive was not attributed to low species palatability but rather an ability to grow close to the soil surface.

Species diversity patterns were explained best by Huston's

(1979) model for species diversity. Species diversity was highest on the community site, which experienced intermediate disturbance.

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Reviewers

Recognition is due the following individuals who have contributed their time and professional expertise to review manuscripts for the *Journal of Range Management* in the past year. Their contribution to the quality of this journal and the advancement of the discipline is highly significant.

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(continued on page 79)

Recovery of Compacted Soil on Pastures Used for Winter Cattle Feeding

G. R. STEPHENSON AND ANNE VEIGEL

Abstract

Soil bulk density measurements were taken from pastures used for winter feeding to determine the effects of different stocking rates on soil compaction and recovery. Samples were taken from paired ungrazed (control) pastures, normally grazed pastures (10 head per ha), and pastures grazed 4 times normal. Results show that significant differences occur in soil bulk density with increased stocking rates, and that 2 growing seasons with protection from grazing and trampling are insufficient time for complete recovery.

Key Words: soil bulk density, cattle trampling, soil compaction

Soil compaction is a universal process associated with use or activity occurring on the soil surface. The major effect is reduction of pore space through which water moves into and through the soil, thereby reducing infiltration and percolation, increasing runoff, and encouraging erosion (Lull 1959). The extent that a soil is compacted is determined by a complex interaction of the compacting force, soil water content, texture, and porosity. Soil bulk density is usually the parameter used to measure soil compaction.

Considerable work has been done evaluating the impact of grazing animals on soil compaction and the associated response of runoff and infiltration. Laycock and Conrad (1967) found that studies conducted in the more humid regions reported consistently that bulk density was higher in grazed areas than in similar ungrazed areas. However, studies in arid rangelands gave conflicting results: some reporting no differences in bulk density between grazed and ungrazed areas, while other studies reported consistently high bulk density values for grazed areas. Laycock and Conrad credited these conflicting results to "varying soil, moisture, or other conditions." In their own work, they detected bulk density differences between grazed and ungrazed plots only in midsummer and attributed this to changes in soil moisture, finding also that these 2 parameters were highly correlated.

Van Haveren (1983) gave a comprehensive review of previous work relating soil compaction, as measured by bulk density, to such hydrologic factors as reduced infiltration, increased runoff, erosion, and impacts on plant growth. Van Haveren determined that bulk densities of coarse textured soil were not affected by grazing intensity, whereas bulk densities of fine textured soil increased significantly with increased grazing intensity.

Willatt and Pullar (1983) performed studies in Australia on soil compacted by sheep, replicating tests under different stocking rates. Their results showed that increases in bulk density and bearing capacity of the soil and decreases in hydraulic conductivity were correlated to increasing stocking rate. Changes in plant composition and reduction in yield were related to increases in stocking rate.

Orr (1975), in a study on heavily grazed bluegrass range in South Dakota, found that more than 1 year of protection from grazing and trampling was necessary for significant soil response and that recovery continued for up to 4 years. It wasn't until the second year of protection that the compacted soils showed significant increases in macropore volume. Both Laycock and Conrad (1967) and Lull (1959) cautioned against using soil bulk density as evidence of compaction unless moisture conditions and other physical characteristics of the soils in the study sites are very similar.

Realizing that maximum compaction of soils of different texture will occur at different moisture levels, we chose a study site with homogeneous soil physical characteristics and approximately the same soil moisture conditions. We used comparative data for both the trampled and untrampled fields, leaving animal stocking rate as the only critical variable. The objective of our research was to evaluate compaction and recovery of soils following different cattle stocking rates on pastures used for winter feeding.

Description of Study Area

This study was conducted at the USDA-ARS Reynolds Creek Experimental Watershed in southwest Idaho (Fig. 1). Six separate pastures of newly seeded alfalfa (*Medicago sativa* L.)-bromegrass (*Bromus biebersteinii* R.) mix were used to evaluate the effects on soil compaction of varied animal stocking rates during winter feeding. Pastures were approximately 0.81 ha in size. The control and treatments were replicated, i.e., the control with no cattle; 10 head/ha; and 40 head/ha (hereafter referred to as treatments 1, 2, and 3, respectively). The stocking rate of 10 head/ha is standard for winter feeding cow-calf operations in this region. Cattle are usually brought in from the range by mid October, culled, placed in winter feeding pastures, and fed hay until transferred back to the range the following spring. Most cows calve during this winter feeding period.

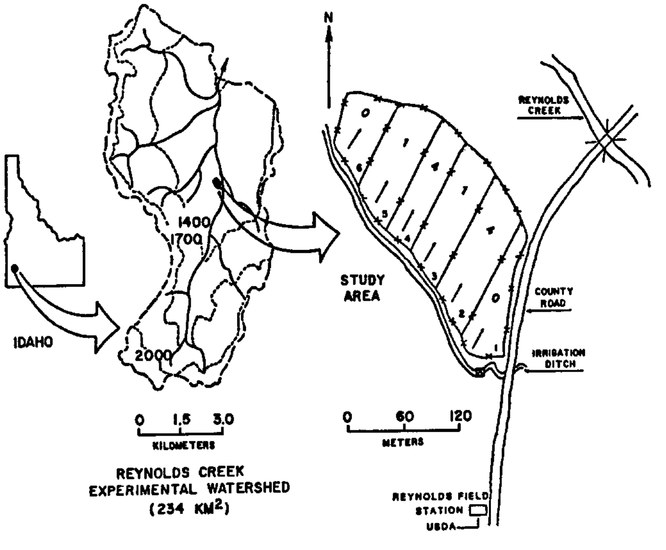

Fig. 1. *Location map showing arrangement of pastures for winter feeding. Plots are numbered right to left. Numbers 0, 1, and 4, are treatment levels.*

For this 4-year study the cattle were placed in the test pastures in early December and removed the following April during 1979 and 1980. Baled hay for feeding was distributed around the pastures daily to prevent excessive concentration of cattle in any one portion of the pastures.

At the time of this research, authors were geologist, and research associate—Cooperator University of Idaho; USDA-Agricultural Research Service, Northwest Watershed Research Center, 270 South Orchard, Boise, Ida. 83705. Stephenson is currently senior hydrogeologist, Dames & Moore, 7500 N. Dreamy Draw Drive, Suite 145, Phoenix, Ariz. 85020, and Veigel is environmental scientist, Morrison-Knudsen Engineers, Inc., 1120 Lincoln Street, Suite 1200, Denver, Colo. 80203.

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Following removal of the cattle in spring, the fields were corrigated and irrigation started. The pastures were irrigated for 24-hour periods, 3 times each growing season. The area receives about 25 cm of precipitation each year. Natural runoff rarely occurs.

The Mollisol soil in the study pastures is of the Harmehl Series, a member of the fine loamy over sandy, mixed, mesic family (Stephenson 1977). A profile description is given in Table 1. Prior to initiation of the study, in October 1979, 240 soil samples were taken from 0–12 cm depth for bulk density determination. The mean value of these samples was 1.34 g/cc with a range from 0.98 to 1.68.

Table 1. Soil properties, Harmehl Loam.

Horizon	Depth (cm)	Texture
A_{11}	0 - 12	Loam
A_{12}	12 - 42	Loam
B_{1t}	42 - 70	Gravelly loam
B_{2t}	70 - 87	Gravelly clay loam
B_{3t}	87 - 97	Gravelly, cobbly clay loam
R	97	Basalt bedrock

Hay was cut and baled in early July and mid September. Any growth occurring after the last cutting was left for grazing.

Method of Study

To evaluate soil compaction related to stocking rate, soil bulk density samples were taken from each pasture in the spring of 1979 and 1980 after the cattle were moved to rangeland, and before irrigation was started. Number of samples per treatment is given in Table 2. Because of accessibility problems, no samples were taken in the spring of 1981. Soil samples were also taken at intervals, up to 16 months after the cattle were removed from the pastures for the last time, in April 1981 (see Table 2). The latter samples (11/81, 4/82, and 8/82) were used to evaluate soil recovery from previous compaction.

Soil samples were taken by hand-driven core sampler with sample size of 7.6 cm diameter by 5.1 cm deep, or by hand dug natural clods. Clod size was kept at about 200 cc. Care was taken to remove any hay or other organic matter from the surface of the sample, and to sample only between hay plants. Each field was sampled randomly within quadrants. Core samples were placed in moisture cans, weighed, and oven dried for 48 hours at 105° C, and reweighed. The clod samples were treated with Saran (Dow Saran F 310)[1] before weighing, then oven dried and reweighed. Sampling methods and analysis procedures are those given by the USDA-SCS (1982).

One-way analysis of variance was used to test the significance of the mean bulk density values between and within treatments for the period the cattle wintered in the fields, and for the 16-month recovery period after the cattle were removed.

Discussion of Results

Soil bulk density samples were grouped according to the replicated stocking rate treatments and mean values were obtained. Table 2 gives the mean bulk density values of all samples for each treatment for the period of study.

During the time the cattle were on the fields, soil bulk density values for treatment 2 averaged 1.48 g/cc, while treatment 3 bulk density values averaged 1.58 g/cc. For treatment 1, the control, soil bulk density values averaged 1.36 g/cc throughout the study period. Following removal of cattle from the pastures for the last time in April 1981, bulk density values for pastures in treatments 2 and 3 recovered to nearly that of treatment 1, the control.

One-way analysis of variance (ANOV) was used to determine statistical relationships between stocking rates and soil compaction and recovery as determined by soil bulk density measurements. ANOV was run on the combined 1979 and 1980 data, the period of time animals were on the field for which samples were taken, to determine if the different stocking rates caused significant changes in soil bulk density. The analysis indicated that significant differences occurred between the 3 treatments at the 1% level (Table 3, part A).

Table 3. ANOV for the years cattle were on the fields (1979 and 1980).

Treatment*	Total D.F.	Factor M.S.	F. Ratio
A (Between Treatments)*			
1 vs. 2	366	1.0594	185[1]
2 vs. 3	382	1.0763	136[1]
1 vs. 3	367	4.1882	604[1]
B (Between Sample Sets)**			
1	175	0.0123	2.70[3]
2	190	0.0339	5.14[2]
3	191	0.2140	26.8[1]

[1]Significant at 1% level of probability.
[2]Significant at 5% level of probability.
[3]Not significant.
*Treatment 1 (0 cattle/ha)
Treatment 2 (10 cattle/ha)
Treatment 3 (40 cattle/ha)
**1979 sample set vs. the 1980 sample set.

When comparing the 1979 sample sets with the 1980 sample sets for each treatment, there was no significant difference for treatment 1, a significant difference at the 5% level for treatment 2, and a significant difference at the 1% level for treatment 3 (Table 3, part B). These significant differences for treatments 2 and 3 indicate that more than 1 year's growing season, with protection from trampling and grazing, is necessary for recovery of the compacted soils, even under normal stocking rates.

Table 2. Mean, standard deviation, maximum and minimum bulk density (g/cm^3) values[1] and soil water content for each treatment for period of study.

	Treatment 1 (0 cattle/ha)						Treatment 2 (10 cattle/ha)						Treatment 3 (40 cattle/ha)					
Sample date	n[2]	$\overline{X}$	σ	Max.	Min.	% H_2O	n[2]	$\overline{X}$	σ	Max.	Min.	% H_2O	n[2]	$\overline{X}$	σ	Max.	Min.	% H_2O
4/79	96	1.36	0.049	1.46	1.24	19	96	1.49	0.051	1.62	1.32	17	96	1.61	0.065	1.75	1.45	18
4/80	80	1.38	0.085	1.60	1.07	19	95	1.46	0.103	1.69	1.21	17	96	1.55	0.109	1.85	1.33	18
11/81	42	1.34	0.115	1.63	1.09	18	45	1.48	0.175	1.79	1.05	12	48	1.61	0.136	1.99	1.28	11
4/82	24	1.35	0.094	1.61	1.18	20	24	1.41	0.044	1.48	1.34	19	24	1.51	0.089	1.60	1.34	20
8/82	20	1.34	0.078	1.51	1.21	17	18	1.37	0.039	1.44	1.32	13	20	1.38	0.058	1.47	1.28	17

[1]Bulk density values are means of 2 replications
[2]n = number of samples including both replications.

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[1] Product names are provided for reader convenience and do not imply any endorsement by the USDA-Agricultural Research Service.

To determine if increased stocking rates caused long-lasting detrimental effects by excessively compacting the soil, the one-way ANOV was used to compare the data from treatments between years animals were on the pastures, April 1979 and April 1980, with data for the 16-month period after they were removed and the pastures left idle, through August 1982. Statistically, the effects of soil compaction and recovery within the 2 grazed pastures showed a significant difference for both at the 1% level of probability (Table 4).

Table 4. ANOV for the years cattle were on the pastures vs. the years after cattle were removed.

Treatments*	Total D.F.	Factor M.S.	F. Ratio
6	234	0.2670	45.12[1]
3	235	0.6429	69.37[1]

[1] Significant at 1% level of probability.
*Treatment 2 (10 cattle/ha)
Treatment 3 (40 cattle/ha)

Figure 2 shows mean soil bulk density for the replicated treatments versus stocking rate for the period of time since the cattle were last removed. The data derived from the means of April 1979 and April 1980 give an estimated base from which recovery of the compacted soils can be observed.

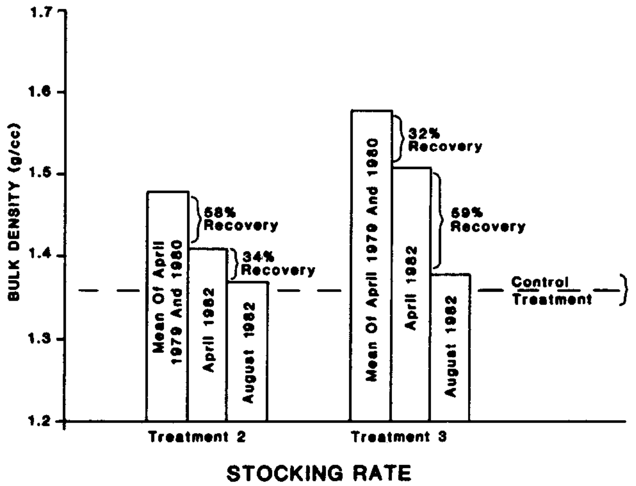

Fig. 2. *Soil bulk density versus stocking rate for recovery period.*

Referring to Figure 2 and comparing soil bulk density of the noncompacted soil in the control treatment with treatments 2 and 3, the compacted soil treatment 2 recovered to 58% of its noncompacted condition after 12 months of no animal activity; whereas, the compacted soil treatment 3 recovered only 32%. After 16 months, mean soil bulk density values for both treatments 2 and 3 were within 9% of total recovery ($P > 0.01$).

ANOV was used to test statistical significance of the soil bulk density data for the recovery period. Although absolute evidence is not available, 1979 and 1980 observations indicate that recovery of the compacted soils probably started in April 1981 when the livestock were removed from the pastures for the last time. Since no soil samples were collected at that time, the November 1981 data were used as the base set and tested against the April 1982 and August 1982 data for treatments 2 and 3. Results show the differences to be significant at the 1% level (Table 5).

Table 5. ANOV for the years after cattle were removed from the pastures.

Treatment*	Total D.F.	Factor M.S.	F. Ratio
2	88	0.1055	6.39[1]
3	91	0.3836	30.69[1]

[1] Significant at 1% level of probability
*Treatment 2 (10 cattle/ha)
Treatment 3 (40 cattle/ha)

Summary and Conclusions

Conclusions from this study are:

1. Soil bulk density variations between treatment 1 (the control), treatment 2 (10 cattle per ha), and treatment 3 (40 cattle per ha) were statistically significant, indicating that increased stocking rate increased the soil bulk density.
2. The mean soil bulk density values of treatments 2 and 3 showed a 92% recovery 16 months after protection from grazing and trampling when compared to the control field. This shows that recovery of these compacted soils was nearly complete after 2 growing seasons for both the normal and 4 times normal stocking densities. This is in close agreement with Orr (1975), who found that more than one season of protection was necessary for significant soil recovery.

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First Call for Papers
1988 SRM Convention
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Titles are now being solicited for papers to be presented at the 41st Annual Meeting of the Society for Range Management, February 14-19, 1988. Please complete the following form (one form per title) and **submit to the program Chairmen by June 1.** Senior authorship limited to 1 paper; junior authorship limited to 3 papers.

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Remember! Deadline for titles is June 1, 1987

Shrub Litter Production in a Sagebrush-Steppe Ecosystem: Rodent Population Cycles as a Regulating Factor

ROBERT R. PARMENTER, MARK R. MESCH, AND JAMES A. MACMAHON

Abstract

This study examines the impact of long-tailed vole *(Microtus longicaudus)* and deer mouse *(Peromyscus maniculatus)* population changes and their feeding behavior on shrub populations and the resulting litter production in a shrub-steppe ecosystem in southwestern Wyoming. Rodent populations were monitored on 3 replicate plots over a 3-yr period. Populations peaked in autumn 1983 and declined to lower levels in 1984–86. Damage to shrubs (in the form of bark-stripping and girdling) was observed after the winter of 1983–84, but not after the winters of 1984–85 and 1985–86. We assessed damage to shrubs on 4 sites. Extent of damage, mortality, and biomass-to-litter transformations were quantified. We found that: (1) 21% of all shrubs and 28% of the big sagebrush *(Artemisia tridentata)* sustained rodent damage; (2) 1% of all shrubs were killed as a result of girdling; (3) mean biomass lost from shrubs that suffered damage was 36%; (4) total aboveground biomass loss occurring on big sagebrush was 231 kg/ha or 4% of the standing crop. These results indicate that rodents feeding on big sagebrush can periodically increase annual rates of litter production by as much as 69% above "normal." Rodents in the sagebrush-steppe ultimately influence ecosystem-level nutrient cycles by accelerating shrub litter production, and may affect plant species composition via feeding-induced shrub mortality.

Key Words: ***Artemisia tridentata*, herbivory, *Microtus longicaudus*, *Peromyscus maniculatus*, rodents**

The role of herbivorous animals in determining the structure and functioning of ecosystems has generally been appraised on the basis of trophic interactions, i.e., the proportion of net primary production (NPP) actually consumed by the herbivores. For most ecosystem-level analyses, the amount of NPP handled by herbivores (both vertebrate and invertebrate) is less than 20% (Chew 1974, Bormann and Likens 1979, Swift et al. 1979, Zlotin and Khodashova 1980). Rather than being important as consumers of energy, herbivores may act as ecosystem regulators, influencing not only plant species composition (via selective herbivory), but also the rates at which energy transfers take place (Chew 1974, 1978, Swift et al. 1979, MacMahon 1981). Such regulatory functions may involve very meager energy expenditures, but can have dramatic and far-reaching effects on the ecosystem. Examples of such animal-plant interactions include pollination of flowers, dispersal of seeds, transmission of diseases, alteration of soils, inoculation of fungal-spores, and so on. These phenomena have what Odum and Odum (1976) term a "high energy quality ratio;" that is, the amount of energy flow affected by the interaction is far greater than the amount of energy spent during the interaction.

In contrast to their relatively minor role in energy consumption, herbivores may dramatically affect the rates of nutrient cycling (Kitchell et al. 1979). Herbivores normally feed on living plant parts that contain a disproportionately high concentration of essential nutrients (compared to woody parts or detritus), and therefore can consume a large percentage of the vegetation's nutrient stores (Swift et al. 1979). Some herbivores also induce nonconsumptive wastage of plant parts (e.g., meristem feeders, stem borers, and bark ringers), that cause pulses of nutrients to be added to the decomposition process via release of nutrients stored in normally long-lived plant parts (e.g., tree trunks or shrub stems) (Crawley 1983).

The role of rodents as consumers of primary production in many ecosystems appears to be minor, although impacts on vegetation during population outbreaks can be severe. In a review of the literature, Golley (1973) reported that in 12 of 17 studies, rodents consumed less than 5.5% of the available primary production. He further suggested that, because of the rapid turnover rates exhibited by rodent populations, rodents may influence nutrient cycling and decomposition rates via litter production and fecal deposition (Golley 1973). In support of this hypothesis, results of studies in the meadow-steppe of the USSR have demonstrated that the presence of voles *(Microtus arvalis)* causes a substantial increase in litter production and an even greater increase in litter mineralization, resulting in overall faster nutrient cycling (Zlotin and Khodashova 1980).

In the shrub-steppe ecosystem of the Intermountain Basin of North America, the ubiquitous deermouse *(Peromyscus maniculatus)* is usually the numerically dominant rodent species. By virtue of their numbers, deer mice can potentially account for a substantial proportion of the NPP normally consumed by rodents. Voles (*Microtus* spp.) constitute only a small proportion of the total rodent fauna (e.g., Rickard 1960, Brown 1967, Maxwell and Brown 1968, Parmenter and MacMahon 1983) and are patchily distributed (Long 1965, Lechleitner 1969, Randall 1978). Consequently, their contribution to total NPP consumption should be minimal. Microtines, however, are renowned for their tremendous population irruptions (Piper 1909, Murray 1965), peaking at reported densities of 7,000–29,000 voles per hectare (Piper 1909, Spencer 1959). When rodent populations reach cycle peaks, extensive damage to both herbaceous and woody vegetation occurs (Piper 1909, Hubbard and McKeever 1961, Mueggler 1967, Phillips 1970, Frischknecht and Baker 1972, Sturges 1983). Rodent consumption of woody vegetation is generally restricted to the plant's cambium and phloem layers (after having stripped off the dry, outer bark). The amount of plant material consumed is relatively small; but if the rodents' feeding activity completely surrounds a stem, then the remaining plant above the "girdling" site dies. This type of feeding activity results in a biomass-to-litter transformation which is orders of magnitude greater than the amount of biomass actually eaten. Hence, an important aspect of the rodents' influence in the shrub-steppe ecosystem may be to periodically increase litter production, which ultimately accelerates nutrient cycling.

The purpose of this study was to determine the extent and distribution of nonconsumptive damage to shrubs by long-tailed voles (*Microtus longicaudus longicaudus*[Merriam]) and deer mice (*Peromyscus maniculatus nebrascensis* Coues), and to estimate the amounts and proportions of aboveground shrub biomass converted to litter.

Study Site

The study site was located 8 km southwest of Kemmerer, Wyo.,

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(Lat. 41°43'30"N, Long. 110°38'15"W) (T.20N, R.117W, Sec. 9) at an elevation of 2,255 m. Terrain was characterized by rolling hills with a north-south strike. Precipitation (mostly snow) averages 22.6 cm/yr, but is highly variable. Mean monthly temperatures range from -8° C in January to 17° C in July (Parmenter and MacMahon 1983).

Vegetation in the area was shrub-steppe (West 1983), and was composed of 2 physiognomically distinct plant associations. The first, with which this paper deals, was dominated by big sagebrush (*Artemisia tridentata* Nutt.), antelope bitterbrush (*Purshia tridentata* DC.) and Utah serviceberry (*Amelanchier utahensis* Koehne). Understory vegetation was predominantly grasses (*Oryzopsis* spp., *Poa* spp. and *Bromus* spp.) and a variety of forbs. This association of plants was patchily distributed throughout the area, occurring most frequently in moister areas (e.g., along ephemeral stream courses and the leeward side of hills and ridges where deep winter snowpacks accumulate). These patches of tall shrubs were surrounded by areas of much shorter vegetation, dominated by the diminutive low sagebrush (*Artemisia arbuscula* Nutt.), cushion plants (*Arenaria congesta* Nutt., *Artemisia frigida* Willd., and *Phlox hoodii* Richards) and grasses (*Oryzopsis* spp. and *Poa* spp.).

Methods

Shrub-feeding Rodent Species

Direct observations of rodent shrub-feeding behavior could not be made, because the feeding activity took place beneath the winter snowpack. In addition, we were unable to ascribe shrub damage to a particular rodent species, because stems damaged by different rodent species were identical in appearance (see below). Therefore, we combined published natural history reports and documented incidences of rodent damage to shrubs with our own field and laboratory observations to identify the potential shrub-feeding rodent species. Our field observations included the presence and patterns of rodent tracks in the snow, as well as winter activity and nesting data on deer mice obtained during a 1983–84 radio-telemetry study (data provided by L. Broome, Department of Biology, Utah State University, 1985).

We conducted feeding experiments in the laboratory to determine if voles and deer mice would eat sagebrush stems. Three long-tailed voles and 3 deer mice were housed in glass cages, with each cage having a 5-cm-deep layer of sand across the bottom. The rodents were provided with nest boxes and bowls of water. We first placed stems (20–30 cm long) of big sagebrush in the rodents' cages (6 stems/rodent) in the presence of other foods (native seeds and green vegetation) for 5 days, and periodically checked the stems for evidence of feeding activity. We then deprived the rodents of all food except the sagebrush stems for 48 h, and again inspected the stems for evidence of feeding activity.

Rodent Trapping

Rodents were trapped on three 2-ha grids of Sherman live traps. Each grid consisted of 225 traps arranged in a 15 × 15-station square (10-m station interval) with a single trap at each station. Traps were baited with peanut butter and rolled oats and left open continuously for 4 consecutive days and nights during each trap period. Traps were checked daily; and captured rodents were identified, toe-clipped, and then released. Trap periods occurred at approximately 6-wk intervals (May through September) during 1983–85 and in early May 1986.

Vegetation Sampling

Preliminary inspection of shrubs in both plant associations revealed that instances of shrub damage were confined to the patches of tall shrubs. For this reason, we restricted our plant sampling efforts to the tall shrub patches. To ascertain the areal proportion of tall shrub patches on the study site, we used a planimeter to measure the sizes of all tall shrub patches on a 1:4800 scale aerial photograph of the area. Tall shrub patches delineated on the aerial photograph were verified by ground-truth examination.

Vegetation surveys took place during midsummer (July and August) in 1984 and 1985, and in May 1986. Four 30-m transect lines were arbitrarily chosen based on the criterion that lines were enclosed within the tall shrub patches. Relative abundance and percentage cover of shrub species on each line was determined using the line intercept method (Canfield 1941). Shrub canopy area was estimated by assigning a particular geometric configuration (circle, triangle, or ellipse) to each individual shrub and measuring the appropriate dimensions. Shrub height was also recorded.

Each shrub along the transect line was inspected for rodent damage. Damage to shrubs ranged from small areas (<10 cm^2) of stripped bark along the main stem to complete girdling of branches. This latter type of damage resulted in parts of the shrub being killed. These dead parts were cut off at the girdling point with pruning shears and weighed in the field using Pesola® scales. After removing and weighing all dead parts on a shrub (attributable to rodent feeding), the remaining parts of the shrub were cut off at ground level and weighed. Through this procedure we were able to determine the total aboveground biomass of the damaged shrub and the proportion of the shrub killed by girdling. [Note: Our shrub biomass measurements were all fresh weights, although the dead shrub parts had dried out considerably and lost most of their leaves by the midsummer sampling time. Hence, our values represent conservative estimates of shrub-biomass losses.]

Results and Discussion

Shrub-feeding Rodent Species

Only 3 species of rodents on our plots were active during the winter: the long-tailed vole, the deer mouse, and the sage vole (*Lagurus curtatus levidensis* [Goldman]). Long-tailed voles, along with other microtines, have been implicated in bark-stripping, particularly during periods of winter snowpack (Bailey 1900, Piper 1909, Hubbard and McKeever 1961, Mueggler 1967, Frischknecht and Baker 1972). The long-tailed vole also inhabits the tall shrub patches in which all of the observed shrub damage occurred (Long 1965, Lechleitner 1969, this study [see below]). We believe the long-tailed vole was a major participant in the shrub-feeding activity on our study plots.

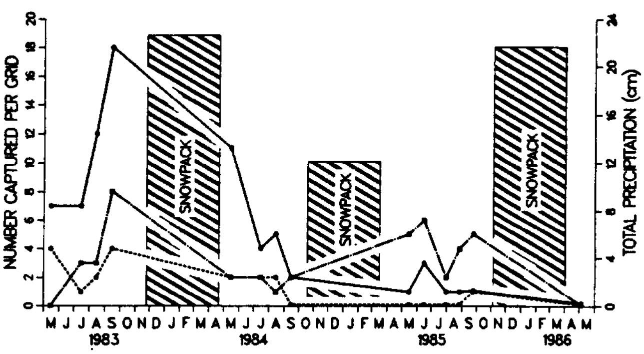
In our laboratory feeding trials, all 3 long-tailed voles and all 3 deer mice exhibited identical behavior: they ate none of the big sagebrush stems when seeds and green vegetation were present but ate the bark and cambium layers of all 6 sagebrush stems when alternative foods were absent. The results indicate that although big sagebrush is not a preferred food, it is readily eaten when better foods are not available. The stripped pieces of stem appeared identical to damaged shrubs observed in the field. Stems damaged by voles were indistinguishable from those damaged by deer mice.

The deer mouse is not known to regularly eat shrub parts (Williams 1959, Johnson 1961, Becker 1977), although it may shift its diet during periods of food shortage. This was demonstrated in our laboratory feeding experiment. Winter field observations of deer mouse tracks and radio-telemetry data collected during the winter of 1983–1984 showed that deer mice were active in patches of tall shrubs. Inspection of deer mouse nests revealed that they were made almost entirely from strips of big sagebrush bark (L. Broome, personal communication, 1985). While we do not know for certain if the deer mice in the study area were feeding on shrub stems or simply collecting bark for nesting material, it seems probable that deer mice contributed to the damage inflicted on the shrub population.

The sage vole is active all year and feeds predominantly on green vegetation, especially sagebrush (Walker 1975). However, the trap-capture locations of this species, combined with radio-telemetry data on microhabitat use (R. Parmenter, unpublished data), indicate that sage voles on our study plots stayed in areas of short vegetation which did not suffer any observable shrub damage. Therefore, we do not believe that sage voles contributed to the winter shrub damage.

Rodent Population Changes

The populations of both long-tailed voles and deer mice were greater during the winter of 1983-84 than in subsequent periods (Fig. 1). Rodent populations peaked in September 1983, and had declined somewhat by May 1984. The populations continued to decline during the summer of 1984 and began the winter of 1984–85 at considerably reduced levels. [Note: We did not measure population sizes during periods of snowpack; hence, the true form of the winter population changes depicted in Figure 1 may not be linear.]


Microtus longicaudus

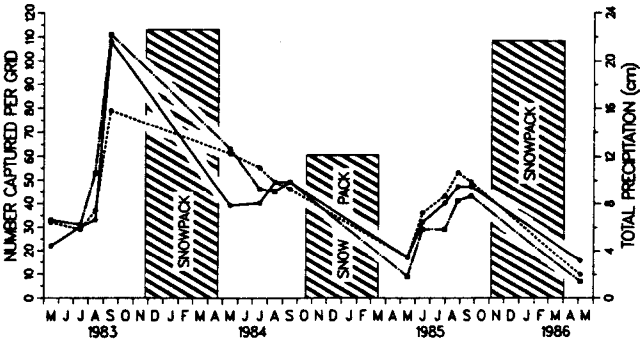

Peromyscus maniculatus

Fig. 1. *Rodent population changes on 3 trap grids (solid, dashed, and dash-dot lines) near Kemmerer, Wyo. Shaded columns represent periods of permanent winter snowpack: column width corresponds to duration of snowpack; column height corresponds to the total amount of precipitation received during the snowpack period (precipitation data from S. Smith, Department of Biometeorology, Utah State University).*

Captures of long-tailed voles were restricted to traps located in the tall shrub associations, and the areal amount of tall shrub vegetation varied among plots; therefore, differences in absolute population sizes among grids were partially attributed to differing quantities of suitable habitat. Vole populations on all 3 replicate grids, however, exhibited similar fluctuations over time.

Rodent Impacts on Vegetation

The patches of tall shrub vegetation in the sample areas were dominated by big sagebrush (Table 1). Sagebrush density in the patches, measured in 1981, was approximately 16,000 shrubs/ha (Alan Carpenter, Department of Range Science, Utah State University, unpublished data). Based on the aerial photo measurements, the tall shrub association comprised 43% (86 ha) of the total land area (200 ha) covered in the photograph.

We observed damage to shrubs only after the winter of 1983–84; extensive inspections of shrubs on the plots following the winters of 1984–85 and 1985–86 produced no observable evidence of rodent shrub-feeding activity. The 1984 damage was confined to the tall shrub patches and was evident in the spring, after snowmelt. Rodents had stripped the bark primarily from big sagebrush (Table 2), although several antelope bitterbrush (4 of 6 shrubs sampled) and a single rabbitbrush (*Chrysothamnus viscidiflorus* [Hook.] Nutt.) were also damaged. Shrubs in Transect 4 did not sustain any damage by rodents. Although both voles and deer mice had been trapped in the area of Transect 4 during the summers of 1984 and 1985, we do not know for certain if the rodents remained in this area during the winter months. When the data from Transects 1–4 are combined, 28% of the big sagebrush population and 21% of the total shrub population suffered some degree of damage. Only 1% of the big sagebrush individuals were completely killed by the girdling.

Table 1. Percentage cover of shrub species in tall shrub vegetation on sample transects near Kemmerer, Wyoming.

Shrub species	Transect Number 1	2	3	4
Artemisia tridentata	34.7	54.1	27.0	11.4
Chrysothamnus viscidiflorus	0.8	0	13.2	10.8
Purshia tridentata	7.2	1.5	0	0
Symphoricarpos sp.	3.1	0	0.3	0

Table 2. Assessments of rodent damage to big sagebrush *(Artemisia tridentata)* near Kemmerer, Wyoming, during the winter of 1983–84. No damage was observed after the winters of 1984–85 or 1985–86.

Transect number	Number of shrubs sampled	Percentage of shrubs damaged	Percentage with biomass losses	Mean (± SE) percentage of biomass lost per damaged shrub
1	23	39	17	25 ± 4
2	37	22	11	48 ± 21
3	16	38	6	19 ± 0
4	5	0	0	0

Comparison of our results with previously published estimates of shrub damage and/or mortality during rodent population irruptions (Hubbard and McKeever 1961, Mueggler 1967, Phillips 1970, Frischknecht and Baker 1972) are difficult because concomitant values of rodent population sizes were not included in those studies. The percentage of damaged shrubs reported by these authors, however, is quite comparable to our value of 21% (28% of big sagebrush). Hubbard and McKeever (1961) observed that 15% of the bitterbrush on their plots in northeastern California was damaged by voles in 1957–59. Phillips (1970) reported damage of 10–20% of bitterbrush in southern Idaho during 1958 and 1963. Frischknect and Baker (1972) estimated that 28% of the big sagebrush on their central Utah plots was damaged in 1969.

While these damage estimates appear similar, the shrub mortality reported in those same studies was considerably higher than our estimate of 1%. Mortality estimates for bitterbrush ranged from 5% (Hubbard and McKeever 1961) to 38% (Phillips 1970), while big sagebrush mortality varied from 10–84% in Montana during 1962–64 (Mueggler 1967) and 36–73% in Utah (Frischknecht and Baker 1972). The discrepancy between our estimate of mortality and those in other reports may be due to different rodent densities in the study area. Vole densities during the other studies must have been quite high for those authors to discern a population irruption without comparative trapping data. The vole and deer mouse populations during our study were not particularly large, and without extensive trap data we would have had difficulty detecting population changes between years. The magnitude of shrub mortality may reflect rodent densities, although several mediating factors (discussed later) may also be involved.

On our sites (4 Transects combined) 11% of the shrubs lost some biomass due to girdling. If a shrub lost biomass, then the average amount lost was 36% of its wet weight (actual mean biomass loss per shrub = 305 g ± 106 (SE), range = 18–1015 g). The big sagebrush plants in the area had a mean wet weight of 849 g ± 177 (SE) (range = 371–1750 g). Combining these values, the total amount of big sagebrush biomass lost via rodent girdling was 231 kg/ha, or approximately 4% of the total aboveground standing crop of sagebrush.

These results indicate that rodents can have a substantial influence on rates of litter production in the sagebrush-steppe ecosystem. Measurements of "normal" annual litter production from big sagebrush in the Great Basin Desert indicate that between 5.8% (West and Gunn 1974) and 13.4% (Mack 1977) of total aboveground standing crop biomass is converted to litter each year via senescence, drought, winter-kill, insects, pathogens, etc. Leaves and inflorescences comprise a vast majority of the litter; only 0.2% of the standing crop biomass annually converted to litter is woody material (calculated from data in Mack 1977). Assuming that the big sagebrush on our sites produces comparable annual amounts of litter, then the amount of aboveground standing crop biomass killed by rodents (4%) represents a 30–69% increase in total annual sagebrush litter production. In addition, because almost all of the biomass from killed shrub parts was woody stems, the rodent damage equates to about a 20-fold increase in annual production of wood litter from big sagebrush. These values would be substantially larger in situations where extensive shrub mortality occurs, such as those in areas studied by Mueggler (1967) and Frischknecht and Baker (1972).

Given that even moderate densities of rodents can inflict substantial damage and mortality on shrub populations, a potential influence of rodents on the nutrient cycling processes of the shrub-steppe ecosystem is apparent. The large amounts of unconsumed detritus produced by the rodents' feeding activity enters the decomposer food chain and provides a new source of essential nutrients to the remaining plant community. The leaves on shrubs girdled during the winter wither and drop from their branches in the spring, and are quickly decomposed. In our study areas, big sagebrush leaves on the ground beneath shrubs lost 75% of their dry weight in only 4 months (May to September) (M. Allen, Department of Biology, Utah State University, unpublished data, 1985). The remaining twigs and branches are not immediately available to the decomposers, as they persist as "standing dead" shrubs of several years. Eventually, though, they too are incorporated into the litter layer.

Rodent-induced mortality of shrubs influences the population age structure of the target species, as well as the species dominance relationships in the plant community. Mueggler (1967) found that voles preferentially selected mature and "decadent" (senescent) big sagebrush over young individuals. Analysis of damaged and undamaged shrub size classes on our sites revealed that rodents generally selected shrubs without preference to height or canopy coverage (Table 3). While rodents on Transect 1 fed on shrubs with significantly greater canopy areas, no such phenomenon was observed on Transects 2 or 3. Our data suggest that shrub selection based on shrub height and canopy area is generally random, although our tall shrub patches were dominated by mature individuals. Elimination of large shrubs from the population exposes new areas of land for colonization by individuals of the same and other plant species, thereby altering the community structure. If shrub mortality were extensive (e.g., Mueggler 1967, Frischknecht and Baker 1972), dramatic and persistent changes could occur in both the floral and soil components of the shrub-steppe ecosystem (Sturges 1983).

Table 3. Heights (cm) and canopy areas (cm²) of undamaged and damaged big sagebrush *(Artemisia tridentata)* from sample areas near Kemmerer, Wyoming. All values are means ± 1 SE.

Transect number	Shrub Height		Shrub Canopy Area	
	Undamaged	Damaged	Undamaged	Damaged
1	50 ± 6	71 ± 8	1950 ± 255*	4213 ± 743
2	77 ± 5	86 ± 9	3532 ± 664	2906 ± 846
3	85 ± 10	55 ± 8	4824 ± 1113	2473 ± 531
4	98 ± 19	None Damaged	5669 ± 2186	None Damaged

* = Significantly different, t-test, $P \leq 0.05$.

Because shrubs are damaged only periodically by rodents, and then only during the winter months, we hypothesize that bark-stripping by rodents is initiated when (1) population densities become so great as to exhaust the supply of palatable grasses, forbs and seeds, and/or (2) the accessibility of subnivean food resources is reduced by structural changes (ice or crust formations) in the lower levels of the winter snowpack (Langham 1981, Male and Gray 1981). Winters characterized by deep, long-lasting snowpacks would presumably exacerbate the food shortage situation. While these hypotheses have yet to be experimentally tested in the field, they are certainly consistent with the observations reported here (Fig. 1) and in previous studies (e.g., Mueggler 1967, Frischknecht and Baker 1972).

How frequently do rodent populations damage shrub stands? The published reports suggest major, widespread destruction occurs about once every 5 to 10 years, although localized incidences of shrub damage can be observed in virtually every year (Walter Mueggler, Forestry Sciences Laboratory, Logan, Utah, personal communication, 1985). Because many shrub species in the Intermountain Basin have life spans of 80 years or more (Roughton 1972), they may be exposed to as many as 10–15 rodent population cycles. Therefore, rodent feeding activity can be a very important source of litter production and shrub mortality in areas providing suitable rodent habitat.

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Grazing System Influences on Cattle Performance on Mountain Range

JERRY L. HOLECHEK, TIMOTHY J. BERRY, AND MARTIN VAVRA

Abstract

A 5-year study was conducted to evaluate the influences of rest-rotation, deferred-rotation, and season-long grazing systems on cattle diet botanical composition and quality and weight gains on mountain rangeland in northeastern Oregon. The grazing season in each year lasted from 20 June to 10 October. Esophageally fistulated animals were used to evaluate diet quality and botanical composition. All study pastures included forest, grassland, and meadow vegetation types. Each pasture had a north and south-facing slope divided by a riparian zone and creek. The grazing pressure for each system was similar. Grazing intensity was the same as National Forest Allotments in the area. There were no differences ($P>.05$) in weight gains among the 3 systems when data were pooled across years. Crude protein, in vitro organic matter digestibility, and acid detergent fiber percentages in fistula samples did not differ ($P>.05$) among systems for any year of study or for data pooled across years. Mid-season movements of cattle under the rest-rotation system had little influence on their diet and performance compared with cattle under the season-long system. Key forages in cattle diets were Idaho fescue *(Festuca idahoensis)*, bluebunch wheatgrass *(Agropyron spicatum)*, and common snowberry (*Symphoricarpos albus)*. Cattle diet botanical composition under the 3 grazing systems did not differ ($P>.05$).

Key Words: ruminants, nutrition, cattle diet, nutrient analysis

Although rest-rotation and deferred-rotation grazing systems have proven effective from vegetation, soil, and wildlife standpoints in mountainous areas, their influences on livestock nutrition and production are not completely understood. In Utah Laycock and Conrad (1981) found cattle daily gains on mountain range did not differ between rest-rotation and season-long grazing systems. Skovlin et al. (1976) found no cattle weight gain differences between deferred-rotation and season-long grazing systems at the Starkey Experimental Range and Forest in northeastern Oregon. Comparisons of cattle diet nutritional quality among rest-rotation, deferred-rotation, and season-long grazing systems on mountain ranges have not been reported.

The objectives of our study were to compare cattle diet botanical composition and quality and cattle performance among rest-rotation, season-long, and deferred-rotation grazing systems during 5 years on mountain rangeland in northeastern Oregon.

Study Area and Methods

The study area was located on the Starkey Experimental Range and Forest in the Blue Mountains of northeastern Oregon. A thorough description of the Starkey Range is given by Skovlin et al. (1976). The average annual precipitation is 53 cm and comes primarily as snow and rainfall in the winter and spring (Table 1). A complete description of the vegetation on the study pastures is given by Ganskopp (1978). The percentage relative cover of important forage species on the 4 study pastures is given in Table 3.

Table 1. Summary of precipitation data (cm) at the Starkey Experimental Forest and Range.

Month	24-year $\bar{x}$	1976	1977	1978	1979	1980
January	6.53	6.86	1.02	5.08	5.21	5.11
February	4.45	2.29	2.54	4.06	6.07	2.79
March	4.52	2.54	2.11	3.56	4.27	4.75
April	4.42	5.08	2.79	6.68	5.84	3.48
May	5.31	4.39	4.80	4.01	5.00	6.66
June	4.42	3.71	1.83	3.12	1.55	6.88
July	1.63	0.05	0.13	2.54	0.74	1.27
August	1.98	6.86	7.42	3.43	6.96	0.48
September	2.77	3.71	9.42	4.11	1.02	2.97
October	4.29	2.67	3.76	7.11	7.85	1.25
November	5.52	4.06	7.75	4.06	6.05	3.91
December	6.93	0.00	9.40	3.20	2.08	6.60
Total	52.77	42.22	53.00	50.96	52.64	46.15

Vegetation types included in each of the 4 study pastures were grassland (south facing slopes), forest (north facing slopes), and meadow (riparian zone). All pastures were divided by Meadow Creek and the associated riparian zone. South facing slopes, north facing slopes, and riparian zones occupied about 65%, 31%, and 4%, respectively, of each pasture.

The 4 study pastures were delineated and fenced so they would be as equal as possible in grazing capacity, vegetation composition, vegetation structure, and terrain. Size of each pasture is given in Table 2. One pasture was used for the season-long grazing system. The deferred-rotation system involved alternating grazing between early (June 10–August 15) and late use (August 16–October 10) in consecutive years on the 1 pasture. A 4 pasture–2 herd rest-rotation grazing system was applied to the remaining 2 pastures. The grazing schedule involved 1 pasture at season-long use; 1 pasture grazed early to mid-season (June 20–August 15), 1 pasture grazed mid-season to grazing season end (August 16–October 10); and 1 pasture rested.

Berry (1982) evaluated grazing pressure under the 3 systems in 1979 and 1980. His data, summarized in Table 2, show grazing pressure was nearly equal among the 3 systems. The stocking rate of the pastures was similar to that on National Forest allotments in the immediate area and many other parts of the western United States.

Hereford/Angus crossbred yearling heifers weighing 320 ± 10 kg and owned by a cooperating rancher were used to evaluate livestock performance. These heifers had been grazed on the Starkey range the previous summer as calves. During each year of study, the rest-rotation, deferred-rotation, and season-long grazing systems were stocked with 20, 20, and 10 head of yearling heifers, respectively. Three of the animals assigned to each system were owned by Oregon State University and equipped with esophageal fistulas. The grazing season lasted 120 days in each year of study. The performance of animals (weight gains) assigned to each system was evaluated in late spring (20 June to 18 July), early summer (19 July to 15 August), late summer (16 August to 12 September), and fall (13 September to 10 October). Fistulated animals were not used for livestock performance evaluation. Heifers were weighed without shrink at the onset of grazing and at the end of each period.

Diet samples from each grazed pasture were collected twice every other week during all 5 years of study. Collections on each

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Table 2. Grazing pressure under rest rotation (RR), season long (SL) and deferred rotation (DR) grazing systems.[1]

System	Total Production of forage (kg/ha)	Utilization (%) (uplands)	Utilization (%) (Riparian zone)[2]	Area (AUM's)	Animal Unit Months (Ha/AUM)	Stocking Rate Forage	Metric Tons of Available Available Forage	Grazing Pressure (AUM)/ Metric Ton of
RR	160	29	52[3] - 73%[4]	67 - 57[5]	48	2.58	19.8	2.4
SL	181	19	50	50	24	2.09	9.1	2.6
DR	128	20	70	74	24	3.09	9.5	2.5

[1] Production and utilization data were collected in 1979 and 1980 and pooled across years.
[2] Larry Bryant, Unpublished data, PNWFRES, Forest Service, LaGrande, Oregon.
[3] Ungrazed and grazed pastures.
[4] Grazed pastures only.
[5] RR1 = 67 ha, RR2 = 57 ha.

Table 3. Percentage relative cover of primary forage species on grazing system pastures and their percentage by weight contribution to cattle diets for data pooled across years and periods.

Species	% Cover[1]					Cattle Diet % Composition[12]					
	RR1	RR2	SL	DR	$\bar{x}$	RR1 $\bar{x}$	RR2 $\bar{x}$	RR[3] $\bar{x}$	SL $\bar{x}$	DR $\bar{x}$	Diet $\bar{x}$
Bluebunch wheatgrass *(Agropyron spicatum)*	16	8	7	8	10	8	14	11	12	13	13
Idaho fescue *(Festuca idahoensis)*	8	15	15	7	11	11	14	13	16	10	12
Elk sedge *(Carex geyeri)*	6	7	6	7	6	8	3	6	6	3	5
Sandberg bluegrass *(Poa sandbergii)*	7	15	16	16	14	3	6	5	5	3	4
Kentucky bluegrass *(Poa pratensis)*	8	7	7	8	8	10	6	8	7	8	7
Miscellaneous grasses	15	4	8	11	9	22	20	21	20	25	21
Total grasses	60	56	59	57	58	62	63	63	66	66	65
Clover (*Trifolium* sp.)	1	1	1	1	1	2	1	2	2	3	2
Western yarrow *(Achillea millefolium)*	3	2	2	2	2	5	5	5	2	3	4
Miscellaneous forbs	17	20	15	18	17	14	16	15	11	15	15
Total forbs	20	23	18	21	20	21	22	21	18	21	21
Common snowberry *(Symphoricarpos albus)*	7	8	9	8	8	11	8	10	9	11	10
Ninebark *(Physocarpus malvaceus)*	8	8	6	7	7	3	3	3	2	1	2
Miscellaneous shrubs	5	5	8	7	7	3	4	4	5	1	2
Total shrubs	20	21	23	22	22	17	16	16	16	13	14

[1] RR1 = Rest rotation pasture 1, RR2 = Rest rotation pasture 2, SL = Season long pasture, DR = Deferred rotation pasture.
[2] There were no statistical differences ($P<.05$) between grazing systems for any diet species or category.
[3] $\bar{x}$ of RR1 and RR2.

pasture were always made during the same week. This resulted in the collection of 12 samples from each grazed pasture for each period. Fistulated animals were moved to preselected areas and allowed to feed uninhibited until at least 1 kg of grazed forage was acquired. Fistula samples were dried in a forced-air oven at 40° C for 7 days and then ground through a 20-mesh screen. Data by Acosta and Kothmann (1978) indicate that oven drying for an extended period as in our study can elevate fiber values compared to freeze drying methods. Although our drying methods may have elevated fiber and reduced digestibility values, we doubt that it had much influence on treatment differences. Crude protein (Kjeldahl procedure) was determined by AOAC (1980) methods. The in vitro digestion technique of Tilley and Terry (1963) was modified by Vavra et al. (1973) and used to determine organic matter digestibility. Acid detergent fiber was determined using methods of Goering and Van Soest (1970). Both crude protein and acid detergent fiber were converted to an organic matter basis. Diet botanical composition of fistula samples was determined by the technique of Sparks and Malechek (1968).

Differences in diet botanical composition, diet quality and daily gains among systems were evaluated using a completely randomized one-way analysis of variance model (Steel and Torrie 1980). Animals in each pasture were used as replicates for this analysis because pastures for each grazing system were not replicated. We recognize this as an important limitation to our study. Statistical comparisons were made between grazing systems within each period and year. LSD mean separation was used to compare grazing system means. Covariance analysis was used to adjust average daily gains for initial weights at the beginning of each period.

Results and Discussion

Diet Botanical Composition

Idaho fescue *(Festuca idahoensis)*, bluebunch wheatgrass *(Agropyron spicatum)*, Kentucky bluegrass *(Poa pratensis)*, elk sedge *(Carex geyeri)*, and common snowberry *(Symphoricarpos albus)* were the most important forage species found in cattle diets (Table 3). Other researchers on similar but different pastures at the Starkey Range from those in the present study have shown these to be the primary forages for cattle (Pickford and Reid 1948; Holechek et al. 1982b,c; Holechek and Vavra 1983a). Seasonal trends in forage selection were consistent with the other studies and therefore will not be discussed.

No differences ($P>.05$) occurred between grazing systems for any forage species or category when diet botanical composition data were pooled across seasons and years (Table 3). However, there were some yearly and seasonal differences ($P<.05$) in grass, forb, and shrub consumption between the rest-rotation and season-long grazing systems.

Our research indicates rest-rotation grazing does not increase ($P>.05$) use of secondary forages, such as Sandberg bluegrass *(Poa sandbergii)* compared to season-long or deferred-rotation grazing (Table 3).

Diet Quality

Grazing systems had a small influence on overall cattle diet quality during the 5 years of study (Tables 4, 5 and 6). With seasonal advance, cattle diets showed a general decline in quality (lower crude protein and digestibility; higher acid detergent fiber) until the fall period when quality improved. Diet quality was lowest in the late summer period due to forage maturation. In years with late summer and fall rains (all years except 1980), forage regrowth occurred in the grassland openings. This explains why diet quality improved during the fall period in all years except 1980.

Table 4. Percent crude protein (organic matter basis) in diet samples by year, period, and grazing system.

Year Period[1,2]	Rest-rotation	Season-long	Deferred-rotation
1976			
Late spring	14.5	14.7	12.5
Early summer	11.1	11.3	9.3
Late summer	13.3	13.7	
Fall	11.1	11.0	
$\bar{x}$	12.5	12.7	10.9
1977			
Late spring	16.7^{a}	13.8^{b}	
Early summer	9.1^{a}	10.9^{b}	
Late summer	8.2	8.3	8.4
Fall	9.6	8.4	8.8
$\bar{x}$	10.9	10.4	8.6
1978			
Late spring	12.6	12.4	13.0
Early summer	12.1	11.0	11.6
Late summer	8.7	8.5	
Fall	10.8	9.1	
$\bar{x}$	11.0	10.2	12.3
1979			
Late spring	13.4	12.3	
Early summer	14.4	13.0	
Late summer	10.6^{a}	13.0^{b}	9.8
Fall	11.9	10.2	10.6
$\bar{x}$	12.6	12.1	10.2
1980			
Late spring	13.0	12.7	13.2
Early summer	12.4	12.1	12.1
Late summer	9.5	9.8	
Fall	8.2^{a}	9.7^{b}	
$\bar{x}$	10.8	11.1	10.6
Grazing System Overall $\bar{x}$	11.6	11.3	10.9

[1] Means with different letters are significantly different ($P<.05$).
[2] Statistical tests apply only across columns: overall means of all 3 grazing systems were compared statistically but yearly means were compared only for season-long and rest-rotation system.

Table 5. Percent in vitro organic matter digestibility in diet samples by year, period, and grazing system.

Year Period[1,2]	Rest-rotation	Season-long	Deferred-rotation
1976			
Late spring	69.3	69.4	68.0
Early summer	59.2^{a}	54.7^{b}	57.8^{ab}
Late summer	56.6	56.8	
Fall	52.1	55.2	
$\bar{x}$	59.3	59.0	62.9
1977			
Late spring	68.0	69.9	
Early summer	46.3	48.9	
Late summer	52.3	51.9	53.6
Fall	53.8	53.6	52.5
$\bar{x}$	55.1	56.1	53.0
1978			
Late spring	62.7	62.8	62.3
Early summer	62.6	62.0	62.9
Late summer	52.2	54.4	
Fall	48.1	52.2	
$\bar{x}$	56.4	57.8	62.6
1979			
Late spring	62.3	61.5	
Early summer	54.9	52.7	
Late summer	55.2	57.8	50.6
Fall	52.2^{a}	47.7^{b}	49.8
$\bar{x}$	56.2	54.9	50.2
1980			
Late spring	64.3	64.8	64.3
Early summer	58.4	59.2	54.6
Late summer	55.0	57.4	
Fall	45.2^{a}	57.7^{b}	
$\bar{x}$	57.7	59.8	59.4
Grazing System Overall $\bar{x}$	56.5	57.5	57.6

[1] Means with different letter are significantly different ($P<.05$).
[2] Statistical tests apply only across columns; overall means of all 3 grazing systems were compared statistically but yearly means were compared only for season-long and rest-rotation systems.

The years in which cattle grazing pressure under the rest-rotation system was double the season-long system (1976, 1978, 1980) are of particular interest. In these years, period differences between grazing systems were generally nonsignificant ($P>.05$). One exception was the fall period in 1980 when cattle diets in the season-long pasture had lower ($P<.05$) acid detergent fiber and higher crude protein and digestibility values than the rest-rotation pasture. The relatively dry summer in 1980 compared to other years greatly reduced fall regrowth in the grassland openings. The heavier grazing pressure associated with the rest-rotation system appears to have forced cattle to select lower quality diet than those on the season-long pasture in the fall of 1980.

The movement of cattle to a fresh pasture at the end of the early summer period in 1977 and 1979 under the rest-rotation system had little effect on diet quality characteristics compared to the season-long system. This indicates in most years forage maturation is far more important than forage availability as a determinant of cattle nutritional status under the stocking rates (30–35% utilization of forage) used in this study.

Inadequate diet crude protein concentration may be an important nutritional constraint on cattle production on the Starkey Range. Protein requirements for growing yearling heifers, as outlined by the NRC (1984), indicate 320 kg heifers require 9.7 crude

Table 6. Percent acid detergent fiber (organic matter basis) in diet samples by year, period, and grazing system.

Year Period[1][2]	Rest-rotation	Season-long	Deferred-rotation
1976			
Late spring	49.9	51.1	52.1
Early summer	48.5	51.4	53.1
Late summer	61.4	59.6	
Fall	61.3	60.6	
$\bar{x}$	55.3	55.7	52.7
1977			
Late spring	57.0^{a}	65.1^{b}	
Early summer	59.6	56.4	
Late summer	67.0^{a}	64.6^{ab}	62.1^{b}
Fall	64.9	67.3	62.9
$\bar{x}$	62.1	63.3	62.5
1978			
Late spring	54.4	53.5	54.4
Early summer	56.2	59.0	57.1
Late summer	60.3	61.1	
Fall	57.9	62.4	
$\bar{x}$	57.2	59.0	55.8
1979			
Late spring	54.9	54.2	
Early summer	62.7	61.1	
Late summer	58.2	61.1	60.2
Fall	61.4^{a}	65.4^{b}	66.1
$\bar{x}$	59.3	60.4	63.2
1980			
Late spring	58.3	57.0	56.9
Early summer	60.1	58.3	60.5
Late summer	61.9	59.1	
Fall	68.0^{a}	62.8^{b}	
$\bar{x}$	62.1	59.3	58.7
Grazing System Overall $\bar{x}$	59.2	59.6	58.5

[1] Means with different letters are significantly different ($P<.05$).
[2] Statistical tests apply only across columns; overall means of all 3 grazing systems were compared statistically but yearly means were compared only for season-long and rest-rotation systems.

protein on an organic matter basis for a .8-kg gain. Diet crude protein levels were inadequate for this level of gain during the latter half of the grazing season in 1977, 1978, and 1980. Crude protein deficiencies were most severe in the late summer period. This is consistent with other research involving cattle nutritional status on the Starkey Range (Holechek et al. 1981, Holechek and Vavra 1983a).

Common snowberry plays a critical role in permitting cattle to meet their protein requirements during the latter half of the grazing season because of its high palatability and crude protein content (11+%). This species had nearly all leaf material removed by late summer in the drought year of 1977.

The increase in diet acid detergent fiber content with seasonal advance reflected the increased consumption of grass and indicated a decline in forage intake. Holechek and Vavra (1982) found a significant ($P<.05$) negative correlation between forage intake and cattle diet acid detergent fiber concentration on other pastures at the Starkey Range.

Cattle diet in vitro digestibility differences between systems are difficult to interpret with the exception of the fall in 1980 when late summer drought occurred. Both diet digestibility and acid detergent fiber values suggest grazing system had little influence on cattle diet energy status.

Cattle Weight Gains

Grazing systems did not ($P>.05$) affect cattle weight gains in any year of study or when data were pooled across years (Table 7). Cattle weight gains did differ ($P<.05$) for some seasons within years.

After movement of cattle at mid-season in 1977, under rest-rotation, weight gains increased compared to a decrease for the season-long pasture in 1977. This difference is difficult to explain because diet quality characteristics did not differ ($P>.05$) between the 2 systems. In 1979 weight gains declined after mid-season movement under the rest-rotation system. However, weight gains also declined under the season-long pasture. Because there were no differences ($P>.05$) between the rest-rotation and season-long systems in the late summer of 1977, we doubt movement influenced cattle performance. Smoliak (1960) and Hormay (1970) have reported forced movements of cattle to another pasture can result in weight losses. Cattle in all our pastures were trailed to a scale at the end of each period. Therefore our data reflect only animal response to the new pasture and not extra handling and movement responses associated with rest-rotation grazing.

Table 7. Average daily gain (kg) for cattle by year, period and grazing system.

Year Period[1][2]	Rest-rotation	Season-long	Deferred-rotation
1976			
Late spring	0.73	0.78	0.58
Early summer	0.68^{a}	0.53^{b}	0.39^{c}
Late summer	0.70	0.63	—
Fall	0.56	0.66	—
$\bar{x}$ Daily gain	0.68	0.64	0.48
1977			
Late spring	0.95	0.76	—
Early summer	0.08^{b}	0.70^{a}	—
Late summer	0.71^{a}	0.05^{b}	0.74^{a}
Fall	0.31	0.31	0.12
$\bar{x}$ Daily gain	0.51	0.55	0.43
1978			
Late spring	0.86	0.92	0.71
Early summer	0.65	0.60	0.80
Late summer	0.15^{b}	0.30^{a}	—
Fall	0.36^{b}	0.55^{a}	—
$\bar{x}$ Daily Gain	0.51	0.57	0.76
1979			
Late spring	0.11	0.08	—
Early summer	1.05	1.31	—
Late summer	0.49	0.61	0.38
Fall	0.40	0.38	0.50
$\bar{x}$ Daily gain	0.51	0.60	0.44
1980			
Late spring	1.49	1.62	1.57
Early summer	0.10	0.38	0.15
Late summer	0.49	0.51	
Fall	−0.04	0.02	
$\bar{x}$ Daily gain	0.51	0.63	0.86
Overall $\bar{x}$	0.54	0.58	0.59

[1] Means with different letters are significantly different ($P<0.05$).
[2] Statistical tests apply only across columns; overall means of all 3 grazing systems were compared statistically but yearly means were compared only for season-long and rest-rotation systems.

Experimental Limitations

Correlation analysis was used to determine how well diet quality characteristics were associated with average daily gains using individual periods for each year as samples ($n = 50$). Coefficients of determination were 0.28, 0.23, and 0.07 for crude protein, in vitro organic matter digestibility, and acid detergent fiber with average daily gain, respectively. Trends in cattle weight gains during late spring and early summer in 1979 were highly inconsistent with other years (Table 7). We have no explanation for the low weight gains of cattle in the late spring of 1979 compared to other years since diet quality was similar to other years. It was definitely not a pasture effect as all cattle responded similarly. We did run the correlations excluding data for late spring in 1979 ($n = 48$). The coefficients of determination showed little improvement ($r^2 = 0.36$, crude protein; $r^2 = 0.29$, IVOMD; $r^2 = 0.22$, ADF). Multiple correlation using all 3 nutritional characteristics slightly improved the association ($R^2 = 0.42$, $n = 48$). These correlations suggest factors other than nutrition probably influenced cattle performance. Holechek (1980) found combining diet quality characteristics with forage intake data greatly improved associations with weight gains compared to only diet quality characteristics. Digestible energy intake and crude protein intake combined explained 83% of the variation ($n = 24$) in weight gains for cattle on forest and grassland pastures on the Starkey Range. Unfortunately, forage intake data were not collected in our study due to monetary and labor limitations.

An important limitation of our study concerns the lack of plant replication in pastures. Rest-rotation pasture 2 and the season-long pasture were very similar in terrain and composition. However, the south slope of rest-rotation pasture 1 was composed primarily of a bluebunch wheatgrass/Sandberg bluegrass plant community (Table 2). On rest-rotation pasture 2 and the season-long pasture, the south slope was dominated by the ponderosa pine/Idaho fescue and Sandberg bluegrass/bluebunch wheatgrass plant communities. The terrain on rest-rotation pasture 1 was much steeper and this appeared to influence use of the different plant communities. Lack of replications coupled with the confounding influences of terrain and vegetation differences between pastures weaken the inferences for our study.

We believe evaluation of animal travel using digital pedometers (Anderson and Kothmann 1977) could have provided useful information. During most periods of study, cattle were observed to better use the inaccessible portions of the rest-rotation and deferred rotation pastures compared to the season-long pasture. This could have increased energy expenditure involved in travel. Our data indicate little difference in diet quality among systems. However, higher utilization levels for the uplands (Table 2) indicate cattle under rest-rotation and deferred-rotation systems may have had to increase their travel to select a diet comparable to those under season-long grazing.

Conclusions

Based on our results, rest-rotation, deferred-rotation, and season-long grazing systems did not differ ($P > .05$) in terms of cattle weight gains or cattle diet quality. The grazing pressure (AUM/metric ton of forage) was nearly identical between systems and typical for many National Forest Allotments in the western United States. Our results indicate the pasture change associated with rest-rotation and deferred-rotation systems have little to no influence on weight gains compared to season-long grazing if cattle movements are under 8 km. It appears rest-rotation and deferred-rotation grazing systems can be applied to rugged mountainous rangelands in the northwestern United States with small to no influence in cattle weight gains compared to season-long grazing if stocking rates are comparable to those in our study. However, improved cattle performance does not appear to be a reason to initiate rest-rotation or deferred-rotation grazing.

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Dietary Relationships among Feral Horses, Cattle, and Pronghorn in Southeastern Oregon

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Abstract

Management of sympatric ungulates on multiple use lands requires knowledge of how species exploit resources available to them. We examined seasonal food habits, dietary overlap, and dietary quality of sympatric feral horses *(Equus caballus)*, cattle *(Bos taurus)*,, and pronghorn *(Antilocapra americana)* in southeastern Oregon from May 1979 through March 1981. Seasonal diets of each ungulate species were determined by microhistological analysis of feces. At least 88% of the mean annual diets of horses and cattle consisted of grasses. Principal species consumed by these ungulates were bottlebrush squirreltail (*Sitanion hystrix* (Nutt.) J.G. Smith), bearded bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. & Smith), and Thurber needlegrass (*Stipa thurberiana* Piper). Because dietary overlap between horses and cattle was high each season (62–78%), we concluded a strong potential existed for exploitative competition under conditions of limited forage availability. Pronghorn diets consisted largely of woody sagebrush *(Artemisia)* species in fall and winter, and a mixture of forbs in spring and summer. Dietary overlap between horses and pronghorn varied from 7% (summer) to 26% (winter). Overlap between cattle and pronghorn varied from 8% (winter) to 25% (spring). These lower levels of overlap indicate a wider buffer between noncompetitive coexistence and exploitative competition. Pronghorn generally selected diets containing higher levels of crude protein (CP) and lower levels of acid-detergent fiber (ADF) than horses or cattle. We observed few differences in seasonal dietary quality between horses and cattle.

Key Words: food habits, diet quality, fecal analysis, ungulates, sympatry, resource partitioning

The principal goal of resource management on multiple use lands is to provide sustained yields of a variety of plant and animal products. The Wild Free-Roaming Horse and Burro Act (PL 92-195) of 1971 recognized feral horses as "an integral part of the natural system", and mandated their preservation and protection "in thriving ecological balance with other legitimate uses of public lands." Prior to 1971, unrestricted removal of feral horses from public rangelands tended to maintain populations at relatively low levels. After passage of PL 92-195, McGuire (1973) predicted the law would reverse this tendency. Indeed, annual rates of increase for 2 herds in southeastern Oregon are estimated to be about 20% (Eberhardt et al. 1982). At this rate, a herd will more than double in 4 years. Such population growth may increase the potential of competition for resources shared by horses, cattle, and pronghorn.

To achieve an ecological balance among communities of sympatric organisms, management must be based on knowledge of how species use and partition resources available to them (Hudson 1976). Dietary partitioning among ungulates may be explained on the basis of (1) body size, (2) type of digestive system (cecal or ruminant), (3) rumino-reticular volume, and (4) mouth size (Hanley 1982, Demment and Van Soest 1985). This food selection framework predicts large cecal digestors (horses) and small ruminants (pronghorn) be positioned at opposite ends of dietary gradient with graminoids at one end and forbs and shrubs at the other. Based on this reasoning cattle should be positioned nearer to horses than pronghorn (Hanley and Hanley 1982). In view of this framework, we examined seasonal food habits, dietary overlap, forage quality, and dietary quality of sympatric horses, cattle, and pronghorn in southeastern Oregon. We hypothesized (1) horses and cattle would select highly similar diets consisting principally of graminoids, while pronghorn would select diets composed largely of forbs and shrubs, and (2) pronghorn would select diets of higher nutritional quality than horses or cattle.

Study Area

The study was conducted approximately 130 km southeast of Burns, Ore., on a 670-km² area administered by the Vale District, Bureau of Land Management. Elevations vary from 1,200 m at Burns Junction to 1,700 m on nearby Sheepshead Mountains.

Mean annual precipitation at Burns Junction is 208 mm. Summer thunderstorms contribute to total precipitation but most rain falls during spring. Snow accumulates throughout winter and is greatest during January. Annual snowfall at Burns Junction averages 107 mm. Mean annual temperature is 9.6° C, with mean monthly extremes of -2.5° C (January) and 22.5° C (July).

The study area lies within the salt desert shrub and shrub-steppe regions described by Franklin and Dyrness (1973). Salt desert shrub communities are restricted to low elevations and are often intermingled with communities dominated by Wyoming big sagebrush (*Artemisia tridentata* spp. *wyomingensis* Beetle.) Principal shrubs of these salt desert shrub communities are shadscale saltbrush (*Atriplex confertifolia* (Torr. & Frem) Wats.), spiny hopsage (*Grayia spinosa* (Hook). Moq.), and bud sagebrush (*Artemisa spinescens* Eat.). Important grasses associated with these shrubs are bottlebrush squirreltail and cheatgrass brome (*Bromus tectorum* L.).

Uplands support shrub-steppe communities dominated by Wyoming big sagebrush. Principal grasses are bearded bluebunch wheatgrass, Sandberg bluegrass (*Poa sandbergii* Vassey), Thurber needlegrass, and bottlebrush squirreltail. Low sagebrush (*Artemisia arbuscula* Nutt.)/Sandberg bluegrass communities are common on the shallow, stony soils of ridgetops.

Methods

Field work extended from May 1979 through March 1981. Monthly data were pooled seasonally as follows: spring, March–May; summer, June–August; fall, September–November; and winter, December–February.

Food Habits

Botanical composition of diets was determined by microscopic examination of fresh fecal material (Sparks and Malechek 1968). Five independent fecal samples per month were prepared for each studied species of ungulate. Each sample was a composite (equal by weight) of feces collected from 6–12 observed individuals so that 30–60 individuals of each species were sampled monthly. One

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Table 1. Mean percent composition (± S.E.) of important[1] forages in seasonal diets of feral horses.

Forage class/species	Summer 1979 (93)[2]	Fall 1979 (102)	Winter 1980 (122)	Spring 1980 (136)	Summer 1980 (114)	Fall 1980 (139)	Winter 1981 (141)
Graminoids							
Agropyron spicatum	32 (8.3)	14 (0.9)	9 (0.7)	24 (4.9)	24 (1.7)	6 (0.6)	9 (3.0)
Bromus tectorum	7 (4.3)	3 (1.2)	2 (1.6)	15 (5.8)	18 (4.2)	4 (2.0)	3 (0.3)
Poa sandbergii	3 (1.1)	9 (2.5)	13 (8.0)	11 (3.2)	1 (0.7)	15 (3.2)	11 (6.3)
Sitanion hystrix	29 (7.5)	43 (3.7)	45 (8.2)	24 (2.4)	8 (2.1)	36 (1.1)	49 (5.4)
Stipa thurberiana	14 (1.9)	17 (3.8)	15 (1.2)	19 (0.4)	28 (4.5)	13 (5.7)	7 (0.6)
Other graminoids	2 (0.3)	T[3]	2 (0.5)	2 (1.2)	4 (2.7)	0	T
Unknown graminoids	4 (0.4)	3 (0.6)	4 (0.1)	3 (0.4)	4 (0.8)	5 (0.8)	7 (0.4)
Total graminoids	91 (1.0)	89 (2.4)	90 (1.9)	98 (0.3)	87 (3.5)	79 (2.6)	86 (3.2)
Forbs							
Phlox hoodii	4 (1.1)	5 (2.4)	5 (1.9)	1 (0.5)	5 (1.1)	13 (1.8)	10 (2.1)
Phlox longifolia	1 (0.3)	1 (0.2)	1 (0.7)	T	T	0	1 (0.9)
Unknown forbs	2 (0.1)	1 (0.5)	1 (0.3)	1 (0.2)	1 (0.6)	1 (0.7)	1 (0.6)
Total forbs	7 (1.1)	7 (2.7)	7 (1.4)	2 (0.6)	6 (0.9)	14 (2.1)	12 (2.5)
Shrubs							
Artemisia arbuscula/A. tridentata ssp. *wyomingensis*	0	1 (0.5)	T	0	0	T	0
Atriplex confertifolia	T	T	3 (1.3)	T	1 (0.8)	4 (0.6)	1 (0.6)
Ceratoides lanata	2 (0.9)	3 (2.3)	T	T	6 (2.1)	3 (1.4)	1 (0.9)
Total shrubs	2 (0.9)	4 (1.9)	3 (1.9)	T	7 (2.7)	7 (1.0)	2 (1.3)

[1] Species comprising at least 1% of any seasonal diet; complete species list found in McInnis (1985).
[2] Number of fecal groups comprising the mean of 3 samples per season.
[3] Trace; less than 0.5%.

microscope slide was prepared for each sample and examined at the rate of 20 systematically selected fields at 100x magnification. Identification of plant species was based on comparison with epidermal characteristics of reference materials. Monthly means were expressed as percent relative density and pooled to yield 3 independent replications per season. We judged fecal analysis the only practical method for determining diets of these free-ranging herbivores. Although forage species may vary in digestibility and discernibility, we believed fecal analysis provided adequate data to rank forages important to the studied herbivores (McInnis et al. 1983). Highly digestible and poorly discernible species may be underestimated.

Dietary Overlap

Percent overlap of a forage species shared by a pair of ungulate species (horses vs. cattle; horses vs. pronghorn; and cattle vs. pronghorn) was defined as the lesser percentage consumed by 1 ungulate. Total dietary overlap was calculated within each season as the sum of overlaps of individual forages (Whittaker 1975, Anthony and Smith 1977, Hurlbert 1978). This index may vary from 0% (no overlap) to 100% (complete overlap).

Forage Quality

Samples of important forage species were collected concomitant with fecal material. Between 1–4 samples (50–100 g each) of plant parts selected by studied ungulates were analyzed each season for CP (Kjeldahl nitrogen × 6.25) and ADF (Van Soest and Wine 1967). Crude protein is correlated with desirable nutritional components, and serves as a reliable index of a plant's nutritional value (Sullivan 1962). Acid-detergent fiber represents the fibrous portion of a feed and shows a reasonably strong inverse relationship with digestibility and dietary quality (Van Soest 1963). Data were expressed on a percent dry matter basis and averaged by species within seasons over years.

Dietary Quality

Percent CP and ADF in seasonal diets of each ungulate species was calculated following Westoby (1974):

$$N_i = \Sigma_{a_{ij}x_j}$$

where Ni is the dietary composition of the ith nutrient, a_{ij} is the ith nutrient content of the jth forage species and xj is the dry weight composition of the jth forage species. N_i was calculated for each mean monthly diet yielding 3 values per season for each ungulate species. Occasionally ungulates consumed plants not analyzed for nutrient content. When this occurred for a species in which previous and subsequent seasonal values of a_{ij} were established, the mean value was used. For species not analyzed, values of similar species were used. Mean values of a forage class were used for unidentified species. In this manner, 100% of each diet was accounted for.

Data were analyzed as a completely randomized design using factorial analysis of variance to examine effects of the 3 ungulate species and 7 seasons on dietary CP and ADF. Differences among means were established ($P<0.05$) with Duncan's multiple range test (Steel and Torrie 1960).

Results

Food Habits

Feral horses were predominantly grazers throughout the year, and grasses comprised 88% of pooled seasonal diets. We observed little variation in total grass consumption among most seasons, but usage peaked in spring (Table 1). The principal grass consumed was bottlebrush squirreltail, forming a mean annual composition of 33%. Following in order of importance on an annual basis were bearded bluebunch wheatgrass (17%), Thurber needlegrass (16%), Sandberg bluegrass (9%), and cheatgrass brome (7%). Usage of these species varied seasonally. Bearded bluebunch wheatgrass and cheatgrass brome together comprised roughly 40% of combined spring and summer diets, but were used lightly during fall and winter. Consumption of bottlebrush squirreltail followed an opposite pattern and accounted for nearly 50% of pooled winter diets.

Cattle primarily consumed grass throughout the year. Grasses, forbs, and shrubs formed 89, 4, and 7%, respectively, of the mean annual diet (Table 2). When pooled across seasons and years, bearded bluebunch wheatgrass and bottlebrush squirreltail respectively formed 20 and 40% of the diet. On an annual basis, these species were followed in order of importance by cheatgrass brome (9%), and Sandberg bluegrass (5%). Consumption of bearded bluebunch wheatgrass, cheatgrass brome, and Sandberg bluegrass was higher in pooled spring-summer diets than fall or winter. Conver-

Table 2. Mean percent composition (± S.E.) of important[1] forages in seasonal diets of cattle.

Forage class/species	Summer 1979 (101)[2]	Fall 1979 (116)	Winter 1980 (94)	Spring 1980 (99)	Summer 1980 (117)	Fall 1980 (156)	Winter 1981 (126)
Graminoids							
Agropyron spicatum	40 (8.6)	10 (1.8)	7 (2.7)	19 (4.6)	36 (2.1)	15 (2.0)	15 (2.3)
Bromus tectorum	7 (2.3)	6 (1.3)	8 (0.8)	16 (4.1)	18 (1.8)	7 (2.8)	2 (1.2)
Poa sandbergii	7 (2.5)	4 (1.0)	1 (0.5)	8 (2.6)	11 (2.7)	3 (1.7)	4 (0.5)
Sitanion hystrix	16 (3.6)	58 (3.3)	61 (3.8)	31 (6.5)	9 (2.9)	50 (3.7)	58 (2.6)
Stipa thurberiana	4 (0.9)	11 (3.1)	3 (0.8)	4 (0.9)	7 (1.6)	1 (0.3)	1 (0.8)
Other graminoids	12 (6.0)	0	1 (0.6)	6 (3.0)	5 (0.8)	1 (0.9)	1 (0.4)
Unknown graminoids	5 (1.2)	3 (0.5)	3 (0.8)	7 (2.4)	8 (4.3)	7 (0.7)	6 (0.5)
Total graminoids	91 (1.9)	92 (1.1)	84 (4.8)	91 (1.6)	94 (1.7)	84 (0.9)	87 (0.8)
Forbs							
Phlox hoodii	2 (1.3)	1 (0.5)	T[3]	2 (0.4)	2 (0.9)	0	0
Phlox longifolia	1 (0.6)	0	0	1 (0.6)	1 (0.5)	0	0
Other forbs	0	1 (0.8)	0	3 (0.8)	0	0	0
Unknown forbs	4 (0.9)	1 (0.6)	1 (0.2)	3 (0.9)	3 (0.9)	3 (1.3)	1 (0.7)
Total forbs	7 (1.2)	3 (0.8)	1 (0.3)	9 (1.9)	6 (1.8)	3 (1.3)	1 (0.7)
Shrubs							
Artemisia arbuscula/A. tridentata spp. *wyomingensis*	T	T	0	T	T	0	0
Atriplex confertifolia	2 (0.4)	3 (0.6)	14 (4.1)	0	0	11 (1.9)	12 (0.2)
Ceratoides lanata	T	2 (1.1)	1 (0.5)	T	T	2 (0.1)	0
Total shrubs	2 (0.9)	5 (1.3)	15 (4.6)	T	T	13 (2.0)	12 (0.2)

[1] Species comprising at least 1% of any seasonal diet; complete species list found in McInnis (1985).
[2] Number of fecal groups comprising the mean of 3 samples per season.
[3] Trace; less than 0.5%.

sely, consumption of bottlebrush squirreltail was greater during the fall-winter period. Use of forbs and shrubs varied seasonally. Forbs occurred more frequently in spring and summer diets than fall and winter, while shrub consumption generally followed the reverse trend. Shadscale saltbrush was the most heavily consumed shrub, and formed 13% of pooled winter diets.

Unlike horses and cattle, pronghorn consumed mainly forbs and shrubs throughout the year. Mean annual dietary composition of grasses, forbs, and shrubs was 13%, 44%, and 42%, respectively. Seasonal use of these forage classes fluctuated widely, and coincided with the availability of forbs. Forb use peaked during summer months, then declined through fall and winter (Table 3).

Table 3. Mean percent composition (± S.E.) of important[1] forages in seasonal diets of pronghorn.

Forage class/species	Summer 1979 (84)[2]	Fall 1979 (132)	Winter 1980 (80)	Spring 1980 (52)	Summer 1980 (127)	Fall 1980 (149)	Winter 1981 (147)
Graminoids							
Bromus tectorum	1 (0.2)	7 (0.9)	3 (0.8)	4 (0.6)	2 (1.2)	3 (0.5)	4 (0.6)
Poa sandbergii	2 (0.8)	5 (0.8)	16 (4.2)	9 (1.3)	4 (0.5)	10 (0.7)	12 (3.1)
Sitanion hystrix	1 (0.5)	1 (0.6)	2 (1.6)	3 (0.7)	T[1]	0	0
Other graminoids	T	T	T	T	T	T	T
Unknown graminoids	0	T	1 (0.5)	T	1 (0.6)	T	1 (0.3)
Total graminoids	4 (0.4)	13 (0.5)	23 (5.6)	16 (1.8)	8 (1.3)	13 (1.4)	17 (3.1)
Forbs							
Balsamorhiza hookeri	17 (2.1)	1 (0.9)	2 (0.4)	4 (0.8)	18 (1.9)	3 (0.8)	1 (0.6)
Iva axillaris	0	0	0	2 (1.1)	3 (0.8)	1 (0.6)	0
Phlox hoodii	3 (0.5)	1 (0.3)	0	2 (0.6)	2 (1.8)	1 (0.3)	7 (4.3)
Phlox longifolia	17 (3.9)	8 (2.2)	15 (3.3)	6 (0.5)	21 (1.3)	14 (2.5)	7 (2.8)
Phoenicaulis cheiranthoides	29 (5.7)	3 (1.3)	2 (0.9)	10 (3.6)	27 (7.9)	9 (4.3)	T
Sphaeralcea munroana	T	10 (4.6)	0	6 (1.7)	0	3 (2.4)	0
Other forbs	6 (2.0)	0	0	11 (1.4)	3 (0.4)	T	0
Unknown forbs	7 (0.9)	4 (0.4)	2 (0.2)	6 (0.1)	6 (0.8)	3 (0.5)	6 (1.4)
Total forbs	79 (1.2)	27 (6.3)	21 (4.6)	47 (5.2)	80 (2.8)	35 (1.3)	21 (1.3)
Shrubs							
Artemisia arbuscula/A. tridentata spp. *wyomingensis*	17 (0.8)	59 (6.2)	56 (1.7)	37 (6.1)	12 (3.3)	52 (1.8)	58 (4.5)
Atriplex confertifolia	0	T	T	T	0	0	4 (0.3)
Other shrubs	T	T	0	0	T	0	1 (0.5)
Total shrubs	17 (0.9)	60 (6.0)	56 (1.6)	37 (6.2)	12 (3.4)	52 (1.8)	63 (4.2)

[1] Species comprising at least 1% of any seasonal diet; complete species list found in McInnis (1985).
[2] Number of fecal groups comprising the mean of 3 samples per season.
[3] Trace; less than 0.5%.

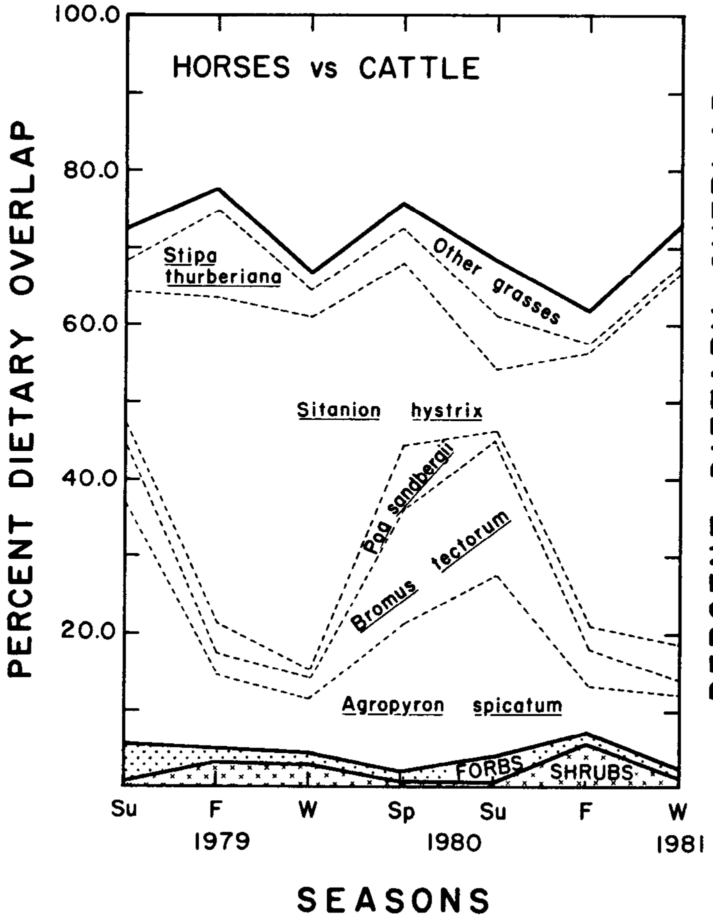

Fig. 1. *Seasonal dietary overlap between feral horses and cattle. Topmost line represents total overlap.*

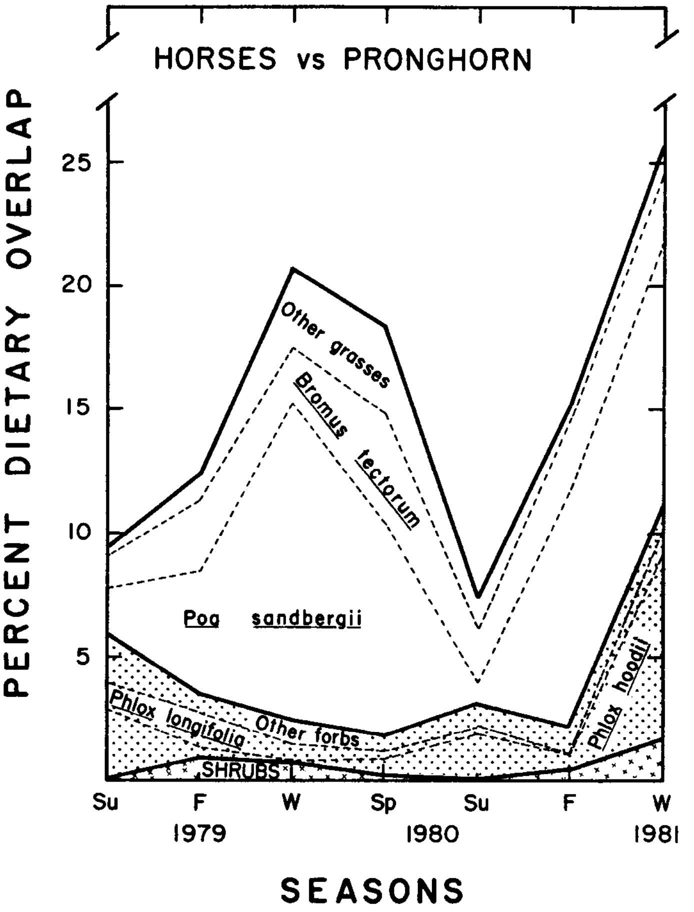

Fig. 2. *Seasonal dietary overlap between feral horses and pronghorn. Topmost line represents total overlap.*

Longleaf phlox (*Phlox longifolia* Nutt.), wallflower phoenicaulis (*Phoenicaulis cheiranthoides* Nutt.), and Hooker balsamroot (*Balsamorhiza hookeri* Nutt.) were the most heavily consumed forbs. During fall, forbs became less available due to advancing phenological development, and pronghorn switched to a diet dominated by shrubs. Low sagebrush and Wyoming big sagebrush could not be distinguished microhistologically, but collectively formed more than 50% of fall and winter diets.

Dietary Overlap

Of 21 taxa identified in the collective annual diets of feral horses and cattle, 81% were used in common. Dietary overlap averaged 70% on an annual basis, and exhibited modest but inconsistent seasonal variation (Fig. 1). When pooled across seasons, grasses formed 94% of total overlap. Collectively, bottlebrush squirreltail and bearded bluebunch wheatgrass formed roughly 50% or more of total overlap every season. Cheatgrass brome contributed nearly 30% of total overlap in summer 1980, but only 10% in summer 1979. Horses and cattle consumed more than twice the amount of this grass during the summer of 1980 (Tables 1 and 2), possibly because greater mean precipitation during May–June 1980 (22.6 mm) compared with the same period in 1979 (11.7 mm) may have increased the yield and retarded phenological development of this species resulting in increased palatability.

Twelve (48%) of 25 forage species identified in the collective annual diets of feral horses and pronghorn were used commonly by both species of ungulates. On an annual basis, overlap averaged 16% and ranged from 7 to 26% (Fig. 2). Diets were most similar during winter months, and least similar in summer. When pooled across seasons and years, grasses (principally Sandberg bluegrass) contributed 70% of total overlap.

Thirty-one forage species were observed in the collective diets of cattle and pronghorn. Thirteen (42%) of these were consumed by both species of herbivores. As in the comparison of pronghorn with horses, dietary overlap between pronghorn and cattle was not high. Although the index clearly peaked during spring, trends in other seasonal fluctuations were inconsistent among years (Fig. 3). On an annual basis, the index averaged 14%, and reached its lowest level during winter 1980. Common use of Sandberg bluegrass and cheatgrass brome collectively formed roughly 50% or more of the total overlap during most seasons.

Forage Quality

Seasonal levels of CP in important forages (Table 4) agreed with other studies conducted in the Great Basin (Hickman 1975, Spalinger 1980). Concentrations of CP in all forage classes were similar in spring, generally declined through summer and fall, and reached their lowest levels in winter. This trend was most pronounced in grasses and least in shrubs. Acid-detergent fiber content of all forage classes increased with decreasing levels of CP as the growing season progressed (Table 4). On the average, shrubs varied less than grasses or forbs in ADF throughout the year, and contained less ADF during all but spring months when levels were similar among all forage classes.

Dietary Quality

In most cases, estimates of dietary quality were based on forage species of which more than 95% were analyzed for CP and ADF. However, only about 75% of pronghorn diets in fall and winter were based on analyzed plants.

For each species of ungulate, dietary CP peaked in spring, steadily declined through the year, and reached its lowest level in winter (Table 5). Although all herbivores consumed diets containing roughly 16% CP during spring, pronghorn selected plants containing consistently higher levels of CP than horses or cattle in

Table 4. Seasonal mean composition (% dry matter) of crude protein and acid-detergent fiber in forages available to feral horses, cattle and pronghorn.

Species/Season	n	Crude Protein $\bar{x}$	Crude Protein SE	Acid-Detergent Fiber $\bar{x}$	Acid-Detergent Fiber SE
Graminoids					
Agropyron spicatum					
spring	3	16.3	2.9	34.2	2.5
summer	3	5.7	1.9	47.4	2.2
fall	2	3.7	0.6	54.3	1.6
winter	4	2.3	0.3	57.1	1.2
Bromus tectorum					
spring	3	17.4	4.0	23.6	5.4
summer	3	6.1	2.8	43.2	3.4
fall	3	3.0	0.3	52.5	1.1
winter	1	2.3		54.9	
Poa sandbergii					
spring	3	13.9	3.6	31.0	4.0
summer	3	3.0	0.3	49.0	0.6
fall	3	4.3	0.8	51.1	1.3
winter	2	6.8	0.0	51.2	0.4
Sitanion hystrix					
spring	3	17.5	3.1	34.9	3.1
summer	2	6.5	3.3	48.2	3.7
fall	3	6.1	1.5	56.9	0.9
winter	4	3.7	0.1	54.7	1.3
Stipa thurberiana					
spring	3	14.0	1.7	38.7	6.6
summer	2	6.5	1.6	50.4	3.6
fall	2	4.0	1.3	51.6	0.6
winter	2	3.3	0.4	56.9	2.3
Forbs					
Phlox longifolia					
spring	1	14.2		33.0	
summer	2	7.2	1.5	47.1	0.6
winter	2	5.8	0.1	62.3	1.1
Balsamorhiza hookeri					
spring	1	11.0		25.6	
summer	1	10.2		32.6	
Phoenicaulis cheiranthoides					
spring	1	27.3		19.0	
summer	1	10.8		30.3	
Iva axillaris					
summer	1	11.0		27.3	
fall	1	17.0		30.5	
Shrubs					
Artemisia arbuscula					
summer	1	10.0		32.6	
fall	1	9.3		34.8	
Artemisia tridentata ssp. wyomingensis					
spring	1	14.5		23.7	
summer	1	13.9		26.2	
fall	3	11.3	0.3	30.0	2.0
winter	3	10.5	0.6	32.1	0.5
Atriplex confertifolia					
spring	1	15.6		15.9	
summer	1	14.6		19.0	
fall	2	8.4	0.0	25.9	5.4
winter	3	8.2	0.8	30.8	1.2
Ceratoides lanata					
spring	1	10.8		46.3	
summer	1	10.2		42.2	
fall	2	7.2	1.7	44.8	0.1
winter	1	8.8		41.3	

every other season (Table 5). Within seasons, significant differences were not observed in dietary CP between horses and cattle. Levels of ADF in all ungulate diets were lowest in spring, increased steadily through the year, and generally reached their highest levels in winter. Pronghorn selected diets containing less ADF than horses or cattle during every season. Dietary ADF was signifi-

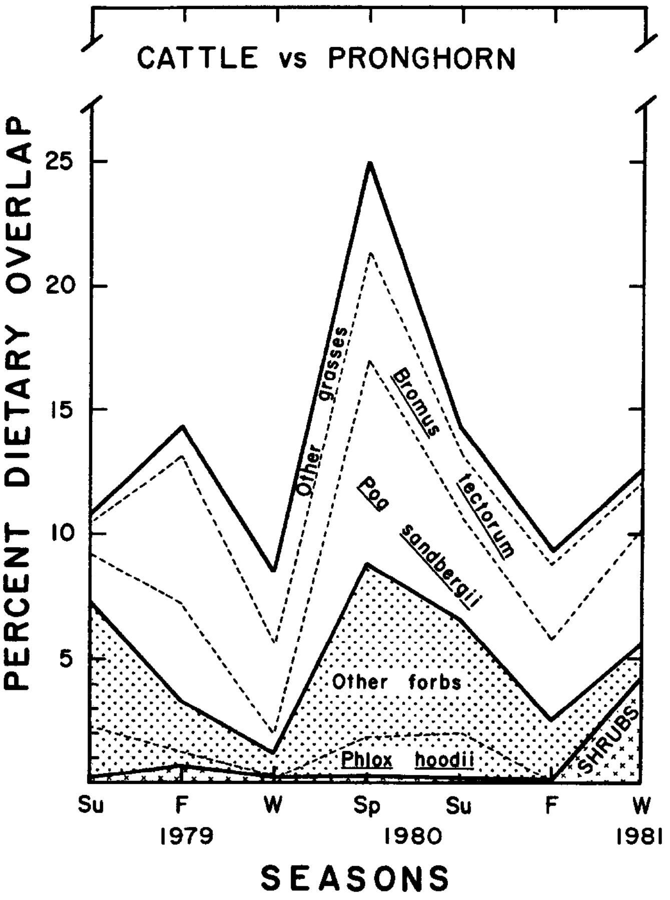

Fig. 3. *Seasonal dietary overlap between cattle and pronghorn. Topmost line represents total overlap.*

Table 5. Mean dietary composition (% dry matter) of crude protein and acid-detergent fiber for feral horses, cattle, and pronghorn.[1]

Season	Feral Horses $\bar{x}$	Feral Horses SE	Cattle $\bar{x}$	Cattle SE	Pronghorn $\bar{x}$	Pronghorn SE
Crude Protein						
Summer 1979	6.2^{a}	0.1	6.1^{a}	0.1	9.8^{a}	0.2
Fall 1979	5.2^{b}	0.1	5.5^{b}	0.1	9.2^{b}	0.1
Winter 1980	4.3^{c}	0.2	4.2^{c}	0.3	8.3^{c}	0.1
Spring 1980	15.8^{d}	0.1	16.5^{d}	0.2	16.0^{d}	0.5
Summer 1980	6.5^{a}	0.1	5.8^{ab}	0.1	9.5^{ab}	0.1
Fall 1980	5.4^{b}	0.1	5.7^{ab}	0.1	8.7^{c}	0.1
Winter 1981	4.2^{c}	0.1	4.1^{c}	0.03	8.5^{c}	0.2
Acid-Detergent Fiber						
Summer 1979	46.6^{a}	0.1	46.5^{a}	0.3	35.1^{a}	0.7
Fall 1979	54.0^{bc}	0.1	53.9^{b}	0.2	38.8^{b}	0.8
Winter 1980	54.6^{c}	0.2	51.9^{c}	0.8	43.2^{c}	0.2
Spring 1980	32.9^{d}	0.7	31.8^{d}	0.2	25.6^{d}	0.1
Summer 1980	46.8^{a}	0.6	46.5^{a}	0.2	35.9^{a}	0.6
Fall 1980	52.9^{u}	0.2	51.6^{c}	0.4	40.0^{b}	0.7
Winter 1981	55.2^{c}	0.3	52.5^{c}	0.3	41.5^{e}	0.9

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[1] Ungulate and seasonal effects significant ($P<0.01$) within each nutritional category; $N = 3$; means of each nutritional category compared within herbivore species across seasons are not significantly different ($P>0.05$) if followed by the same superscript; means compared across herbivores within seasons are not significantly different ($P>0.05$) if underlined.

Table 6. Results of t test comparing pooled winter diets (1980 and 1981) of feral horses and cattle.[1]

Species	Mean Dietary Composition Horses	Mean Dietary Composition Cattle	Computed t values	Significance[2]
Agropyron spicatum	9	11	–0.6000	ns
Bromus tectorum	3	5	–1.1780	ns
Poa sandbergii	12	3	2.0467	*
Sitanion hystrix	47	60	–2.7646	**
Stipa thurberiana	11	2	5.6554	***
Total graminoids	88	86	0.8997	ns
Total forbs	10	1	5.1512	***
Total shrubs	3	14	–3.7163	**

[1] Based on paired t test comparing monthly proportions of each food item between horses and cattle; $n = 6$.

[2] ns, *, **, and *** respectively refer to not significant; $P<0.1$; $P<0.05$; and $P<0.01$.

cantly different between horses and cattle only during winter.

Discussion and Conclusions

While forbs and shrubs may be locally important in diets of free-ranging horses (Hansen 1976, Krysl et al. 1984) and cattle (Uresk and Rickard 1976, Johnson 1979), most studies concluded these ungulates are primarily grass consumers throughout the year (Skiles 1984). Within shrub-steppe communities horses and cattle consumed year-round diets containing roughly 90% grass (Vavra and Sneva 1978). Most workers found substantial dietary overlap between these herbivores in a variety of vegetation types (Olsen and Hansen 1977, Salter and Hudson 1979, Hanley and Hanley 1982, Krysl et al. 1984). Dietary overlap between feral horses and cattle grazing common sagebrush-grassland range in eastern Oregon average 67, 69, and 72% during spring, summer, and winter, respectively (Vavra and Sneva 1978). Conversely, pronghorn sparsely use grasses (Skiles 1984). Previous comparisons have shown little overlap in food habits of sympatric pronghorn and horses (Olsen and Hansen 1977, Meeker 1979, and Hanley and Hanley 1982), or pronghorn and cattle (Olsen and Hansen 1977, Johnson 1979, Hanley and Hanley 1982).

In this study, ungulates were classified as principally grass consumers (horses and cattle), or forb and shrub consumers (pronghorn). Horses and cattle showed predilection for many of the same forages, and dietary overlap was substantial (62–78%) every season. Conversely, pronghorn shared relatively few food items with horses or cattle. These results support our first hypothesis and agree with Hanley's (1982) food selection framework.

Dietary overlap is not sufficient evidence for exploitative competition (Colwell and Futuyma 1971), and consequences of overlap partially depend upon availability of the resource. In one case exploitation would not occur between 2 species sharing a common abundant resource which is not limiting (Sale 1974, Lawlor 1980). On the other hand, competition may increase if availability is reduced by common utilization (Nelson 1982). Interspecific competition must be judged on the basis of 2 criteria (Wagner 1983): (1) 2 species compete when they share a resource that is present in short supply, and (2) in using the resource, each species reduces the other's population performance to levels below what these measures would be in the absence of the other species. Although it is beyond the scope of this study to test the hypothesis of competition among horses, cattle, and pronghorn, our data provide insight into potential exploitative interactions among these species.

The theory of competitive exclusion (Hardin 1960) proposed 2 species cannot coexist on the same limiting resource. Ecologically similar species may coexist by partitioning resources among themselves (Schoener 1974), particularly during the lean season (Smith et al. 1978). In the present study, winter was the presumed season of lowest forage availability. Horses and cattle consumed significantly different proportions of some food items during this season (Table 6), but total overlap still averaged 70% (Fig. 1). High dietary overlap and similarity of habitat selection (McInnis 1985) suggest competition could occur between horses and cattle.

In the pronghorn-horse and pronghorn-cattle comparisons, low dietary overlap (Fig. 2 and 3) may suggest a wider buffer between noncompetitive coexistence and exploitative competition. However, Vavra and Sneva (1978) demonstrated a potential for higher levels of dietary similarity (20–49%) when drought reduced availability of foods preferred by pronghorn and they switched to diets high in large perennial grasses. Wagner (1983) concluded competition for forage between grazers and browsers was most likely to occur on depleted range where food habits of such herbivores converged.

Our second hypothesis stated pronghorn would select diets of higher nutritional quality than horses or cattle because of their smaller size and higher metabolic rate (Hanley and Hanley 1982). Indeed, pronghorn consumed consistently lower levels of ADF; and higher proportions of CP during every season except spring (Table 5). The effect of higher metabolic rates of small animals is that they require more protein and energy per unit weight than larger animals (Bell 1971, Schwartz and Ellis 1981). Schwartz et al. (1977) observed consumption of less fibrous diets by pronghorn than cattle, bison or sheep. This trend may reflect differences in feeding strategies of these herbivores. Large body size and large gastro-intestinal volume (e.g., horses and cattle) are adaptations to exploitation of high cellulose diets (grasses) while small body size and small gastro-intestinal volume (e.g., pronghorn) are adaptations to exploitation of high cell soluble diets (forbs and shrubs) (Hanley and Hanley 1982).

An essential difference between ruminant and cecal digestors is that in the former group, passage rate of digesta and intake is depressed by increasing levels of dietary fiber (Janis 1976, Hanley 1982). To maintain an adequate level of nutrient absorption, ruminants increase mass flow of digesta through the gastro-intestinal tract by selecting diets lower in fiber, especially when forage quality is limiting (Bell 1971, Janis 1976, Hanley 1982). In our study nutrient quality of most forages was lowest in winter (Table 4), and cattle selected diets containing significantly less ADF than horses (Table 5). We observed no other significant differences in the quality of diets consumed by horses and cattle.

Comparative data on the nutrition of free-ranging ungulates are scarce. Requirements of CP for domestic horses vary from 8.5% for maintenance to 14% during the first 3 months of lactation (NRC 1978). In the present study, newborn foals were observed between late March and May (McInnis 1985), and CP varied from roughly 4% in winter to nearly 16% in spring (Table 5). Based on comparison with percent CP requirements, horses in our study were apparently deficient during all but spring months. However, equids have evolved a digestive strategy which allows them to compensate for low quality forage by increasing throughput and intake rates (Janis 1976). Thus, horses may have received adequate levels of CP by processing more feed than ruminants.

Beef cows require 7–8% CP for maintenance and 9–10% for lactation (NRC 1984). Raleigh (1970) reported cattle grazing sagebrush-bunchgrass vegetation in southeastern Oregon consumed diets containing about 19% CP in early May and 3% in mid-September. Cattle in the present study exceeded the requirements for lactation in early spring when calves were born, but dietary CP declined rapidly through summer and apparently failed to meet lactation requirements then (Table 5). Further declines through fall and winter caused diets to be deficient in CP during those periods.

Although nutritional requirements of pronghorn are largely unknown, Schwartz et al. (1977) speculated the CP requirement for deer (*Ocodoileus* spp.) may be comparable (6–7% for maintenance and 13–16% for growth). Smith and Malechek (1974) determined dietary CP of pronghorn declined from 22–10% between early May and late September on desert ranges in Utah, but concluded maintenance requirements were met throughout all periods studied. If pronghorn requirements for CP are similar to those of deer, diets consumed by pronghorn in our study were probably adequate for maintenance each season (Table 5). However, levels necessary for growth were reached only during spring. As forage matured during summer months, dietary CP declined, and may have been inadequate to meet the needs of lactating females.

Our estimates of dietary protein may have underestimated actual proportions consumed for 2 reasons: Firstly, hand-compounded samples contain less protein and more fiber than diets actually selected by free-ranging herbivores (Edlefsen et al. 1960, Kiesling et al. 1969). This may be especially true for pronghorn because their small mouths allow them to be more selective of plant parts than animals with large mouths (Hanley 1982). Secondly, estimates of dietary quality were based on forage species occasionally totaling less than actual amounts consumed. Since estimates for horses and cattle approached or reached 100% of actual diets, dietary CP and ADF of these herbivores was probably not markedly affected. However, CP and ADF levels in pronghorn diets during fall and winter were probably somewhat higher than suggested by our results (Table 5). Despite these deficiencies, our results provide an initial comparison of seasonal dietary quality for feral horses, cattle, and pronghorn.

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Livestock and Wildlife Population Distributions in Relation to Aridity and Human Populations in Kenya

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Abstract

In response to the demand for inventories of livestock and wildlife populations in Kenya, animal censuses were completed during the period 1977 to 1983 using low level, systematic reconnaissance flights. Total stocking levels, ratios of livestock to wildlife, and ratios of cattle to sheep and goats were estimated in terms of tropial animal units for each administrative district. The total stocking level, the ratio of cattle to sheep and goats, and human population density were negatively correlated to aridity. In the driest districts, livestock were low in absolute density but their per capita importance to the human population was high.

Key Words: animal census, aerial surveys, cattle, sheep, goats, stocking levels

Livestock and wildlife are important natural resources of Kenya and their management requires an inventory to provide a basis for measuring trends in population sizes and distributions. Previous inventories emphasized specific regions or animal groups. They were not designed to provide a national overview.

Since 1977, the Kenya Rangeland Ecological Monitoring Unit (KREMU) developed the methods and subsequently conducted inventories of livestock and wildlife in the rangelands of Kenya. The earliest surveys stratified Kenya on the basis of eco-units and eco-regions (Stelfox et al. 1979). However, these ecological units did not correspond to the needs of planners concerned with district development. In 1982, KREMU modified its survey design to provide results on the basis of administrative districts. KREMU also initiated censuses of livestock in the "high-potential" districts.

This report summarizes the results of KREMU's animal censuses from 1977 to May 1983 in terms of administrative districts. Many of the districts were surveyed several times but the high potential districts were surveyed only once. The results and discussion are restricted to livestock and wildlife as aggregated groups. Species-specific details are described by Peden (1984).

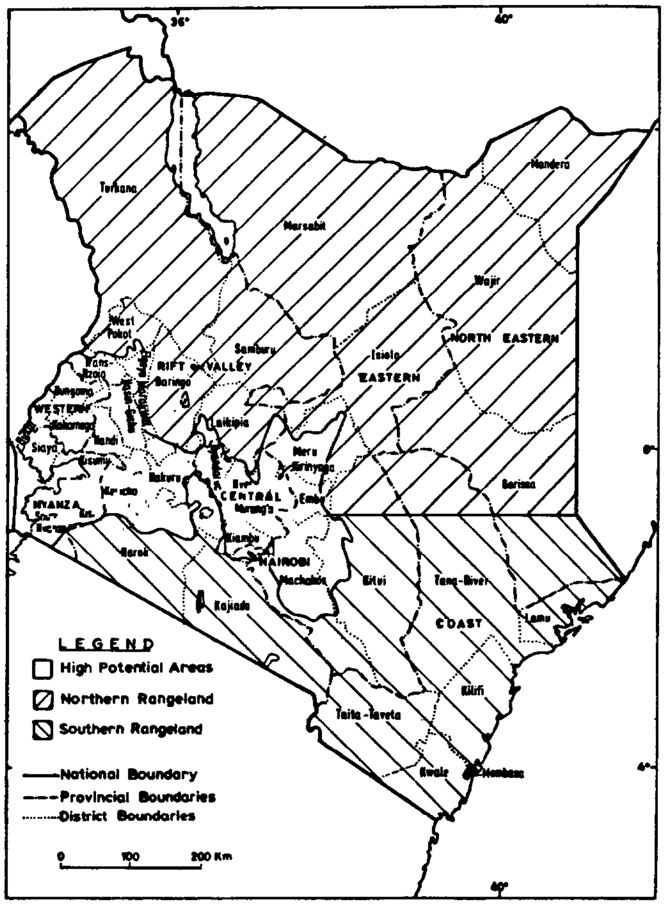

Fig. 1. *Districts of Kenya.*

Methods

KREMU's method of censusing animal populations follows that of Norton-Griffiths (1978). Surveys of 38 administrative districts (Fig. 1) were conducted using systematic reconnaissance flights. Most flights were oriented in an east-west direction, but some north-south flights were undertaken when the terrain imposed too much danger for east-west flying at low altitude. There was some variation from survey to survey with respect to flying heights above ground level, to strip width, to transect spacing and to aircraft speed (Table 1). Flying heights ranged from 91 to 122 m. Strip width varied from 224 to 400 m. Transect spacing was either 5 or 10 km apart and aircraft speeds varied from about 150 to 200 km per hour. Identical methods would have provided better year to year comparisons but the variations were a necessary part of developing and testing KREMU's methods.

During the survey flights, observers on board the aircraft photographed animal herds including more than ten animals to improve the accuracy of counting large groups. For each district and each observer, a linear regression was used to predict the corrected count (photo count) from the visual count. These regressions were used to adjust every visual count even if a matching photograph was not taken. For herds less than 10 in size, the visual counts were used directly. Correction of visual counts through the use of photo counts does not give a complete correction for observer biases. Although its magnitude has yet to be measured, visibility bias is known to be greater in "high-potential" areas, where more dense vegetation prevails, than in rangelands. It was assumed that 30% of the livestock were not seen in "high potential" areas and thus an additional correction factor of 1.43 was used to increase estimates. The observations made in the rangelands were not adjusted after the photo corrections had been made.

From 1977 to 1983, KREMU conducted many aerial surveys to obtain various population estimates. Not until 1982 was a consistent effort made to summarize data on the basis of district boundaries (except for Baringo and Kajiado). Consequently, most of the survey data were re-sorted and collated to provide district summaries. For some districts, such as Garissa, the period of data collection spanned a considerable length of time. This reflects the fact that the district data sets had to be synthesized from independent surveys done at different times. Thus some animals may have

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Table 1. Variations in field procedures of KREMU's surveys.

Place	Date	Fly height (m)	Strip width (m)	Approx. speed km/h	
All rangelands	1977–78	91	224	150	Cessna 185
Southern rangelands	1980	91	250	190–210	Partenavia
Baringo	1980	122	415	190–210	Partenavia
Northern rangelands	1981	122	400	190–210	Partenavia
Kajiado	1981	122	490	190–210	Partenavia
Baringo	1982	122	364	190–210	Partenavia
Laikipia	1982	122	400	190–210	Partenavia
Kajiado	1982	122	418	190–210	Partenavia
Turkana	1982	122	400	190–210	Partenavia
High potential land	1982–83	122	361	190–210	Partenavia
Southern rangelands	1983	91	263	190–210	Partenavia

migrated during the period of the survey and some been missed or counted more than once. In comparing districts, the surveys summarized herein were not collected at the same time every year for every district. For example, for reasons of security, Wajir and Mandera districts have not been surveyed since 1978.

For each set of data, population estimates and standard errors were obtained using Jolly's method number 2 (Norton-Griffiths 1978, Jolly 1969). Only those data which gave a representative coverage of specific districts were used. In cases in which 2 or more censuses were available, the average population size for the district was calculated.

The stocking levels of the various districts were compared in terms of 250 kg tropical animal units (Field et al. 1983). The TLU equivalents used in this report are given in Table 2. The weights assigned to individuals of each species are taken from Watson et al. (1978) and Ecosystems (1978). These TLU equivalents are approximate values only. The weights of individual animals vary greatly from birth to adulthood, from season to season, and from place to place. Nevertheless, the TLU provides a useful comparative index of stocking levels. For each district, the average ratios of cattle to sheep and goats, livestock to wildlife, and livestock to the 1979 human population density (Central Bureau of Statistics 1981) were calculated. The only animals used in calculating total stocking levels were those listed in Table 2. During the surveys, other animals were seen, but the estimates were not considered to be either reliable or important for the purpose of this paper. Animals seen but not included were predators, hippos, warthogs, dik diks, duikers, reedbuck, bushbuck and oribi. If included, these would contribute to slightly higher estimates of the wildlife stocking level.

Table 2. Animal weights (kg) and tropical animal unit equivalents (TLU).

Animal	TLU	kg
Cattle (*Bos.* spp.)	0.7	180
Sheep and goats *(Ovis aries & Capra hircus)*	0.1	18
Donkeys *(Equus asinus)*	0.6	150
Camels *(Camelus dromedarius)*	1.2	300
Wildebeest *(Connochaetes taurinus)*	0.5	125
Elephants *(Loxodonta africana)*	6.9	1500
Zebra (*Equus* spp.)	0.8	200
Kongoni (*Alcelaphus* spp.)	0.5	125
Hunter's hartebeest *(Damaliscus hunteri)*	0.5	125
Topi *(Damaliscus korrigum)*	0.5	112
Waterbuck (*Kobus* spp.)	0.4	105
Ostrich *(Struthio camelus)*	0.5	115
Thomson's gazelle *(Gazella thomsonii)*	0.1	15
Grant's gazelle *(Gazella grantii)*	0.2	40
Impala *(Aepyceros melampus)*	0.2	40
Rhino (*Diceros* spp.)	3.3	815
Sable *(Hippotragus niger)*	0.5	125
Gerenuk *(Litocranius walleri)*	0.1	25
Eland *(Taurotragus oryx)*	1.4	340
Buffalo *(Syncerus caffer)*	1.8	450
Lesser kudu *(Strepsiceros imberbis)*	0.2	40
Giraffe (*Giraffa* spp.)	3.0	750
Oryx *(Oryx beisa)*	0.4	100
Greater kudu *(Tragelaphus strepsiceros)*	0.8	200

In the high-potential districts, wildlife were not included in the estimates of total stocking level. It was assumed for the purpose of this analysis that these species contribute relatively little to the total biomass of high-potential districts. Because of hazardous flying conditions, areas above 2,500 m were not surveyed.

An aridity rating for each district was developed by calculating an area-weighted average of Braun's (1980) moisture availability zones within the districts. This index ranges from 1 to 7 where a value of 1 refers to a very humid region and 7 refers to very arid conditions. Linear regressions were used to relate the total stocking level, animal ratios, and human density to the aridity index.

Results

Thirty-eight administrative districts (Fig. 1) were used to demonstrate spatial variation in average stocking densities in Kenya. No data were available for Nairobi, Elgeyo-Marakwet, and Mombasa. Livestock densities in Kenya (Table 3) varied from a low of 3.3 TLU/km^2 in Marsabit to a high of 66.4 in Keriocho District. The "high-potential" districts of Trans Nzoia, Uasin Gishu, Nandi, Nakuru, Kericho, and those of Western and Nyanza provinces all had livestock densities greater than 20 TLU/km^2. With the exception of Narok District, the livestock in the rangeland districts averaged less than 20 TLU/km^2. Wildlife densities, which were estimated only in the rangeland districts, varied from 0.1 in West Pokot to 21.4 in Narok. In Lamu and Taita-Taveta districts, the stocking level of wildlife exceeded that of livestock species, while in all other rangeland districts stocking levels of livestock were greater. The relative abundance of wildlife was expressed as the ratio of livestock to wildlife, and has a value of less than one if wildlife TLU exceed that of livestock. As the relative abundance of livestock increases, this index becomes larger. The observed ratios ranged from a low of 0.3 in Lamu to a high of 105 in West Pokot. Assuming that wildlife contributed little to the total stocking rate in the high-potential districts, the livestock stocking level can be considered to be almost identical to the combined total of livestock and wildlife. On the basis, total stocking levels in TLU equivalents (Table 3) ranged from a low of 3.9 TLU per km^2 in Marsabit District to a high of 66.4 in Kericho District.

The index of average aridity ranged from a very humid value of 1.1 for Kisii District to a very arid value of 7.0 for Marsabit and Mandera districts (Table 3). Total stocking levels were greater in the most humid districts (Fig. 2) and lower in the drier districts. These stocking levels were negatively correlated to aridity (R = –0.70).

The ratio of cattle to sheep and goats was correlated (R = –0.82) to the natural log of the aridity index (Fig. 3). This ratio varied from a low of 1 in Mandera to a high of 120 in Bungoma District

Table 3. Average stocking levels (TLU per km^2), aridity index, and human population density (no. per km^2) for 38 districts in Kenya, 1977-1983.

District	Livestock	Wildlife	Total animals	Ratio lvst./ wildlife	Ratio cattle/ sheep & goats	Aridity	Humans	Lvst./1000 humans
Baringo	9.8	0.2	9.9	59	7	4.6	21	478
Bungoma	39.5	—	39.5	—	124	1.4	164	241
Busia	23.2	—	23.2	—	70	1.8	183	127
Embu	12.9	—	12.9	—	12	3.5	97	133
Garissa	7.4	2.3	9.8	3	11	6.6	3	2552
Isiolo	9.6	1.4	11.0	7	4	6.7	2	5647
Kajiado	17.5	5.0	22.5	4	8	5.3	8	2303
Kakamega	22.4	—	22.4	—	55	1.3	295	76
Kericho	66.4	—	66.4	—	75	1.6	161	412
Kiambu	9.1	—	9.1	—	22	2.6	280	32
Kilifi	6.2	1.3	7.5	5	10	5.0	35	179
Kirinyaga[1]	136.7	—	136.7	—	1012	1.9	202	674
Kisii	26.4	—	26.4	—	83	1.1	396	67
Kisumu	33.1	—	33.1	—	45	2.4	230	144
Kitui	5.4	1.2	6.1	5	7	5.7	16	342
Kwale	10.7	0.6	11.3	18	8	4.4	35	307
Laikipia	18.4	8.9	27.3	2	18	4.9	14	1333
Lamu	2.4	9.5	11.8	<1	36	5.0	7	369
Machakos	15.6	—	15.6	—	10	4.8	72	216
Mandera	7.0	0.4	7.5	16	1	5.9	4	1750
Marsabit	3.3	0.6	3.9	6	3	7.0	1	2538
Meru	13.5	—	13.5	—	22	3.5	84	161
Muranga	31.3	—	31.3	—	58	1.9	262	120
Nakuru	32.6	—	32.6	—	13	3.1	91	360
Nandi	52.0	—	52.0	—	57	1.3	109	477
Narok	24.9	21.4	46.3	1	14	4.4	13	1901
Nyandarua	26.2	—	26.2	—	10	2.7	69	403
Nyeri	18.6	—	18.6	—	22	2.5	143	126
Samburu	7.9	2.0	9.9	4	6	5.7	4	1795
Siaya	38.7	—	38.7	—	64	2.8	188	206
South Nyanza	31.6	—	31.6	—	67	2.8	143	221
Taita Taveta	3.4	8.8	12.2	<1	23	6.0	9	391
Tana River	5.1	2.0	7.2	3	8	6.6	2	2125
Trans Nzoia	32.0	—	32.0	—	53	2.6	125	256
Turkana	5.7	0.3	6.0	21	2	6.6	2	2478
Uasin Gishu	46.2	—	46.2	—	27	2.3	89	519
Wajir	6.4	0.7	7.1	10	5	7.0	3	2560
West Pokot	9.4	0.1	9.5	105	16	4.5	18	537

[1] Indicates data of questionable reliability.
— indicates no data availabile.
"lvst." abbreviation for livestock.

(Table 3). High ratios indicate a relatively high proportion of cattle compared to sheep and goats while low ratios characterize a relatively low proportion of cattle. Nation-wide, this ratio was lowest in the more arid regions indicating that the relative biomass of cattle is greater in wetter areas and that of sheep and goats is greater in arid regions.

Human population densities varied from less than 2 persons per km^2 in Marsabit and Isiolo districts to more than 200 in Kakamega, Muranga, Kisumu, Kiambu, and Kisii districts (Table 3). Human density was also correlated (R = -0.86) to the natural logarithim of the aridity index (Fig. 4). Those districts with the greatest human densities were characterized by the wettest agroclimatic zone. The number of livestock per person was greatest in the driest districts (Table 3). Districts such as Kisii and Kakamega which have high human densities had less than 100 TLU per 1,000 people, while there were more than 2,000 TLU per 1,000 persons in the drier districts.

Discussion

After 6 years of censusing animal populations in Kenya, KREMU has accumulated a large body of data. Those data described in this report present a synthesis of all surveys which could be summarized on a district basis. Except for Nairobi, Elgeyo-Marakwet and Mombasa, all parts of the country have been surveyed at least once.

Because species composition varies so much from district to district, the concept of the tropical animal unit was used to provide a common denominator. However, choosing a TLU equivalent for a particular kind of animal was difficult. This value must account for differences in the age-sex composition, for differences among subspecies and varieties within a given group, and for differences associated with the nutrition and the environment in which the animals live. Nevertheless, the TLU equivalent gives a useful standard by which stocking levels across diverse habitats can be compared. Future monitoring will require estimates of the age-sex structure of the animal populations and measures of individual weights of animals of various taxonomic, nutritional, and age classes in order to obtain more accurate estimates of stocking levels.

The use of the term "stocking rate" has been avoided because the current survey activities are too infrequent for this measure to be made. The stocking rate is "the actual number of animals or animal units on a specific area for a specific period of time" (Heady 1975). The population censuses reported herein provide a "snap shot" in time of the changing animal populations without reference to the length of time they are actually present on the rangelands being surveyed. More frequent censuses and measures of animal movements will be necessary to give a complete picture of stocking rates.

While there was, on average, a negative correlation between stocking levels and the aridity index (Fig. 2), the stocking levels for

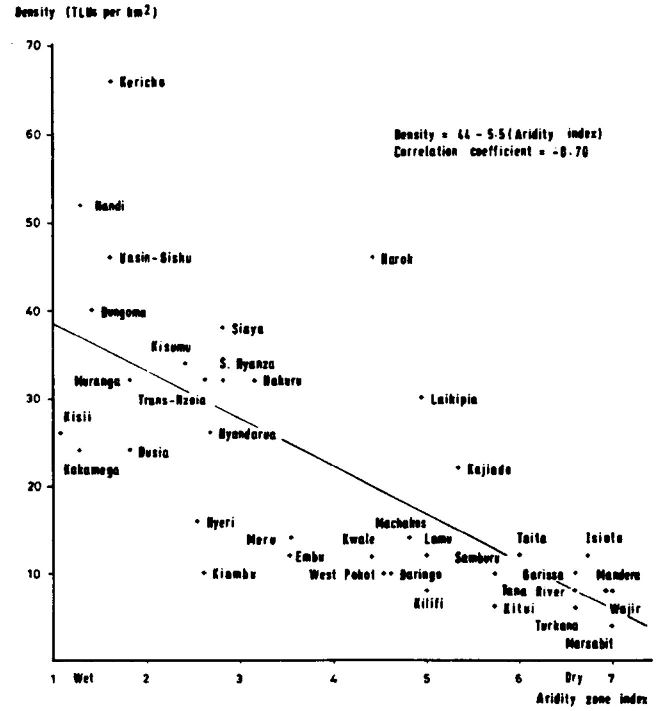

Fig. 2. *Relation between total animal density and the aridity index.*

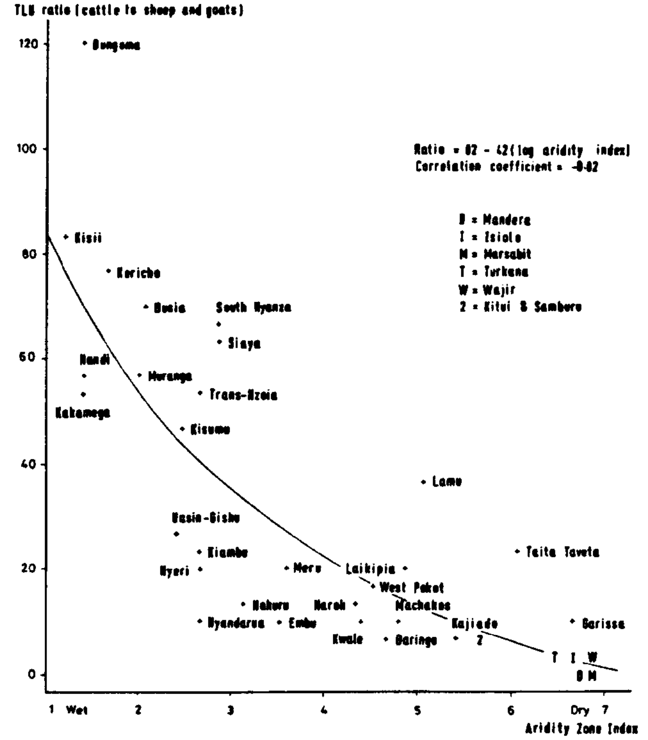

Fig. 3. *Relation between the ratio of cattle to sheep and goats and the aridity index.*

several districts were either well above or well below the regression line. Stocking levels, in general, were low in the driest areas and high in the most humid districts. On one hand, districts such as Kericho, Narok, Laikipia, and Kajiado appeared to have high stocking levels relative to their average level of aridity. These are districts which have well-developed livestock industries. On the other hand, the districts of Kakamega, Kisii, Busia, Nyeri, Embu, Trans Nzoia, Kwale, West Pokot, Kilifi, Baringo, Lamu, and Kitui had relatively low stocking levels. It is likely that factors other than water are keeping animal densities relatively low in these areas. For example, Kakamega and Kisii districts have high human densities (Table 3) and the requirements for human food have been given priority over forage requirements for livestock.

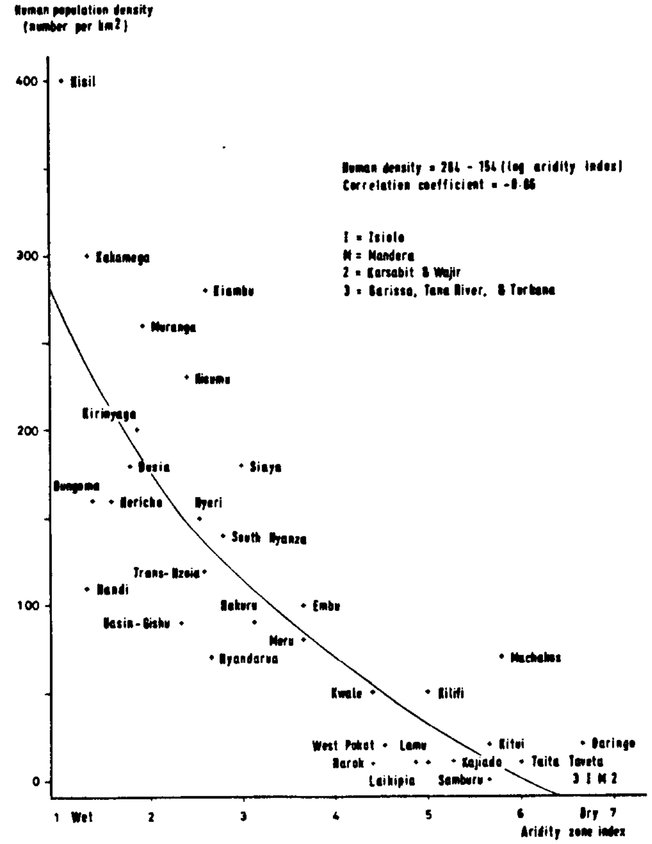

Fig. 4. *Relation between human density and the aridity index.*

On the assumptions that most of the annual production of forages in an area will be consumed by either wildlife or livestock and that the total stocking levels were largely limited by forage, those districts with the lowest ratio of livestock to wildlife represent areas where livestock expansion might be most successful given proper management. Thus districts such as Garissa, Kajiado, Laikipia, and Lamu may have a good potential for livestock expansion. However, the consequence of this would likely be a subsequent decrease in wildlife biomass. Districts such as Baringo and West Pokot, with very high ratios of livestock to wildlife, may have relatively little potential for expanding the livestock industry.

The description of the aridity index (Table 3) provides a district-based summary of the detail given in Braun's (1980) original map. Although much detail was lost, this presentation is directly comparable to the district-based animal census data. Relating total stocking level and the ratio of cattle to sheep and goat ratios to aridity provides one measure of the impact of range-livestock management. After correcting for aridity, the districts of Baringo, Nakuru, and Uasin Gishu appear to have a relatively high proportion of sheep and goats. It is beyond the scope of this paper to explain this finding. However, it may be indicative of loss of habitat or forage plants suitable for cattle. It may also reflect the traditions of the resident human populations.

Both the human population density (Fig. 4) and the livestock density (Fig. 2) were negatively correlated to aridity. Given that these relationships can be explained by the greater productivity of food crops in wetter districts, there is likely to be competition for food. Since the human population gives greater priority to feeding people than to feeding animals, the lowest numbers of TLU of livestock per 1,000 people (Table 3) are found in the most populous districts of Kisii, Kakamega, and Kiambu. In contrast, the districts of Garissa, Isiolo, Kajiado, Marasabit, Tana River, Turkana, and Waji have low human densities but a high number of livestock TLU per 1,000 people. Not only does the reduced human population reduce competition for grazing land, but these areas are for the most part, too dry for production of food crops for human consumption and thus the animals become the primary sources of food and wealth. Thus in the districts where animal densities are lowest, the per capita importance of them is greatest.

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Foraging Ecology of Bison in Aspen Boreal Habitats

R.J. HUDSON AND S. FRANK

Abstract

Studies on several wild and domestic ungulates suggest that large grazers attain higher maximum forage intake rates but require relatively higher forage biomass to do so. In this study, forage intake rates and feeding times of North America's largest wild grazer, the bison *(Bison bison)*, were related to forage biomass during summer and autumn in aspen boreal forest habitats. Irrespective of season, maximum feeding rates of 68 g/min declined by 50% as forage biomass was reduced to 780 kg/ha. This reduction was due primarily to smaller bite sizes. However, bison compensated by increasing cropping bite rates to more than 60 bites/min on heavily grazed swards. Grazing times increased from 9 h/day in summer to 11 h/day in autumn, offsetting slight decreases in average foraging efficiency. During summer, a greater proportion of grazing occurred at night. Upland meadows were preferred habitats for grazing despite relatively low pasture biomass and potential dry matter intake rates.

Key Words:ruminant nutrition, forage intake, forest range

Bison once occupied a vast geographical range and wide variety of habitats. Historically, the main Canadian populations were distributed south of the North Saskatchewan River where they offered a major source of meat and hides for native people, fur traders, and later settlers (Roe 1970). Today, most bison in Canada are privately owned, although approximately 8,000 still exist in parks and reserves. Despite the historical importance of bison and their emerging role as a farm animal, their nutritional ecology remains poorly understood (reviewed by Reynolds et al. 1982). Because almost all populations are confined and highly fragmented, we may never know exactly how they used the forage resources of prairies and parklands (Moodie and Kay 1976, Morgan 1980). However, by examining their response to forage biomass, structure, and quality, we may better understand their original trophic niche.

As North America's largest herbivore, bison offer several insights into potential constraints of body size on nutritional ecology. It is widely accepted that larger herbivores are able to subsist on low quality forages, a fact borne out by comparative studies of digestive efficiency (Richmond et al. 1977, Hawley et al. 1981). Large animals also possess considerable thermal inertia and can thrive in extremely cold environments (Christopherson et al. 1978, 1979). However, large body size has its disadvantages as well; although weight-specific energy requirements of large animals are low (Hudson and Christopherson 1985), bison nevertheless require substantially more forage in absolute terms than do smaller herbivores. These high levels of forage intake could be achieved by: foraging longer, cropping forage faster, taking larger bites, or selecting habitats which allow higher consumption rates. This study was conducted to evaluate these foraging alternatives. In particular, we wanted to test the hypothesis that large grazers such as bison require higher forage biomass to meet their greater daily forage requirements.

Study Area and Animals

Observations were made at the Ministik Field Station, located in the Beaver Hills 50 km south east of Edmonton, Alberta. The area falls within the boreal mixed-wood forest zone (Rowe 1972) but a history of burning and grazing have left few coniferous elements. Until the middle of the last century, the area supported sizable populations of bison particularly during winter.

Deciduous forests, grasslands, and wet meadows were all about equally represented in the study area. The dominant forest overstory was balsam poplar *(Populus balsamifera)* on wetter sites and trembling aspen *(Populus tremuloides)* elsewhere. Upland meadows were comprised of *Poa pratensis* and *Bromus inermis*. Low-

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land meadows supported *Poa, Calamagrostis,* and *Juncus.* The wettest sites, ringed by willow *(Salix)* fens, supported vigorous stands of sedge (*Carex aquatilis, C. rostrata).*

The station has been heavily stocked since 1977 with wapiti *(Cervus elaphus),* moose *(Alces alces),* and bison. At the time of the study, the bison herd consisted of 1 adult bull, 3 subadult bulls, 7 cows, 4 yearlings (including 3 females), and 1 calf. They were thoroughly habituated to human presence and could be observed without disturbance from within 20 m.

Methods

We evaluated activity budgets, habitat selection, and foraging behavior of free-ranging bison during June–July when pastures were green and in September–October when vegetation had cured. The 2 periods were separated by the peak of the rut during August. This provided an opportunity to explore influences of forage biomass and quality on feeding behavior.

Activities and Habitat Selection

Feeding times and habitat selection of herd members were recorded during one 24-hr scan and one 12 h (0600–1800 h) scan in each season. Observation dates were selected to be representative of seasonal meterological conditions. The July scans were conducted when maximum temperatures were 21–25° C. Maximum temperatures during October scans were 10–13° C.

Activity states (feeding/not feeding) and habitats occupied (upland meadows, lowland meadows, sedge meadows, and aspen/-poplar forests) were recorded every 10 min. Because identification of individual animals was sometimes uncertain, particularly at night, hourly tallies had to be made on the basis of sex/age classes. This obviated statistical analysis of differences between seasons.

Foraging Bahavior

We recorded foraging behavior according to a protocol used previously to study wapiti (Hudson and Nietfeld 1985) and moose (Renecker and Hudson 1986) in the same area. While engaged in relatively uninterrupted foraging bouts, selected individuals were observed for 1–5 min intervals during which cropping bite rates were recorded with an electronic event-recorder. We ended measurements when individuals interrupted feeding, e.g., to walk to a different habitat, groom, or interact with other animals. We immediately collected 20 simulated bites to represent the quantities selected by the focal animal. This procedure was necessarily subjective, but on the upland swards used to derive functional relationships, little selectivity was apparent; estimating bite sizes was mainly a matter of estimating the depth within the sward that the animal grazed. Bite sizes estimated from oven-dried weights (60° C to constant weight) were paired with dry forage biomass determined by plucking a single 0.25 m² plot situated within several meters of the location grazed. Consumption rates (g/min) were calculated as the product of bite rate (g/min) and bite size (g/bite) for a total of 37 observations.

Data from subadult bulls, cows, and yearlings were pooled; the single senior bull and calf were excluded from analysis. Because it was difficult to determine the proportion of aboveground biomass available to bison, data for sedge meadow habitats were not used. We estimated maximum foraging rates (A) and vegetation biomass at which foraging rates were reduced to 50% of the maximum (critical biomass, B^{50}) using asymptotic regression (Dixon 1981). The fitted curve was one of the form, $R = A \times B / (B^{50} + B)$, where B is vegetation biomass. This equation is equivalent to the more familiar form, $R = A\,(1 - e^{-kB})$, where $k = \ln(2)/B^{50}$. Interrelationships of bite sizes to forage biomass and biting rates to bite sizes were explored by regression analysis using logarithmic transformations.

Results

Activity Budgets and Habitat Selection

On summer pastures, bison grazed 8.7 h/d but this increased to 10.7 h/day on cured autumn pastures (Table 1). The proportion of time pent grazing between 0600 and 1800 h increased from 46% in July to 61% in October. Subadult bulls, adult cows, and yearlings behaved similarly. Foraging was organized into 4–5 main bouts in both seasons but during July there was less synchrony among sex/age classes (Fig. 1).

Table 1. Proportion of time spent grazing (%).

	Scan[1]	Jul 20	Jul 28	Oct 20	Oct 22
Adult cows (*n*=7)	24 h	38.8	—	45.1	—
	12 h	46.6	51.9	67.7	53.6
Subadult bulls (*n*=3)	24 h	35.4	—	43.1	—
	12 h	42.2	47.4	63.2	55.6
Yearlings (*n*=4)	24 h	34.9	—	45.8	—
	12 h	40.6	46.4	69.1	55.6

[1] Proportion of time spent grazing was calculated on the basis of 12 and 24 hours. Scans on 28 Jul and 22 Oct were conducted for only 12 h (0600–1800 h).

Although activities were not always synchronized, bison tended to remain in one herd, particularly in autumn. Habitats used for grazing ranked similarly in both summer and autumn (Table 2). Most foraging time was spent on grassy upland meadows and least in poplar forests. Although information is limited, bison appeared to use the same proportions of habitats while grazing during daylight and darkness.

Table 2. Proportion of grazing time[1] spent by bison in each habitat in relation to forage biomass.

	July		October	
	20	28	20	22
Sedge meadow	4335±714	kg/ha	6870±999	kg/ha
24 h	28%	—	16%	—
12 h	34%	17%	20%	17%
Upland meadow	550±100	kg/ha	539±190	kg/ha
24 h	43%	—	49%	—
12 h	42%	78%	50%	37%
Lowland meadow	3705±797	kg/ha	2516±296	kg/ha
24 h	28%	—	31%	—
12 h	24%	2%	24%	31%
Forest				
24 h	1%	—	4%	—
12 h	<1%	3%	6%	15%

[1] Grazing times for 24 h and 12 h (0600 – 1800 h) period.

Foraging Rates

The maximum consumption rate of bison feeding on herbaceous vegetation was 67.5 g/min. Although insufficient data were obtained during autumn to fit a separate relationship and test significance, there was no obvious difference between summer and autumn (Fig. 2). When pasture biomass was 779 kg/ha, consumption rates fell to one half of this maximum.

This asymptotic relationship resulted from the interactions of bite size and bite rate. Bite sizes increased logarithmically with forage biomass to almost 1.2 g/bite on pastures supporting approximately 3,000 kg/ha (Fig. 3). Cropping bite rates declined moderately from an observed maximum of 65 bites/min to 46 bites/min over this range of bite sizes (Fig. 4).

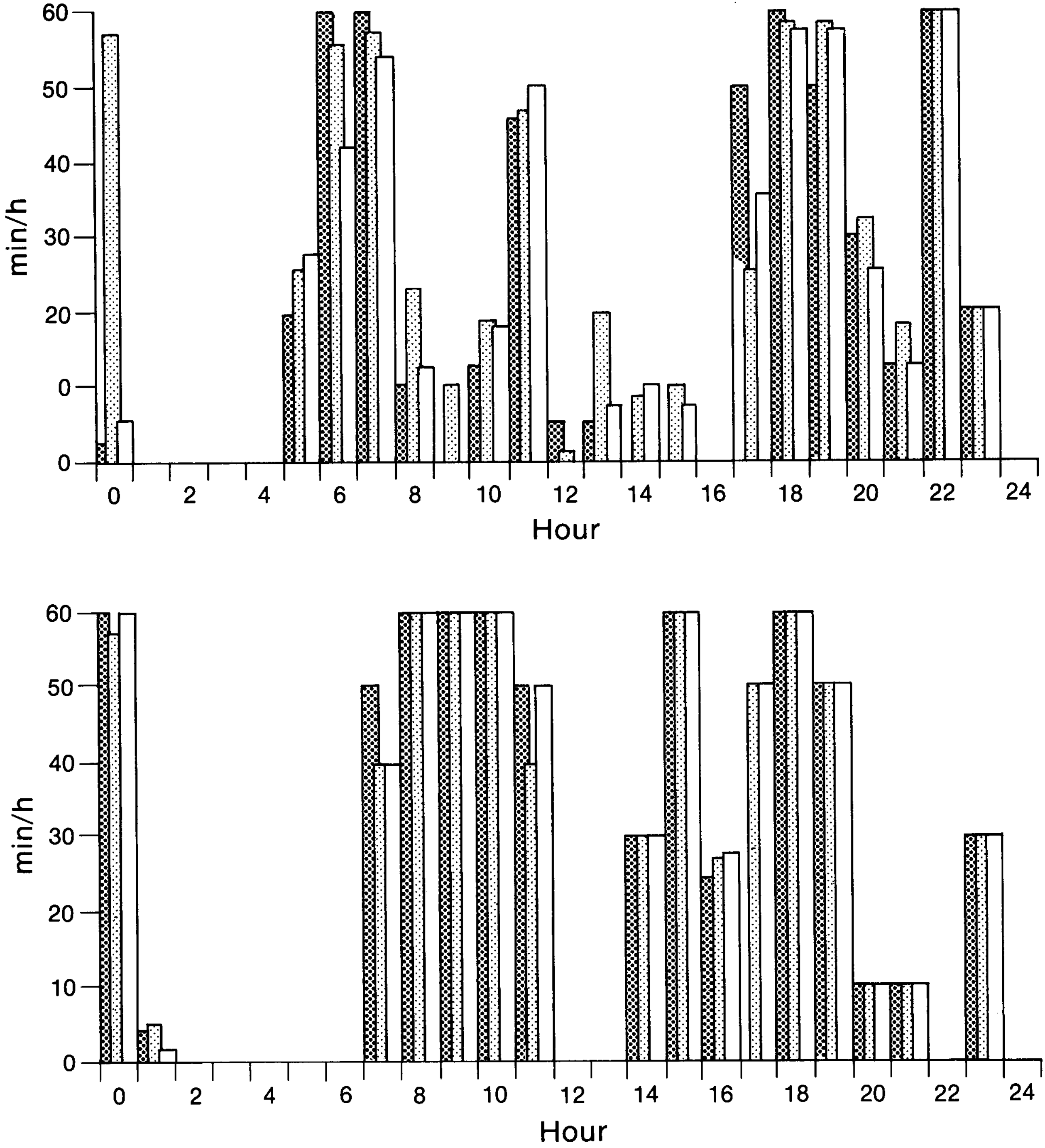

Fig. 1. *Foraging times (min/h) of bison during 24 h on 20 July (above) and 20 October (below). Dark bars–subadult males; medium bars–adult cows; light bars–yearlings.*

Discussion

Foraging Efficiency

Maximum foraging rates of ruminants scale to body size (Clutton-Brock and Harvey 1983, Wickstrom et al. 1984). Compared with 68 g/min for bison, maximum rates determined on summer pastures in the same study area were 18 g/min for wapiti (Hudson and Nietfeld 1985) and 23 g/min for moose (Renecker and Hudson 1986). Estimates of over 60 g/min have been obtained for beef cattle in other parts of central Alberta (Arthur 1984). Therefore, on the basis of body size, maximum feeding rates observed for bison are consistent with expectations.

Larger herbivores are also expected to require higher forage biomass to achieve these maxima (Wickstrom et al. 1984). However, interspecific patterns are not all that clear even with due consideration for habitat structure and forage preferences. In this study, bison foraged more efficiently on sparse pastures than might be expected. In spite of their considerably larger size, the critical biomass (B^{50}) of 779 kg/ha for bison fell within the range of 542 kg/ha (Wickstrom et al. 1984) and 1,000 kg/ha (Hudson and Nietfeld 1985) reported for wapiti in grassland habitats.

The high feeding rate of bison is achieved by large bite sizes and rapid bite rates. Bite sizes on short uniform swards are determined largely by the width of the incisor bar (6.5 cm measured in a single adult bison cow). In our study, bison seldom prehended even long

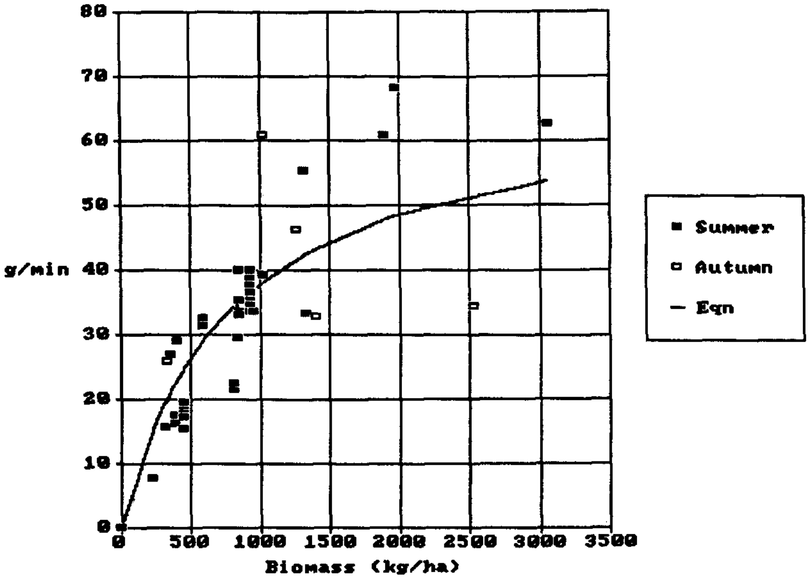

Fig. 2. *Intake rates of bison in relation to forage biomass during summer (closed symbols) and autumn (open symbols):* $Y = (67.5\,X)/(779 + X)$, $r^2 = 0.55$.

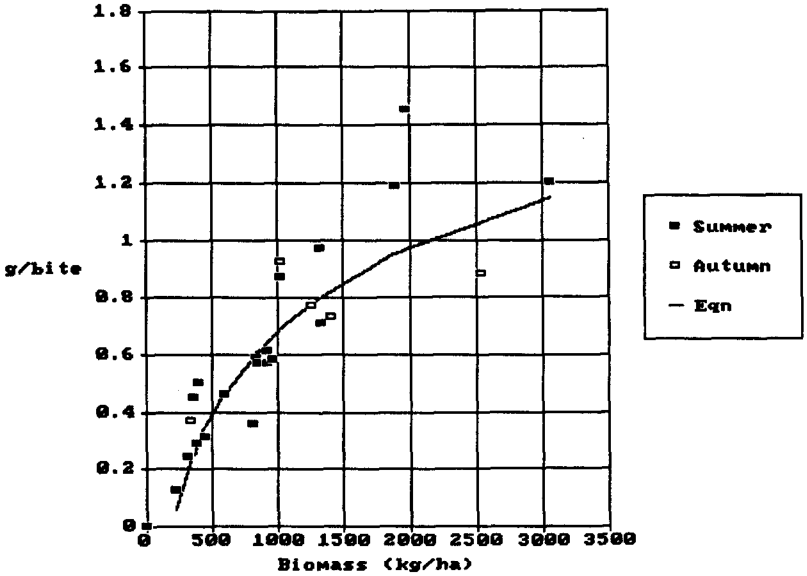

Fig. 3. *Bite sizes of bison in relation to forage biomass during summer (closed symbols) and autumn (open symbols):* $Y = 2.22 + 0.42 \ln X$, $r^2 = 0.74$.

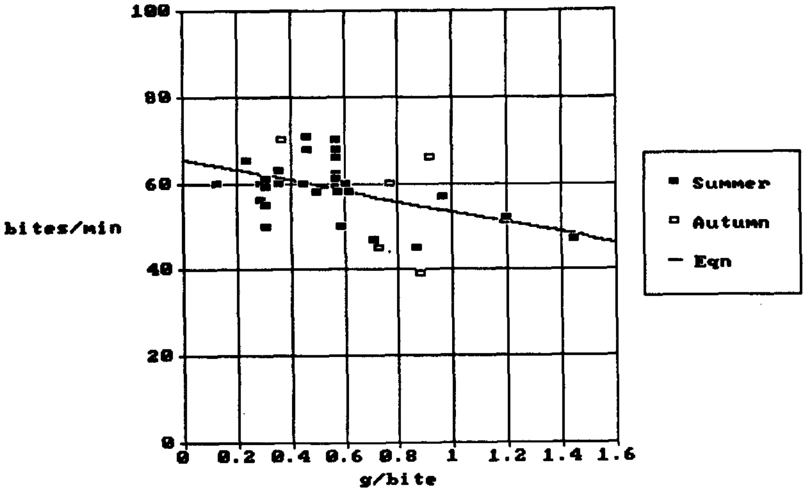

Fig. 4. *Cropping bite rates of bison in relation to bite size during summer (closed symbols) and autumn (open symbols):* $Y = 65.7 - 12.3\,X$, $r^2 = 0.21$.

forage with their tongues in a horizontal plane. The curvilinear relationship of bite size to forage biomass presumably arises because of the vertical distribution of pasture biomass as well as upper limits of mouth volume.

The inverse relationship between biting rates and bite sizes has several explanations (Wickstrom et al. 1984, Hudson and Nietfeld 1985). An obvious explanation is that grazing animals attempt to compensate for smaller bites by feeding faster. However, the decline in bite rates may be imposed by increased handling time required to wet, masticate, and swallow larger bites. Compared with wapiti, cropping bite rates of bison were high at an equivalent forage biomass and declined less sharply with increasing bite sizes. This may mean that bison spend less time selecting and / or less time handling forage. Under the conditions of this study, the superior handling efficiency of bison probably is most important because these pastures offered little opportunity for selection. Although differences in this relationship between summer and autumn forages might be expected, contrasts in fibrousness were not great since most pastures grazed in the autumn showed some regrowth.

Because of the weak relationship between bite rate and and bite size, intake rates of bison on grasslands are determined primarily by bite size, which is strongly influenced by forage biomass. Based on their studies on reindeer and comparisons of published information, Trudell and White (1981) pointed to considerable variation in the relative importance of these two parameters. While the bison represents one extreme, reindeer represent the other in which bite sizes vary little with forage biomass. Trudell and White's (1981) argument that high biting rates of reindeer indicate selectivity is not inconsistent with our seemingly contradictory explanation for bison. At low forage biomass, reindeer may spend more time searching for acceptable forage items; therefore, biting rates increase with forage biomass as long as bite size does not inordinately increase handling times The main feature of selective feeding appears to be constancy of bite sizes.

High foraging efficiency permitted bison to meet their forage requirements without prolonged foraging. Grazing times observed in this study (8.7–10.7 h/d) were no greater than those of wapiti (8–13 h/d) on the same pastures (Gates and Hudson 1983). Average foraging rates (calculated from habitat-specific forage biomass and proportional habitat use) declined slightly from summer (43 g/min) to autumn (39 g/min). However, extending foraging times by 2 h permitted bison to actually increase daily dry matter intakes. Potential daily intakes calculated in this way exceed 5% of body weight. Actual intakes probably were at least 50% lower because feeding rates applied only to uninterrupted feeding at a single station.

Trophic Strategies

By conventional criteria, the digestive efficency of bison is high, particularly on fibrous forage (Peden et al. 1974, Richmond et al. 1977, Hawley et al. 1981). Nevertheless, superior digestion coefficients usually are not reflected in better feed conversion efficiency (kg gain/kg forage) in comparisons with cattle that digest coarse forages less well (Richmond et al. 1977). One reason for these patterns may be that that proportion of acetate among volatile fatty acids increases as digestion proceeds, providing a deficit of glucogenic precursors (Van Soest 1982). This should have minor effects on the efficiency of utilization of metabolizable energy for maintenance, but exert more important reductions in the efficiency of growth. Another penalty of prolonged retention of digesta is reduced intake. Although low dry matter intakes are offset by higher digestibilities, daily intakes of digested organic matter in bison are low compared with many other large grazing ruminants (Foose 1982).

This pattern of digestive adaptation should convey a competitive advantage in circumstances where forage is in limited supply and there are few opportunities to forage selectively. It is a conservative strategy of using limited resources rather completely. To complement this digestive strategy, one would expect bison to forage efficiently on grass swards even at low biomass densities. This study confirms this expectation.

Bison bison like its immediate ancestor *(Bison occidentalis)* is a grassland specialist that seemed to rapidly fill a niche left vacant by megafaunal extinctions at the Pleistocene-Holocene boundary (McDonald 1981). Modern bison evolved as recently as 5,000 years BP when forests and savannas were replaced by grasslands. They dominated this environment as evidenced by the abundance of fossilized bones and dense populations which existed at the time of European exploration and settlement. High foraging efficiency would have permitted the attainment of such high population densities and indeed this adaptation could have been honed by prolonged existence at high densities.

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Seasonal Diets of Camels, Cattle, Sheep, and Goats in a Common Range in Eastern Africa

WANGOI MIGONGO-BAKE AND RICHARD M. HANSEN

Abstract

Although there have been several reports on the food habits of domestic herbivores in various semiarid regions of the world, there has been no previous report on the partitioning of forage resources by camels *(Camelus dromedarius)* and sheep *(Ovis aries)*, goats *(Capra hircus)* and cattle *(Bos indicus)* using a common range. In the semiarid region of northern Kenya, the seasonal exploitation by these herbivores resulting from herding by the nomadic Rendille pastoralists makes the system for management of these rangelands very complex. Information on the food habits of animals utilizing a common range is important in offering a basis for assessing the usefulness of the range components to the animals. Consequently, food habits information becomes an important tool in making management decisions. Camels were predominantly browsers while cattle were predominantly grazers. Sheep and goats were intermediate feeders. Cattle browsed most during the 'green' season when the browse shoots were most abundant and easiest for their large mouth parts to harvest. Camels grazed most during the very dry season when most trees and shrubs had shed their leaves. The observed variations in food habits among the 4 herbivores suggest that they may require different management to obtain optimum production.

Key Words: common use, forage selection, diet similarity, Kenya livestock, pastoralists

Animal husbandry is the most productive use of arid and semiarid areas of the world. More than 2/3 of Kenya is classified as rangeland (over 492,100 km^2). More than half of this area averages less than 370 mm of rainfall annually. The Rendille pastoralists utilize such an area in the lowlands of northern Kenya in their nomadic way of life. Knowledge of plant species commonly selected by grazing and browsing herbivores at different times of the year is fundamental to effective grazing management. The Rendille keep camels, cattle, sheep, and goats, the first 2 being the chief source of milk and the last 2 used mainly for barter. A large increase in human population in recent times, due to a better standard of living, has been accompanied by a tremendous increase in the total livestock numbers in the area. This has resulted in range degradation, especially around settlements and wells (bore holes).

Food habits of single species in semiarid areas of eastern Africa have been described for goats (Edwards 1948, Hornby et al. 1948, Wilson 1957, Knight 1965), cattle (Harker et al. 1956, Lampkin and Quarterman 1962, Payne and McFarlane 1963), and camels (Knoess 1976, Field 1978, Newman 1979). Food habits studies on mixed species in the same region have been described for goats and cattle (Staples et al. 1942) and for camels, sheep, and goats (Field 1979). However, no seasonal diets have previously been reported for common use of camels, goats, sheep, and cattle. The objective of this study was to gather this information as a basis for better management of the semiarid rangelands of eastern Africa used in common by these 4 livestock species. The study was conducted from March 1982 to February 1983.

The study area is located in northern Kenya between latitudes 1° 7′ and 2° 37′ north and longitudes 37° 13′ and 37° 52′ east. It covers an area of approximately 3,450 km^2 through which pastoralists roam with their livestock in search of good pastures. The study period covered 2 wet (green seasons) and 2 dry seasons. McCown (1980) suggested that 'green season' be used instead of 'wet season' when discussing temporal patterns of forage condition since even after the rains have ceased plants continue to grow as long as there is sufficient moisture remaining in the soil. The sequence of seasons during the period of study was the first green season (April–June 1982), first dry season (July–September 1982), second green season (October–December 1982), and second dry season (January–March 1983).

Forage biomass of dwarf shrubs, grasses and herbs (Table 1) was sampled once every month using 1-m^2 quadrat (Brown 1954, Mannetje 1978). Clipped vegetation was divided and sacked in the field on the basis of species, standing dead, herbaceous litter and woody litter. The samples were air dried for 1 month at daytime temperatures of 20° C to 40° C and then weighed. Foliage biomass of trees and shrubs (Table 1) was estimated using the wandering quarter method (Catane 1963) for estimating tree density (Mueller-Dumbois and Ellenberg 1973) by taking crown measurements of each tree or shrub encountered along the transect and converting the crown area to foliage dry weight using correction factors developed for species in the area of study (Lamprey, unpublished).

Table 1. The mean ± standard deviation of major (>5%) plant genera found in the diets of livestock species in the Rendille region of northern Kenya during the first green season (April to June, 1982).

Genus of Plants	Livestock species			
	Camels	Goats	Cattle	Sheep
Trees				
Commiphora	10 ± 5	7 ± 1	—	—
Euphorbia	7 ± 3	—	—	—
Shrubs				
Grewia	10 ± 6	7 ± 3	—	—
Dwarf Shrubs				
Duosperma	10 ± 4	—	—	—
Heliotropium	6 ± 2	6 ± 2	—	—
Indigofera	8 ± 3	7 ± 3	—	—
Justicia	6 ± 4	6 ± 3	—	—
Sericocomopsis	10 ± 5	8 ± 2	—	—
Grasses				
Aristida	—	7 ± 2	19 ± 6	13 ± 5
Brachiaria	—	—	7 ± 4	—
Cenchrus	—	—	6 ± 4	—
Enneapogon	—	—	—	—
Eragrostis	—	—	5 ± 2	7 ± 7
Sporobolus	—	—	5 ± 2	7 ± 7
Tragus	—	—	—	7 ± 5
Chloris	—	—	6 ± 2	—

Once a week 40 individuals from each of the 4 livestock species were randomly selected to provide fecal samples. These were about 2 g each for cattle, 1 pellet for camels, and 4 pellets for sheep and goats. The samples were dried in the shade at daytime temperatures of 20° C to 40° C for a minimum period of 1 week. They were then ground in a Wiley mill through a 1-mm screen. The seasonal

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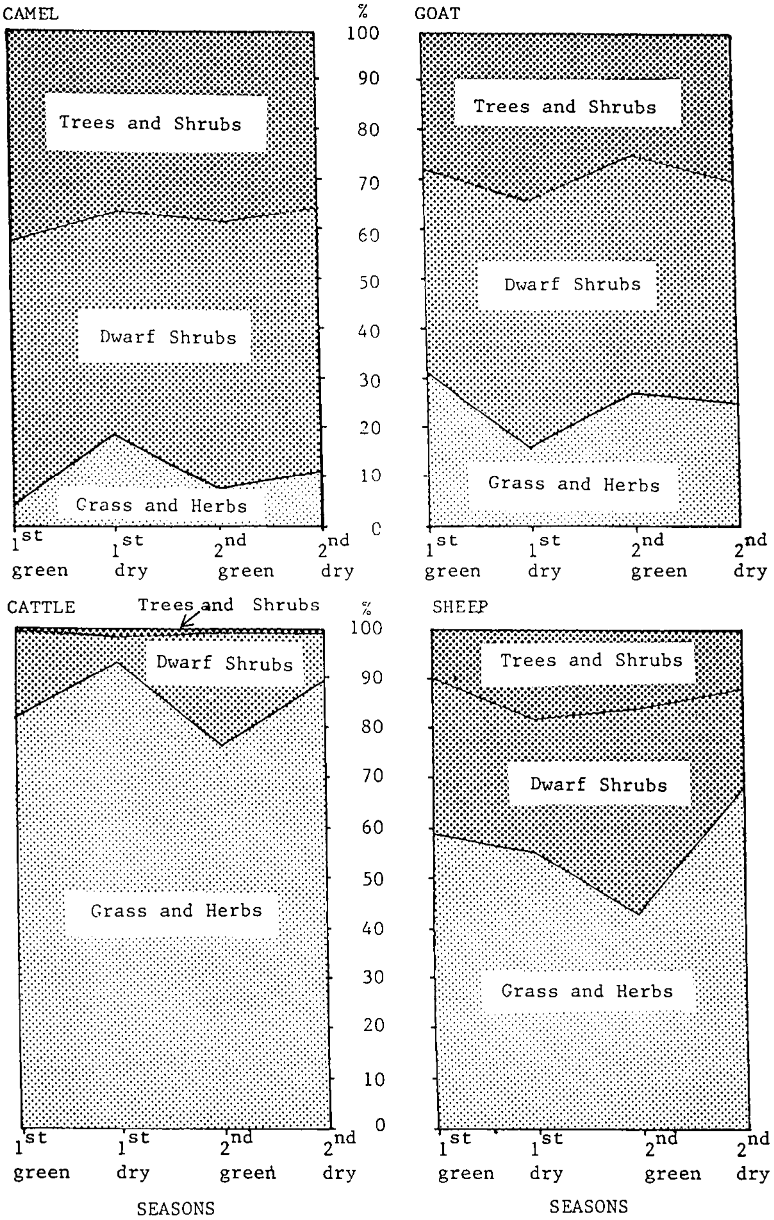

Fig. 1. *Seasonal forage components (%) of the diets of camels, cattle, sheep and goats in the Rendille region of northern Kenya.*

samples of each animal species were composited and a subsample of this was used for the microhistological analysis to get the percent relative density of forage fragments, which is a good approximation for the relative amount of each plant eaten. Five microscope slides were prepared for each seasonal sample and 20 slide fields read per slide.

Although the microhistological technique of diet analysis (Sparks and Malechek 1968) used in this study has been criticized, especially in estimation of diets consisting largely of leafless shrubs (Gill et al. 1983), Holechek and Valdez 1985), the procedure has been shown to be most accurate when the technician has had special training, is experienced in the technique, and has field related experience with the plant species in the area of study (Holechek et al. 1982, Holechek and Gross 1982, Mukhtar and Hansen 1983). If necessary, correction factors may be applied (Vavra and Holechek 1980). The technician (Migongo-Bake) had been taught to identify and quantify plant fragments until all her determinations for hand compounded mixtures of plants from the study area were less than ± 5% of their dry weight. It was observed in the study area that in the dry season when the drought-deciduous browse species had lost their leaves, they became brittle and unpalatable so that only the palatable grasses and drought-tolerant leafy woody plants were selected.

Results

The forages in the diets of the 4 livestock species were categorized as trees-and-shrubs, dwarf shrubs and grass-and-herbs components for each of the 4 seasons (Fig. 1). The major forage species (>5%) in the seasonal diets of the livestock species are shown in Tables 1 to 4. While no individual grass or herb species contributed more than 5% to the diet of camels in any 1 season (Tables 1 to 4) grass-and-herbs as a diet component (Fig. 1) contributed more than 10% of their diet during both dry seasons. The same tendency was observed for goats. Trees-and-shrubs and dwarf shrubs contributed substantially (>10%) to the diets of cattle in the green seasons (Fig. 1). However, no browse species contributed more than 5% to the diet of cattle in any one season (Tables 1 to 4). Individual browse species contributed more than 5% to the diet of sheep in the very green season (October–December). As a forage

Table 2. The mean ± standard deviation of major (>5%) plant genera found in the diets of livestock species in the Rendille region of northern Kenya during the first dry season (July to September, 1982).

Genus of Plants	Livestock species Camels	Goats	Cattle	Sheep
Shrubs				
Cadaba	9 ± 6	6 ± 2	—	—
Balanites	7 ± 4	—	—	—
Grewia	—	8 ± 4	—	—
Dwarf Shrubs				
Duosperma	11 ± 6	12 ± 6	—	—
Heliotropium	7 ± 6	7 ± 5	—	—
Indigofera	9 ± 4	—	—	—
Sericocomopsis	—	6 ± 3	—	—
Grasses				
Aristida	—	—	23 ± 6	16 ± 6
Cenchrus	—	—	—	—
Chloris	—	—	7 ± 5	—
Enneapogon	—	—	—	—
Eragrostis	—	—	17 ± 8	7 ± 3
Sporobolus	—	—	6 ± 5	—
Tetrapogon	—	—	7 ± 4	—
Tragus	—	—	9 ± 6	9 ± 5

Table 3. The mean ± standard deviation of major (>5%) plant genera found in the diets of livestock species in the Rendille region of northern Kenya during the second green season (October to December, 1982).

Genus of Plants	Livestock species Camels	Goats	Cattle	Sheep
Trees				
Commiphora	10 ± 2	—	—	6 ± 2
Euphorbia	7 ± 3	—	—	—
Shrubs				
Grewia	—	6 ± 2	—	—
Dwarf Shrubs				
Duosperma	—	7 ± 1	—	—
Heliotropium	9 ± 1	7 ± 4	—	—
Indigofera	16 ± 4	9 ± 4	—	6 ± 2
Justicia	—	—	—	6 ± 4
Seddera	—	—	—	6 ± 2
Sericocomopsis	8 ± 2	9 ± 2	—	7 ± 4
Grasses				
Aristida	—	—	17 ± 6	7 ± 3
Brachiaria	—	—	6 ± 3	—
Chloris	—	—	7 ± 2	—
Eragrostis	—	—	10 ± 5	—
Sporobolus	—	—	7 ± 4	—
Tragus	—	—	6 ± 3	—

Table 4. The mean ± standard deviation of major (>5%) plant genera found in the diets of livestock species in the Rendille region of northern Kenya during the second dry season (January to March 1983).

Genus of Plants	Livestock species Camels	Goats	Cattle	Sheep
Trees				
Commiphora	6 ± 3	—	—	—
Shrubs				
Cadaba	6 ± 4	6 ± 4	—	—
Dwarf Shrubs				
Duosperma	9 ± 3	8 ± 5	—	—
Heliotropium	6 ± 2	—	—	—
Indigofera	12 ± 3	6 ± 5	—	—
Justicia	6 ± 6	—	—	—
Sericocomopsis	10 ± 5	11 ± 5	—	—
Grasses				
Aristida	—	—	22 ± 3	18 ± 7
Enneapogon	—	—	6 ± 8	6 ± 3
Eragrostis	—	—	12 ± 3	11 ± 4
Sporobolus	—	—	7 ± 3	—
Tragus	—	—	—	9 ± 4

Table 5. Seasonal average rainfall (mm) and forage biomass (kg/ha) in the Rendille region of northern Kenya.

	Seasons First green	First dry	Second green	Second dry
Rainfall	76	0	182	17.5
Forage Types				
Trees-and shrubs[1]	26	16	28	19
Dwarf shrubs	981	442	1061	812
Grass-and-herbs	172	127	225	139

[1] Leaf biomass estimate

component browse contributed more than 30% to the diet of sheep in all 4 seasons (Fig. 1).

Discussion

Although cattle ate predominantly grasses, the browse component of their diet was higher in the green seasons than in the dry season. The amount of browse in the diet was highest during the second green season, which was exceptionally wet and consequently had the highest forage biomass observed in the study period. However, no single browse species made a major (>5%) contribution to cattle diets for any single season. Cattle grazed most during the driest of the 4 seasons (July–September) although grass biomass was at its lowest then. An explanation for this behavior could be that because of their large mouth parts, cattle were not able to select for leaves and twigs from amongst the dry-season-hardened branches of browse. Although more than 50% of the diet of sheep consisted of grasses for all except one season, the browse component of their diet tended to increase during both the very dry season (July–September) and the very green season (October–December). The increase in the very dry season was most likely caused by the much greater decrease in grass relative to browse, while that in the green season was most likely a result of the greater increase in browse biomass relative to grass due to the unusually high rainfall in that season (see Table 5). Goats also tended to browse relatively more during the driest season. However, for camels, which like sheep and goats have mouth parts adapted for browsing, the grass component of the diet was greatest during the driest season. Most trees and shrubs and even some dwarf shrubs, in these semiarid rangelands are drought deciduous. This reduction in leafy browse might have caused the camels to graze, especially in localized stands of *Aristida* spp., common in these rangelands, in order to meet their dietary requirements, which are greater than those of the other 4 livestock species. This dry-season grazing behavior by camels had been observed earlier in this region (Sato 1976, Field 1979) and also in the northwest Sahara (Gauthier-Pilters 1958).

Since most trees in the area of study are drought deciduous, they are important as a diet component only in the green seasons. In the dry season dwarf shrubs thus become major contributors of browse diet to camels, goats and, to some extent, sheep. Most of the grass species in the area of study are annuals and remain either in the form of standing-dead or litter in the dry season. Although grass biomass is very low in the dry seasons it is still the major diet contributor to the diet of cattle and, to a large extent, sheep. The preference of a grass diet by camels in the dry season adds more pressure to a resource that is already in low supply. This increased demand on the grass resource in the dry season might have a negative effect on cattle production, since they are predominantly grazers.

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(continued on page 83)

Elk, Mule Deer, and Cattle Habitats in Central Arizona

MARK C. WALLACE AND PAUL R. KRAUSMAN

Abstract

Elk *(Cervus elaphus)* and mule deer *(Odocoileus hemionus)* distribution and use of habitats shared with cattle (*Bos* spp.) on a ponderosa pine *(Pinus ponderosa)*-bunchgrass range in central Arizona was examined. Cattle were removed from the range in 1961 and reintroduced in 1980. A 48-km survey route was driven through pastures containing cattle and through pastures without cattle to document the effects cattle had on native ungulates during the summers of 1981 and 1982. Location and number of elk, mule deer, and cattle observed along the route were recorded. Locations where animals were seen were used as sample sites to measure habitat variables: forest overstory, plant species composition, elevation, slope, exposure, and distance to water, fencing, meadow, cover, and draws. Distribution of elk and mule deer and habitats used by elk changed when cattle were introduced to the range. Significantly ($P<0.05$) fewer elk and mule deer were seen on pastures grazed by cattle than on pastures not grazed by cattle. Use of habitats by elk shifted from open mesic and silviculturally disturbed areas to more closed forest after cattle were introduced. Use of habitats by deer was not altered when cattle were introduced to the range.

Key Words: habitat selection, discrimination function, ponderosa pine-bunchgrass

Cattle (*Bos* spp.) may alter elk *(Cervus elaphus)* and mule deer *(Odocoileus hemionus)* use of rangelands (Julander and Jeffery 1964, Mackie 1970, Nelson 1982 and Urness 1982). Elk use may decrease in response to cattle grazing (Skovlin et al. 1968) or be unaffected (Long and Irwin 1982). Cattle grazing can even improve elk range (Andersen and Scherzinger 1975). Urness (1982) and Longhurst et al. (1982) argued that livestock grazing pressures have created much more of our western deer habitat and that livestock can be used as a deer management tool. More empirical evidence is needed on the response of elk and deer to grazing by cattle.

In 1979 the U.S. Forest Service established the Circle-Bar pasture in the Chevelon Wildlife Management Area, Apache-Sitgreaves National Forest, Arizona. This area had not been grazed by livestock since 1961 (Adams et al. 1979. Chevelon Canyon allotment analysis. U.S. Forest Serv., Apache-Sitgreaves Natl. Forest, Ariz., mimeo). The development of the Circle-Bar pasture provided a unique opportunity to describe elk and mule deer distributions and habitat use in response to cattle on a central Arizona summer range.

Study Area

The 135-km² study area was characterized by broad, flat plateaus cut by steep, north-draining canyons. Elevations ranged from 2,135–2,500 m. Mean minimum and maximum temperatures during July–August of 1981 and 1982 were 9° C and 26.5° C, respectively. Average annual precipitation in 1981 and 1982 was 46 and 64 cm from the lower to higher elevations, respectively, and similar to a 15-year average (1965–1980) throughout the area (Adams et al. 1979. Chevelon Canyon allotment analysis. U.S. Forest Serv., Apache-Sitgreaves Natl. Forest, Ariz., mimeo).

Ponderosa pine *(Pinus ponderosa)* was the dominant overstory species. Douglas-fir *(Pseudotsuga menziesii)*, limber pine *(Pinus flexilis)*, and white fir *(Abies concolor)* occurred in the canyons and higher elevations. The understory throughout the study area was dominated by Arizona fescue *(Festuca arizonica)*, muhly grass (*Muhlenbergia* spp.), June grass *(Koeleria cristata)*, and bottlebrush squirreltail *(Sitanion hystrix)*. Small open meadows dominated by bluegrass (*Poa* spp.) were scattered throughout the area. Fires and silvicultural disturbances created a patchwork of seral stages. The 1956 Dudley burn (70 ha) was a midsuccessional stand with 3 to 5-m-tall ponderosa pine regeneration and a bunchgrass-buckbrush *(Ceanothus fendleri)* understory during the study period and 1981 and 1982. The 1975 Cliff (20 ha) and 1978 Breed (10 ha) burns were in early successional bunchgrass associations.

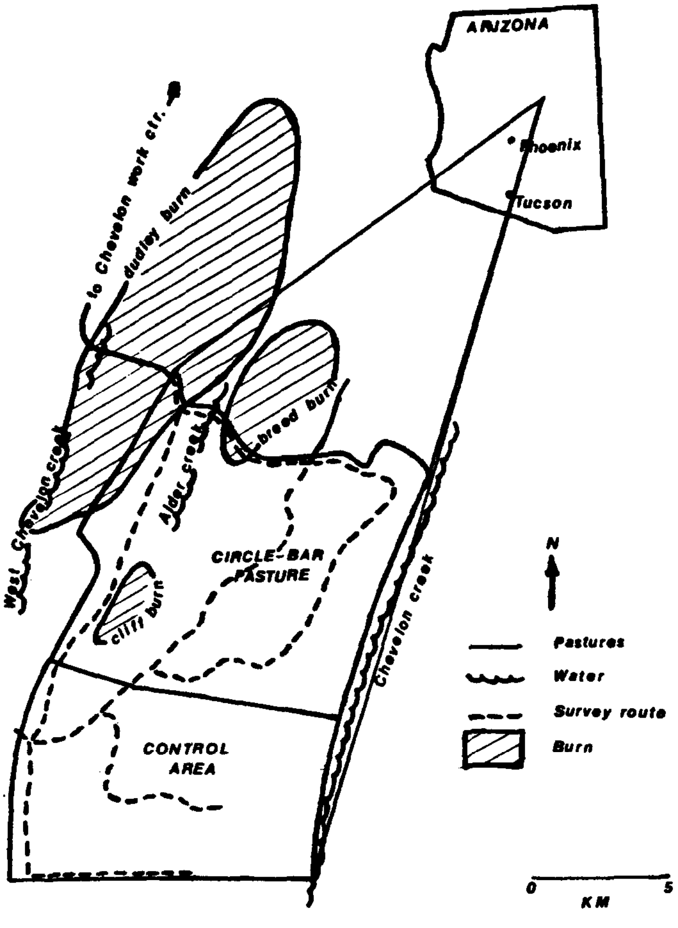

Fig. 1. *Location of the Circle-Bar and control pastures in the Apache-Sitgreaves National Forest, Arizona.*

The study area was divided into 2 pastures: the Control and Circle-Bar pastures (Fig. 1), which were not used by livestock from 1961–1979. In 1980, 400 cows grazed on Circle-Bar.

Materials and Methods

We conducted this study in July–August 1981, and from May–October 1982. Cattle were excluded from both pastures in 1981. In 1982, cattle were excluded from the Control pasture all year but 1,000 yearling steers grazed Circle-Bar pasture from 15 May–30 July. Stray cattle were still on this pasture until October

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1982. For our analysis only data from July and August in 1981 and 1982 are compared. Grazing treatments for this study were as follows: Control ungrazed 1981, Circle-Bar ungrazed 1981, Control ungrazed 1982, and Circle-Bar grazed 1982. Cattle use on the grazed treatment was 1,750 AUM's or approximately 2.96 ha/AUM.

A 48-km survey route (Fig. 1) (26 km in Circle-Bar and 22 km in the Control pasture) was driven 30 kph during the morning and evening hours (0500–0900 and 1600–2000, respectively), 20 times in 1981 and 14 times in 1982. Location and number of elk, mule deer, and cattle observed along the route were recorded. We tested (Mann-Whitney U test [Conover 1980]) for differences between the grazing treatments in numbers of animals seen per kilometer driven and for animal group sizes.

Locations where animals were seen were used as sample sites to measure habitat variables. At each site the elevation, slope, exposure, and distance to water, fencing, meadow, cover, and draws was noted using onsite measurement, aerial photographs, and topographic maps. Hiding cover was defined as vegetation or topography capable of hiding 90% of a standing animal from the view of an observer.

Forest overstory at each site was described with a spherical densiometer to estimate canopy coverage (Strickler 1959) and a 10-factor wedge prism to estimate basal area. A 25-m line-intercept transect (Strong 1966) established in a random direction from each site where animals were observed was used to estimate percentage of total frequency, density, and coverage of understory plant species. A dominant species for trees, shrubs, grasses, and forbs was determined by ocular estimation at each site. These estimates were used as dominant species descriptors for the site.

Nominal scale data were tested with G-factor analysis (Sokol and Rohlf 1969:735-738) using $\alpha = 0.10$. Ratio scale data were examined using discriminant analysis to descriptively explore habitat use by the ungulates (after Ferrar and Walker 1974 and Hudson 1976). Measures of plant species which occurred on less than 5% of the transects were excluded from the analyses. A step-wise (5-step limit) selection procedure was used in the discriminant analyses to determine important variables for differentiating ungulate sites. Variables were selected by the criteria of maximizing Mahalanobis distance. The original data were then reclassified using the derived discriminant function scores to evaluate the effectiveness of the discriminating variables. Analyses were conducted using the Statistical Package for the Social Sciences (Klecka 1975).

Results and Discussion

There was no difference in number of elk seen between years on the Control pasture, and elk numbers did not differ between the Control and Circle-Bar pastures in 1981. Significantly fewer ($P<0.05$) elk were seen, however, on the Circle-Bar pasture in 1982 than in 1981 (Table 1). Also, fewer elk were seen on the Circle-Bar pasture than the Control Pasture in 1982. Skovlin et al. (1968), Mackie (1970), and Knowles and Campbell (1982) also indicated that elk use descreased in pastures where cattle grazed.

Table 1. Median numbers of elk and mule deer seen per kilometer driven on the Control and Circle-Bar pastures during July and August of 1981 and 1982. Cattle grazing occurred only on the Circle-Bar pasture in 1982.

	1981		1982	
	Control	Circle-Bar	Control	Circle-Bar
N[a]	20	20	13	14
Elk	0.21[b]	0.13[b]	0.50[b]	0.01
Mule deer	0.02[bc]	0.07[bc]	0.02	0.00

[a]Number of survey routes driven
[b]Significantly different ($P<0.05$) from the Circle-Bar pasture in 1982
[c]Significantly different ($P<0.05$) between 1981 Circle-Bar and Control pastures.

Observations of elk on the Circle-Bar pasture decreased with the introduction of cattle in 1982 (X = 0.75 elk/km the week prior to 15 May compared with 0.12 elk/km the week after 15 May). Elk observations on the grazed pasture did not again exceed 0.12/km until after 7 September. Nelson and Burnell (1976) indicated a negative interaction with elk being displaced because they are subordinate to and socially intolerant of cattle. Elk seen on the Circle-Bar pasture during the cattle-grazing period, however, were frequently within 15 m of cattle, and interactions observed at salt blocks suggested species dominance was related primarily to number of conspecifics present. Ward et al. (1973), Knowles and Campbell (1982), and Long and Irwin (1982) also found elk and cattle to be socially compatible and observed them feeding in close proximity to each other.

Mule deer were more abundant on the Circle-Bar pasture than on the Control pasture when they were both ungrazed by cattle in 1981 (Table 1). In 1982, however, the number of mule deer on the Circle-Bar pasture decreased and was no longer significantly different from that seen on the Control pasture. McIntosh and

Table 2. Standardized canonical discriminant coefficients for functions discriminating elk and mule deer habitat use along survey routes in Control and Circle-Bar pastures during July and August, 1981 and 1982. Cattle grazing occurred only on the Circle-Bar pasture in 1982.

	1981		1982	
	Control	Circle-Bar	Control	Circle-Bar
Significance of function	<0.003	<0.001	<0.001	<0.002
Cases correctly classed (%)	90.48	93.55	100.00	100.00
Canonical correlation	0.82	0.87	0.95	0.92
Group centroids				
elk:	−0.6649	−1.5177	−1.5238	−2.0390
mule deer:	2.8256	1.8429	5.4856	2.3788
Variables[a]				
Percentage frequency of:				
Sitanion hystrix	0.75165	1.31612	5.15304	
Muhlenbergia spp.			2.11791	
Carex spp.	−0.52365		−3.60399	
Vicia americana	1.11802			−0.73015
Thermopsis pinetorum			0.53073	
Rumex spp.		−0.68652		
Conyza canadensis	−0.40165	−0.60612		
Percentage cover of:				
Ceanothus fendleri		0.91490		1.20261
Poa spp.		−0.49157		
Koeleria cristata				1.39994
Psedocymotperus montanus	1.00054		1.44371	−0.69433

[a]Values are reported only for significant variables ($P<0.01$)

Krausman (1982) also reported this decrease in mule deer occurrance on the Circle-Bar pasture when it was grazed by cattle.

Although fewer mule deer were seen, their distribution did not change dramatically in relation to cattle presence on the Circle-Bar pasture. Deer numbers decreased slowly but deer were consistently seen foraging and drinking with cattle. Hungerford (1970) and Ward et al.(1973) also found mule deer and cattle feeding in close proximity. Knowles (1975) reported that mule deer either moved from the area or used all parts of their home ranges more frequently when cattle were present.

We measured habitat variables on 114 sites where animals were observed during July and August: 29 and 25 elk sites in 1981 and 1982, respectively; 18 and 11 mule deer sites in 1981 and 1982, respectively; and 31 cattle sites in 1982. Elevation, slope, and exposure were major distinguishing components of habitat use in studies by Julander and Jeffery (1964) and Sivinski (1979), but discriminant analysis indicated they were not important for differentiating ungulate habitats on the relatively flat Apache-Sitgreaves National Forest. Selective cutting, pulp wood harvest, and commercial thinning had not created the large openings or dense regrowth common in other forest types or management schemes either. Exceptions were the burns in open (early) or dense (midsuccessional) stages and the open meadows. Of the nonvegetative habitat variables measured for each species, none differed significantly between pastures or years.

Dominant species descriptors for elk sites differed between pastures and years. Elk sites on the Circle-Bar pasture during 1982 were dominated by ponderosa pine, buckbrush, and muhly, whereas, sites on the Control pasture in 1982 and both pastures in 1981 were dominated by Gambel oak, aspen *(Populus tremuloides)*, and mesic grasses. Dominant species for mule deer sites were not significantly different between pastures or years.

Discriminant analyses of understory species of elk and mule deer sites for each pasture and year identified habitat gradients that separated elk sites (negative values) from mule deer sites (positive values) (Table 2). The understory species useful for discriminating elk from mule deer sites were representative of vegetative communities that occurred under different forest canopy or moisture classes. Discriminant function variables which discriminated elk and mule deer sites on all 3 ungrazed pastures represent a similar gradient from open mesic meadow to closed forest with shrub understory.

Observations of elk (open mesic or disturbed sites) were characterized by sedge and bluegrass or early seral weeds (sheep sorrel [*Rumex* spp.] and horsewood [*Conyza canadensis*]). Reynolds (1966) indicated elk used openings more than forested areas and Clary and Larson (1971) found elk use consistently showed an inverse relationship to ponderosa pine basal area. DelGuidice and Rodiek (1982) emphasized the importance of mesic forest openings as summer foraging sites for elk. Observations of mule deer (closed forest with shrub understory) were characterized by shade tolerant grasses and forbs. Reynolds (1966) indicated use by mule deer under ponderosa pine was nearly equal to use of openings, and deer preferred small openings to large ones. Skovlin et al. (1968) reported mule deer used forest more than openings, while Carpenter and Wallmo (1981) emphasized that mule deer use of openings was dependent upon the proximity of cover.

Elk habitats on the Circle-Bar pasture in 1982 differed from those described for the ungrazed pastures. Variables identifying elk sites were shade tolerant forbs (vetch [*Vicia americana*] and anice plants [*Pseudocymopterus montanus*]) that are commonly found under dense ponderosa pine sites. Mule deer sites were still identified by buckbrush and June grass representative of forested areas and shrub understory.

The addition of cattle as a third group enabled us to use 2 discriminant functions in the analysis of the Circle-Bar pasture in 1982 (Table 3). Vetch characterized elk sites which were discriminated from the mule deer sites associated with buckbrush, and cattle sites with bluegrass, muhly, and horseweed.

Table 3. Standardized canonical discriminant coefficients for discriminating elk, mule deer, and cattle habitat use along survey routes in the Circle-Bar pasture during July and August of 1982.

	Discriminant function	
	1	2
Significance of function	<0.002	<0.002
Variance acounted for (%)	61.15	38.85
Canonical correlation	0.42	0.28
Group centroids		
elk:	0.95781	0.902721
mule deer:	1.19381	-1.668953
cattle:	-1.07083	0.132430
Variables[a]		
Percentage frequency of:		
Muhlenbergia spp.	-1.27124	0.81276
Vicia americana	1.11319	1.02026
Percentage cover of:		
Ceanothus fendleri	0.69862	-1.23921
Conyza canadensis	-0.92840	-0.73240
Poa spp.	-1.03976	-0.70033

[a] Values are reported only for significant values ($P \leq 0.01$)

Cattle were much more numerous than elk or mule deer on the Circle-Bar pasture and were observed in most of the available habitats. Cattle use in the meadows, draws, and more open forested sites appeared to displace elk from these habitats, characterized by low basal areas of trees and high canopy coverage of bluegrass or muhly and seral weeds. The presence of cattle did not appear to affect patterns of habitat use by mule deer. Deer remained in forested sites that were dominated by buckbrush.

Skovlin et al. (1968) indicated that elk tolerated light stocking levels of cattle but were inhibited by moderate to heavy stocking. In our study area, a moderate level of cattle stocking affected elk and mule deer distribution and was associated with changes in habitat use by elk. The nutritional consequences of such behavioral responses by elk and mule deer are unknown but are necessary to evaluate the degree and role of competition in interactions with livestock.

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Crude Terpenoid Influence on Mule Deer Preference for Sagebrush

TIMOTHY L. PERSONIUS, CARL L. WAMBOLT, JEFFREY R. STEPHENS, AND RICK G. KELSEY

Abstract

Samples of current year's growth of leaves and stems were collected in February 1983 from basin big sagebrush (*Artemisia tridentata* Nutt. *tridentata*), Wyoming big sagebrush (*A.t. wyomingensis* Beetle and Young), mountain big sagebrush (*A.t. vaseyana* [Rydb.] Beetle), and black sagebrush (*A. nova* Nels.) on a mule deer (*Odocoileus hemionus hemionus*) winter range near Gardiner, Montana. Samples were from both lightly and heavily used plants (form classes) within each taxon. Crude terpenoids were separated into 3 groups: headspace vapors, volatile, and nonvolatile crude terpenoids. Compounds in each group are thought to stimulate the sensory organs of mule deer. Individual compounds were identified and quantified for comparison with preference ranks among taxa and between utilization form classes. Seven compounds were selected by discriminant analysis as indicators among the 4 taxa, with methacrolein+ethanol, *p*-cymene, and the sesquiterpene lactones the most probable preference determinants. Seven other compounds were found useful for separating plants within taxa into form classes. Chemical differences between the 2 form classes, however, were less distinguishable than were those among the 4 taxa.

Key Words: *Artemisia tridentata, Artemisia nova, Odocoileus hemionus hemionus,* forage selection, terpenoids

Knowledge of the motivation behind forage selection by ungulates is vital to predicting and manipulating range forage/herbivore interactions. Given the opportunity to select, mule deer (*Odocoileus hemionus hemionus*) will preferentially browse certain species of sagebrush over others (Hanks et al. 1971, Scholl et al. 1977, Sheehy and Winward 1981, Welch et al. 1981, 1983). Even within a taxon there is differential utilization (Welch et al. 1981, 1983, Behan and Welch 1985). Factors influencing the interactions among plants and herbivores are numerous and frequently complex, but there is substantial evidence that the secondary metabolic products synthesized by a plant can function as mediating agents (Rosenthal and Janzen 1979). Sagebrush species synthesize and store relatively large quantities of terpenoids on their epidermal surface in glandular trichomes (Kelsey and Shafizadeh 1980, Kelsey et al. 1982, Kelsey 1986). Many of the compounds that have been identified in sagebrush species are also known to exhibit a variety of biological activities (Tatken and Lewis 1983, Kelsey et al. 1985). Previous studies relating sagebrush chemistry to mule deer preference have focused on the monoterpene composition and concentrations (Scholl et al. 1977, Welch et al. 1983, Behan and Welch 1985). No significant relationships were found between the monoterpenes and utilization. The monoterpenes represent only a portion of the compounds of sagebrush foliage, however, and other constituents could be involved. This study was undertaken to identify epidermal compounds associated with differences in sagebrush preference by mule deer.

Materials and Methods

Site Description

The study site was a mule deer winter range near Gardiner, Montana, immediately north of Yellowstone National Park. Elevation of the rolling bench at the base of the Absaroka Mountains is 1,950 m. Precipitation averaged about 400 mm during the period 1941 to 1970 (USDA 1981), with about half of this moisture as snow. The area was dominated by basin big sagebrush (*Artemisia tridentata* Nutt. *tridentata*), Wyoming big sagebrush (*A.t. wyomingensis* Beetle and Young), mountain big sagebrush (*A.t. vaseyana* [Rydb.] Beetle), and black sagebrush (*A. nova* Nels). Sampling was restricted to plants from a "natural cafeteria", an area of 30 × 60 m, where the 4 taxa occurred intermixed in nearly equal biomasses. This natural cafeteria was a mosaic of distinct microsites controlled by slope angles, soil properties, and exposure, that in turn resulted in a plant community dominated by a combination of sagebrush taxa not ordinarily found together. Because the natural cafeteria was small, contained nearly equal quantities of each taxon, and had no physical limitations to deer access, utilization within the area should have reflected mule deer preference. Bluebunch wheatgrass (*Agropyron spicatum* [Pursh.] Scribn.) and Idaho fescue (*Festuca idahoensis* Elmer) were important subdominants. Mule deer were consistently observed on the cafeteria browsing sagebrush from late November into April.

Sagebrush Utilization

To document differential utilization on the 4 sagebrush taxa, 1,136 available vegetative leaders were tagged on 124 plants evenly distributed throughout the cafeteria. Tags were installed prior to the 1982–1983 period of winter deer use. Tagged leaders were re-examined after winter browsing to determine the percentage of total leaders browsed. It was not practical to measure length of leader removed as most plants exhibited a browsing history in the form of very irregular and twisted leader growth that could not be measured and pre- and post-browsing accurately.

Sample Collection

In early February, 10 plants were subjectively selected and sampled in each taxon, 5 representing the light-use form class (open, growthy, relatively unbranched crowns), and 5 representing the heavy-use form class (dense, intricately branched crowns, club-like appearance). Form classes can be viewed as indicators of historic preference for individual sagebrush plants (Cook and Stoddart 1960, McNeal 1984, Kelsey 1986). It is not implied that individual plants from different taxa that exhibit the same form class have historically received the same amount of actual use. Instead, it is likely the response is partially under genetic control and will therefore vary among sagebrush taxa. A sample consisted of 15 of current year's leaves and stems which closely approximated the actual tissue consumed by mule deer. Plant samples were sealed in individual air-tight plastic bags, double bagged, placed on dry ice, and transported to a freezer for storage at -20° C until chemically analyzed.

Crude Terpenoid Isolation

Seven to 8 grams of frozen leaf and stem tissue from each sample were brought to room temperature in a sealed plastic bag. The plant material was transferred to a beaker, covered with chloroform (24 ml/g) and stirred gently for 5 min. The extract was filtered through sharkskin paper into a preweighed flask for concentration and weighing as described by Kelsey (1986). Extracted tissue, including nonglandular trichomes that had dislodged from the

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leaves and collected in the filter paper, was dried at 100° C overnight, cooled to room temperature in a desiccator, and reweighed. Crude terpenoid concentrations were calculated as percentage of extracted tissue dry weight.

The most volatile compounds are lost from the extract during concentration, whereas a portion of the less volatile monoterpenes, remain in the final residue. The latter can be separated from the nonvolatile lactones and waxes by steam distillation (Kelsey et al. 1982). After redissolving the concentrated extract in chloroform, steam was bubbled through the solution for 10 minutes. Volatile compounds were captured in a cold water (10° C) condenser and collected in a flask with chloroform and water. Nonvolatile components remained in the distillation flask with condensed water. The resulting volatile and nonvolatile crude terpenoid fractions were concentrated, and weighed, like the initial extract above (Kelsey 1986).

Volatile Crude Terpenoid Analysis

Composition of the volatile crude terpenoid fraction was analyzed by gas-liquid chromatography (GLC). A 0.1 μl sample of extract was injected onto a 4-m × 3-mm stainless steel column packed with 10% Carbowax (TPA) on 80/100 to 100/120-mesh Gas Chrom Q, in a chromatograph with a flame ionization detector and nitrogen carrier gas. Column temperature was programmed for 50–200° C, with a 10°/min rise and final temperature hold (5 min for headspace samples, and 15 min for volatile oils). Chromatograms were printed by a Hewlett Packard 3380 A integrator recorder. Integrater conversion factors for quantifying individual oil components were determined by injecting known quantities of methacrolein as a reference for highly volatile compounds and camphor as a reference for the less volatile monoterpenes. Concentrations were standardized for differences in initial sample size and expressed as percentage of extracted tissue dry weight.

Compounds were identified by comparison of retention times to known references, and by GLC/mass spectrometry. For this analysis, approximately 0.05–0.1 μl of the volatile crude terpenoid oil (neat) was injected onto the GLC column (4-m × 3-mm stainless steel, 10% Carbowax on 80/100 CWHP, He carrier gas) with a programmed temperature of 50–200° C at 10°/min. Mass spectra of the oil components were identified by comparison with known reference samples and published spectra (Stenhagen et al. 1974, Epstein et al. 1976).

Sesquiterpene Lactone Analysis

Analysis of the nonvolatile crude terpenoid fraction centered on isolation, quantification, and identification of sesquiterpene lactones, 1 of the major classes of compounds in this fraction that could influence preference. Other constituents present but not studied included cuticular waxes, some flavonoids, and possibly other unknown compounds.

The concentrated nonvolatile crude terpenoid fractions from each plant sample were dissolved in chloroform, or a mixture of chloroform and ethanol, and diluted to 25.0 ml with the same solvent. A measured volume (between 2 and 6 μl) was injected onto a 1.8-m × 3-mm stainless steel column packed with 3% OV-17 on 100–120 mesh Gas Chrom Q. Oven temperature was set isothermally at 205° C. The sesquiterpene lactone matricarin (5 mg/ml) was used as a reference. Microliter quantities of the diluted extracts were analyzed by thin-layer chromatography (TLC) (Kelsey et al. 1976). TLC and GLC analyses indicated a similar chemical composition for plants of the same species. Therefore, measured aliquots were taken from each extract and combined by taxa to isolate and identify specific sesquiterpene lactones. Compounds were separated and purified by preparative TLC, and then compared with reference samples using TLC, GLC, and infrared (IR) spectroscopy.

Total sesquiterpene lactone concentration in each of the 40 extracts was measured by comparing the integrated area of the lactone moiety absorbence band with that of a reference compound at known concentrations, using a Nicolet model MX-1 Fourier Transform Infrared Spectrometer with liquid sample cells. Deacetylmatricarin, deacetoxymatricarin, and cumambrin B were used as references for basin big sagebrush, mountain big sagebrush, and black sagebrush, respectively. No reference was needed for the extracts of Wyoming big sagebrush because they had no measurable lactone absorbence; there were either no sesquiterpene lacetones present, or only very low concentrations, below the detection limits of the technique.

Headspace Analysis

Sagebrush produces some very volatile compounds that are lost during the rigorous distillation, evaporation, and drying procedures used in the crude terpenoid isolation process. These compounds are likely to escape from the plant into the atmosphere. Mule deer may be able to detect them by smell without having to sample the foliage. These very volatile components were analyzed as headspace vapors using a modification of the procedure reported by Kelsey et al. (1983). Approximately 1 g of frozen whole tissue was sealed in a 60-ml vial fitted with an air-tight rubber septum. The sample was then adjusted to room temperature and placed in an oven at 60° C for 15 min. An air-tight syringe, with a valve for sealing the contents was used to extract 1.0 ml of vapor from the vial. After closing the valve, the vapor was compressed to 0.1 ml (as recommended by the syringe manufacturers), and injected into a column in a GLC as described for the volatile crude terpenoid fraction. The tissue sample was then removed from the vial, dried overnight at 100° C, cooled to room temperature in a disiccator, and weighed. Integrator counts for individual compounds were converted to micrograms after injecting known quantities of camphor and methacrolein as references. All concentrations were standardized to compensate for differences in tissue dry weights. Compounds were identified as described for the volatile crude terpenoids.

Statistical Analysis

The data set consisted of 40 plant samples grouped into 4 taxa of 10 samples each, and 2 form classes of 5 samples within each taxon, with a quantified list of individual compounds for each sample. Stepwise multiple discriminant analysis (Nie et al. 1975) was used to identify those compounds which, when considered together and on a sample-by-sample basis, could be used to separate taxa or form-class groups on a chemical basis. Only individual compounds were entered in the analysis.

A one-way analysis of variance (AOV) was used for comparison of means among taxa. Tukey's Honestly Significant Difference (HSD) multiple range test was used to separate significantly different means ($\alpha = 0.05$). A simple t-test ($\alpha = 0.10$) was used to compare group means between the 2 form classes within a taxon.

Results and Discussion

Utilization and Preference

Mountain big sagebrush was by far the most preferred taxon, Wyoming and basin big sagebrush were intermediate, and black sagebrush was the least preferred (Table 1). This order of ranking is the same as for mule deer in Oregon (Sheehy and Winward 1981), and very similar to mule deer preference observed on a uniform garden in Utah (Welch et al. 1981, 1983).

Chemical Constituents

Many glandular terpenoids exhibit a variety of biological activities (Tatken and Lewis 1983, Kelsey et al. 1985), and their compartmentalization in trichomes allows a relatively high concentration to be maintained where they are most accessible to the sensory organs of herbivores. The complex mixture of compounds can help maximize protection against a variety of herbivorous organisms and their different sensory mechanisms. Mule deer probably depend on both olfactory and gustatory senses for monitoring forage. In our study the chemical analysis was designed to isolate groups of compounds whose individual constituents are likely to be detected by a certain sensory organ. The headspace analysis was used to identify the highly volatile compounds in sagebrush most

Table 1. Percentage of leaders browsed during winter (1982–1983) on 4 sagebrush taxa in the natural cafeteria.

Taxon	Number of leaders tagged	Percentage used
mountain big sagebrush	316	52
Wyoming big sagebrush	328	24
basin big sagebrush	254	19
black sagebrush	238	8

easily detected by smell before eating or immediately after the first bite. The volatile compounds, isolated by steam distillation, were not completely evaporated during the extraction procedure, suggesting they might be detected by both the gustatory and the olfactory senses of mule deer when released by mastication. The nonvolatile crude terpenoid fraction was left with the sesquiterpene lactones, waxes, and other unidentified compounds that are detectable mainly by taste (Burnett et al. 1977).

Eighteen componds were quantified in the headspace vapors, of which 15 were identified (Table 2). Methacrolein and ethanol could not be consistently separated and were considered as one. In the samples that were separable, however, methacrolein constituted 80–90% of the total. Twenty compounds were quantified in the volatile crude terpenoid fractions, and 9 were identified (Table 2). Only 6 of the 32 compounds (Table 2) were common to both of these fractions. In general, the means of nearly every headspace and volatile crude terpenoid compound differed significantly ($P<0.05$) between at least 2 taxa (Table 2). In contrast, the means of only 11 of these individual compounds differed ($P<0.1$) between the 2 form classes of any taxon (Table 3).

Table 2. Mean concentrations of individual compounds in the headspace vapor and volatile crude terpenoid fractions from the 4 taxa of sagebrush. Compounds listed in order of increasing retention time.

Chemical	ATV[1]	ATW	ATT	AN
		Headspace Vapor[2]		
methyl butene	6.64^{b}[3]	8.21^{b}	6.14^{b}	1.44^{a}
acetone	0.84^{a}	5.67^{b}	5.67^{b}	0.00^{a}
methacrolein+ethanol	0.45^{a}	15.96^{b}	30.06^{c}	0.43^{a}
UHN-1†	0.00^{a}	0.00^{a}	0.00^{a}	0.36^{b}
UHV-1†	0.38^{a}	0.00^{a}	0.00^{a}	0.00^{a}
UHV-2†	0.15^{b}	0.00^{a}	0.00^{a}	0.00^{a}
santolina triene	0.00^{a}	3.63^{bc}	1.89^{b}	7.45^{c}
α-pinene	4.07^{b}	0.00^{a}	0.00^{a}	3.12^{b}
camphene	5.92^{b}	2.25^{a}	1.90^{a}	2.09^{a}
β-pinene	1.15^{b}	0.14^{a}	0.17^{a}	0.22^{a}
artemiseole	0.16^{a}	1.96^{b}	1.32^{b}	0.00^{a}
α-phellandrene	0.00^{a}	0.00^{a}	0.00^{a}	0.20^{b}
1,8-cineole	5.33^{c}	0.70^{b}	0.79^{b}	0.00^{a}
ρ-cymene	0.24^{a}	0.13^{a}	0.13^{a}	0.70^{b}
artemisia ketone	0.32^{a}	0.00^{a}	0.00^{a}	0.00^{a}
thujone	0.84^{a}	0.00^{a}	0.00^{a}	0.00^{a}
camphor	1.49^{b}	0.54^{ab}	0.25^{a}	0.15^{a}
		Volatile Crude Terpenoids[4]		
methacrolein	0.00^{a}	0.12^{b}	0.24^{c}	0.00^{a}
artemiseole	0.02^{a}	0.53^{b}	0.41^{b}	0.00^{a}
1,8-cineole	1.10^{b}	0.30^{a}	0.32^{a}	0.04^{a}
ρ-cymene	0.06^{a}	0.04^{a}	0.06^{a}	0.24^{b}
santolina epoxide	0.00^{a}	0.18^{b}	0.43^{c}	0.00^{a}
UETW-1†	0.00^{a}	0.22^{b}	0.34^{c}	0.00^{a}
methyl santolinate	0.00^{a}	0.84^{b}	1.07^{b}	0.00^{a}
thujone	0.73^{a}	0.00^{a}	0.00^{a}	0.00^{a}
UEV-1†	0.14^{b}	0.00^{a}	0.00^{a}	0.00^{a}
camphor	1.82^{ab}	2.11^{b}	1.70^{ab}	0.96^{a}
UEV-2†	0.32^{b}	0.00^{a}	0.00^{a}	0.00^{a}
UETW-2†	0.00^{a}	0.56^{b}	0.37^{b}	0.00^{a}
UEV-3†	0.18^{b}	0.00^{a}	0.00^{a}	0.00^{a}
UETW-3†	0.00^{a}	0.40^{b}	0.31^{b}	0.00^{a}
borneol	0.23^{b}	0.00^{a}	0.00^{a}	0.19^{b}
UEV-4†	0.50^{b}	0.00^{a}	0.00^{a}	0.00^{a}
UETW-4†	0.00^{a}	0.38^{b}	0.46^{b}	0.00^{a}
UEV-5†	0.17^{a}	0.00^{a}	0.00^{a}	0.00^{a}
UETW-5†	0.00^{a}	0.22^{b}	0.31^{b}	0.00^{a}
UEV-6†	0.06^{a}	0.00^{a}	0.00^{a}	0.00^{a}

[1] ATV: *A.t. vaseyana;* ATW: *A. t. wyomingensis;* ATT: *A.t. tridentata;* AN: *A. nova.*
[2] μg/gram of dry tissue
[3] Individual compounds followed by the same letter were not significantly different ($P<0.05$) among taxa using Tukey's HSD multiple range test.
[4] Percentage extracted-tissue dry weight.
†Unidentified compounds.

Table 3. Mean concentrations of individual compounds in the headspace vapor and volatile crude terpenoid fractions that differed significantly ($P<0.1$) between the 2 form classes of each taxon.

			Form Class[4]		
Taxon[1]	Compound[2]	Source[3]	Light-use	Heavy-use	P-value
ATV	acetone	HD	1.67	0.00	.01
	UHV-2†	HD	0.31	0.00	.01
	camphene	HD	2.62	9.22	.04
	camphor	HD	0.40	2.58	.05
	UEV-1†	ES	0.27	0.01	.05
	camphor	ES	0.84	2.79	.02
	UEV-2†	ES	0.43	0.20	.08
	UEV-4†	ES	0.98	0.01	.04
	UEV-5†	ES	0.33	0.00	.06
	UEV-6†	ES	0.12	0.00	.07
ATW	camphene	HD	3.20	1.30	.07
	β-pinene	HD	0.20	0.09	.05
	UETW-2†	ES	0.35	0.77	.09
ATT	acetone	HD	4.57	6.76	.07
	camphene	HD	1.39	2.41	.06
AN	-- none significant --				

[1] ATV: *A.t. vaseyana;* ATW: *A.t. wyomingensis;* ATT: *A.t. tridentata;* AN: *A. nova.*
[2] *Borneol,* ρ-cymene, and UEV-3 concentrations were not significantly different between form classes, but were selected by stepwise multiple discriminant analysis as helpful for distinguishing form classes.
[3] HD = headspace; ES = volatile crude terpenoids.
[4] HD: g/gram dry tissue; ES: percentage extracted-tissue dry weight. † Unidentified compounds.

The total lactone concentration was measured in the nonvolatile crude terpenoid fractions (Table 4). Black sagebrush had the highest average concentration, containing 2 major components, cumambrin A and B, and several unknowns. Wyoming big sagebrush had the lowest lactone concentration, and no individual compounds were identified. Basin big sagebrush and mountain big sagebrush both had significant quantities of lactones but differed in the chemical complexity of their respective fractions. Matricarin, deacetylmatricarin, and deacetoxymatricarin were the dominant sesquiterpene lactones in basin big sagebrush. All 3 have been previously isolated or detected in this taxa (Irwin 1971, Kelsey and Shafizadeh 1979). Mountain big sagebrush lactones were a mixture of many unidentifiable compounds, without a major constituent.

Chemical analysis of individual plants is important because of plant-to-plant variability (Kelsey et al. 1983, and observations in this study). Occasionally, a compound is present in high concentra-

Table 4. Mean concentrations[1] of chemical groups in the 4 sagebrush taxa.

Fraction	ATV[2]	ATW	ATT	AN
total crude terpenoids	19.58^{a}[3]	22.36^{ab}	24.59^{b}	21.94^{ab}
volatile crude terpenoid fraction	5.71^{b}	$6.81.^{bc}$	7.61^{c}	1.82^{a}
nonvolatile crude terpenoid fraction	13.87^{a}	15.55^{ab}	16.98^{b}	20.12^{c}
headspace vapors	28.84^{ab}	39.94^{bc}	49.25^{c}	16.44^{a}
sesquiterpene lactones	2.58^{bc}	0.10^{a}	2.37^{b}	3.05^{c}

[1] Headspace: μg/gram dry tissue. All others are percentage extracted-tissue dry weight.
[2] ATV: *A.t. vaseyana;* ATW: *A.t. wyomingensis;* ATT: *A.t. tridentata;* AN: *A. nova.*
[3] Means followed by the sample letter were not significantly different ($P<0.05$) among taxa using Tukey's HSD multiple range test.

tions in 1 sample but nearly absent in another. Compounds that occur less frequently, but in high concentrations could be overrated as preference indicators if the tissue samples were composited prior to analysis.

Discriminant Analysis

All samples were correctly placed into their respective taxa using 7 compounds identified by discriminate analysis: UETW-4, lactones, 1,8-cineole (volatile), methacrolein (headspace), methyl butene, ρ-cymene (volatile), and santolina triene (Tables 2 and 4). Mean concentrations (Tables 2 and 4) of all these compounds differed significantly between at least 2 taxa.

All 10 samples were assigned the correct form class for mountain big sagebrush, using 5 compounds: acetone, borneol, ρ-cymene, UEV-3, and UEV-2 (Table 3). Eight of 10, and 9 of 10 samples were assigned the correct form class for Wyoming and basin big sagebrush respectively, using only 1 compound each: β-pinene (Wyoming big sagebrush) and camphene (basin big sagebrush) (Table 3). Black sagebrush samples could not be assigned to form classes using chemical criteria.

Chemical Determinants of Preference

Compounds identified by discriminant analysis are indicators of relative preference among and within the 4 sagebrush taxa. For them to actually influence or determine preference, however, they must elicit a positive or negative herbivore feeding response. They must occur in sensibly different quantities among forage choices, and should relate in some way to the observed preferences for different forages.

Of the 7 compounds identified for distinguishing among taxa, methacrolein+ethanol, ρ-cymene, and the lactones are the most probable preference determinants. Methacrolein+ethanol was the largest single constituents of the headspace fraction and correlated negatively and consistently with preference for the 3 big sagebrush taxa (Tables 1 and 2). Both constituents are known irritants, particularly the methacrolein (Tatken and Lewis 1983). Black sagebrush, the least preferred taxon, had the lowest amounts of methacrolein+ethanol, but significantly (4 times) greater quantities of ρ-cymene (another irritant) than any other taxon.

The sesquiterpene lactones may be preference determinants even though their chemical compositions were different for each taxa. Sesquiterpene lactones are bitter tasting and negatively influence white-tailed deer *(Odocoileus virginianus)* and eastern cottontail rabbit *(Sylvilagus floridanus)* preference for *Veronia* species (Burnett et al. 1977). Consequently, those in sagebrush must be suspected. The matricarins and cumambrins could be deterrents since they occurred in high concentrations in the 2 least preferred taxa. The cumambrins caused contact dermatitis on some human patients, while the matricarins did not (Mitchell and Dupuis 1971). Mountain big sagebrush had lactone concentrations similar to basin big sagebrush, but without any major components. This may weaken deterrent effectiveness. Although Wyoming big sagebrush was lactone-free, this does not rule out the possibility of other preference determining compounds. *Artemisia pygmaea* and *A. longiloba* have no lactones, but they do contain sesquiterpene alcohols (Irwin and Geissman 1973, Shafizadeh and Bhadane 1973, Kelsey and Shafizadeh 1979). If sesquiterpene lactones influence mule deer preference, than our data indicate both total concentration and composition must be considered. The potential involvement of UETW-4, 1,8-cineole, methyl butene, and santolina triene in determining preference is less clear, as they either had a positive correlation to preference, no known biological activity, or remain unidentified.

Discriminant analysis may overlook, or ignore, some compounds if their significance among groups is limited to only a few cases. For instance, α-phellandrene (Table 2), an irritant (Tatken and Lewis 1983), only occurs in black sagebrush (the least preferred taxon) and may be influencing preference for that species, but it was not identified as such in the discriminant function. This appears to be the only obvious omission from the discriminant list.

Compounds identified as preference indicators among taxa came from all 3 major groups of crude terpenoids (Table 4). Excluding the sesquiterpene lactones, the concentrations of all chemical groups were negatively correlated with the mule deer preference for big sagebrush subspecies (Tables 1 and 4). Mountain big sagebrush, the most preferred, had the lowest concentrations and basin big sagebrush, the least preferred, had the highest concentrations. The nonvolatile crude terpenoid fraction, detectable by taste only, was the only group of compounds whose quantity had a negative correlation with preference across all 4 taxa. Although the headspace chemicals might be detected by smell without sampling the plant, mastication of the tissue would release all constituents, providing the opportunity for simultaneous stimulation of both sense organs and allowing for synergistic interactions among all epidermal compounds.

Compounds selected to distinguish form classes were nearly all different from those that distinguished the 4 taxa. Camphor occurred in significantly higher concentrations in the heavy-use form class of mountain big sagebrush (Table 3), suggesting that it might be an attractant. It was not selected in the discriminant analysis, however, probably because of the large variation between samples and overlapping ranges of concentrations between form classes. Selecting compounds that are likely determinants of preference for the form classes was not possible.

Determining the importance of sagebrush epidermal chemicals as mediators of herbivory requires further investigation. There are numerous variables. Little information is available on chemical potencies and threshold levels for individual compounds. Carefully controlled feeding trials are necessary to clearly evaluate the effects of specific sagebrush chemicals on the feeding behavior of mule deer and other herbivores.

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Succession of Pinyon-Juniper Communities after Mechanical Disturbance in Southcentral New Mexico

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Abstract

Principal component analysis (PCA) was used to interpret secondary succession of pinyon-juniper stands after cabling or bulldozing. Soil types were used to separate 93 sample units into 3 groupings. A PCA was run on 2 of the groupings. Groups of sample units were defined as community types for each ordination. Stepwise discriminant analysis using environmental variables was used to assist in delineation of community types. Species that contributed the most to the first 3 principal components were compared among community types for each ordination using an analysis of variance and a comparison of the least squares means. Grasses on the deeper soils usually increased after cabling, but after 25 years they had declined to near pretreatment levels. Wavyleaf oak (*Quercus undulata* Torr.) increased after cabling, and on the older cablings it had reached higher cover values than on the other community types. Pinyon and juniper response appeared to be dependent on density and size of trees before cabling. If the stand was near climax before cabling, pinyons rapidly became dominant on the site. If it was seral, there would be more junipers, but their slow growth and the time they require for maturation required more time before they dominated the site. The successional pattern following cabling on relatively deep soils is similar to what was found after fire, but it occurs faster. Cover of grasses and shrubs increased more on rock-free soils compared to sites treated similarly but with rock. The ordinations indicated that succession in pinyon-juniper communities is directional and leads towards climax with a decrease in variability among sites.

Key Words: vegetation changes, Ordination, principal component analysis, botanical composition

Distribution of the pinyon-juniper complex in the Southwest is extensive, covering about 77 million hectares (Pieper 1977). This vegetation type constitutes a valuable resource supplying food and cover for many wildlife species, food and fuel for man, forage for livestock, and watershed, water storage, etc. Since settlement of the American West, distribution and density of trees in the pinyon-juniper complex has increased (West et al. 1975). A decline in forb and grass production has accompanied these increases (Arnold and Schroeder 1955; Johnsen 1962). Livetock grazing, a lower incidence of wildfire, and climatic change are often suggested as reasons for this expansion (Springfield 1976).

Several studies have dealt with community response following disturbance. Dwyer and Pieper (1967) studied the effects of a wildlife on a juniper stand in south central New Mexico. They found the fire mortality of junipers varied according to size, with the smaller trees more susceptible. The forb component was not affected by the fire, and grasses recovered within 2 years. Clary and Jameson (1981) examined understory response after girdling pinyons and junipers and treatment of live oak (*Quercus turbinella* Greene) with herbicide on several soil types in Arizona. They reported increased production for all grasses, most forbs, and about half the shrub species. However, there were measurable differences in vegetation response on different soils.

Hessing et al. (1982) investigated early succession of a pinyon-juniper woodland in a northern Arizona powerline corridor. The study area had been bulldozed, used as an access road and reseeded. The seeding was considered a failure and seedbed preparation added significantly to site disturbance. They reported that only 1 woody species, wolfberry (*Lycium pallidum* Miers) had become established on the site after 5 years. This species is often associated with disturbed areas. Forbs were more abundant of the cleared sites than under the adjacent tree canopy; however, most of these forbs were invaders or annuals. Grasses were significantly less abundant on the cleared site than on neighboring undisturbed site. The authors suggested recolonization of disturbed sites would be a slow process requiring many years. Another powerline study in northern New Mexico by Ludwig et al. (1977) showed similar results in areas which had been bulldozed. Annual forbs dominated these bladed sites for about 4 years, after which these authors propose that grasses would supplant the forbs. They found no difference in density of the trees between the treated site and the control because of reproduction. However, the treated site had significantly less tree cover than the control. Grass cover was significantly greater on the treated site than on the control. Tree

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Table 1. Multiple comparisons of the species percent cover for the groups from the rocky soil. Least squares means were used for the comparison.

	*Lycurus phleoides**	*Muhlenbergia dubia**	*Gutierrezia sarothrae**	*Juniperus deppeana***	*Pinus edulis**
Group	Mean	Mean	Mean	Mean	Mean
uncabled	0.13 B[1]	2.00 AB	0.20 B	4.63 A	11.91 A
1954 cable	0.36 AB	1.05 B	0.57 B	1.87 B	7.21 B
1975 cable	0.60 A	1.07 B	1.40 A	0.25 B	3.10 BC
1975 cable	0.13 B	3.48 A	0.41 B	1.76 B	2.48 C

[1] Means followed by different letters are significantly different (*$P<.05$, **$P<.15$).

establishment occurred within 5 years following treatment, but recovery of the tree canopy to pretreatment values was estimated to require at least 100 years.

A few studies have examined more than the first few years following disturbance. Burkhardt and Tisdale (1969, 1976) investigated secondary succession following fire in western juniper (*Juniperus occidentalis* Hook.) communities in southwestern Idaho. Barney and Frischknecht (1974) did a similar study for stands of Utah juniper-single leaf pinyon (*J. osteosperma* (Torr.) Little -*Pinus monophylla* Torr. & Frem.) in Utah. Arnold et al. (1964) examined succession in Utah pinyon-juniper (*P. edulis* Engelm.) communities in Arizona following fire, grazing, and tree control treatments. Finally, Tausch and Tueller (1977) evaluated succession following chaining of Utah juniper-single leaf pinyon communities in eastern Nevada.

Successional patterns common to both fire and chaining may be summarized from these studies and 3 examples are shown in Figure 1. Generally, following catastrophic disturbance an annual community forms. It is replaced by a perennial grass community, which is replaced by perennial grasses, forbs and half shrubs. This mixed community gradually becomes dominated by shrubs and junipers, and succeeds to climax. The pattern is similar for fire and cabling disturbance. However, rate of change is much faster after cabling than after fire because more plants survive cabling.

These generalized models may not apply to every area and pinyon-juniper community. Clary and Jameson (1981) reported that vegetation on limestone-derived soils responds differently to tree removal than vegetation on basalt-derived soils.

There are many studies of secondary succession in pinyon-juniper communities. Most reported changes the first few years following disturbance. Several have dealt with more than the first few years after disturbance; most of these long-term studies were concerned with succession following fire. Succession studies beyond the first few years after cabling are rare, and none have dealt with succession following cabling in pinyon-one-seed juniper communities. The objective of this study was to determine secondary successional patterns following disturbance by cabling and bulldozing.

Methods

Field Methods

The study area was restricted to the Sacramento Mountains of south central New Mexico. Study sites were selected through interviews with Forest Service personnel and by ground reconnaissance. Cabling and bulldozing were the major treatments sampled. All the known pinyon-juniper treatments were examined before site selection. Selection criteria were soil uniformity, aspect, slope, and elevation to assure environmental similarity among sites.

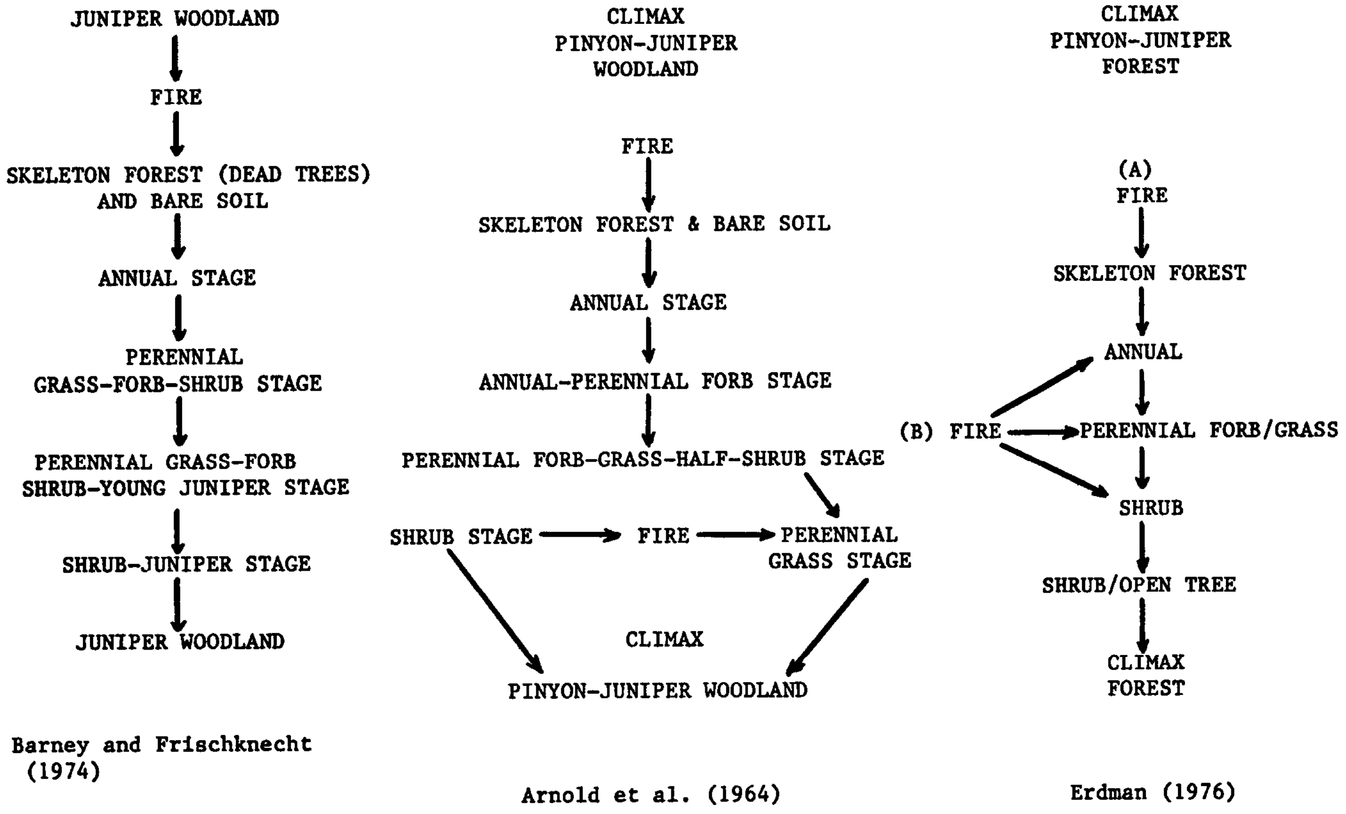

Fig. 1. *General successional models of pinyon-juniper communities.*

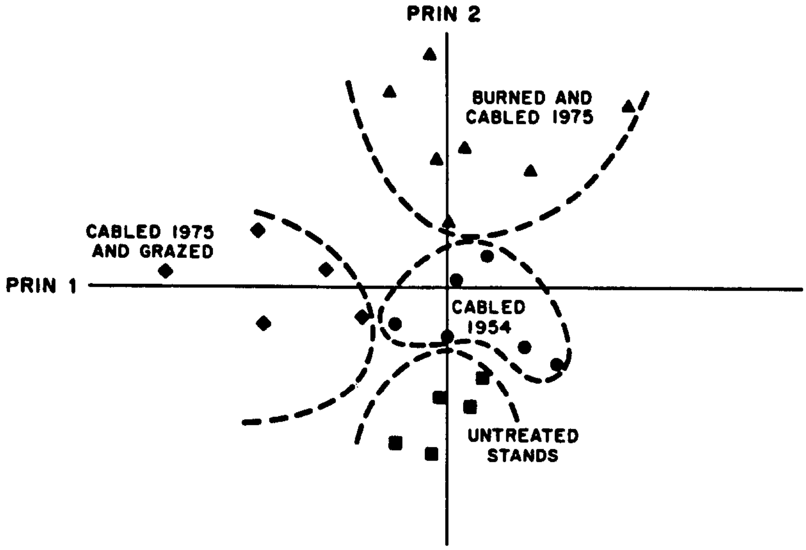

Fig. 2. *Ordination based on the first 2 principal components of the sample units from the* Pinus edulis - Juniperus deppeana / Muhlenbergia dubia *habitat type. Sample units of the uncabled community type are represented by ■, sample units which represent the community type which had been cabled in 1954 are represented by ●, stands from the two community types which had been cabled in 1975 are represented by ▲ for the one with evidence of fire, and by ◆ for the one with the greater grazing. Axis 1 represents successional direction and axis 2, the variation due to different histories of disturbance.*

Sample sites were sampled during the summer of 1982 and 1983. A 15×25 m macroplot was located subjectively on each area, with the long axis parallel to the slope to minimize slope-related variations between sample units. Within the macroplot, two 25 m transects were established randomly using a 25 m tape with the restriction that they were at least 2 m apart. Twenty 2×5 dm microplots were placed at 1 m intervals along each transect, and canopy cover was estimated for each herbaceous species found rooted within the microplot. Forty microplots were sampled per macroplot. Systematic placement of the microplots helped eliminate subjective bias during sampling. Cover classes were used because of the difficulty in precise estimation of percent cover. Cover classes of Daubenmire (1959) were modified to estimate percent cover: Class 1 (0–5%); Class 2 (>5–25%); Class 3 (>25–50%); Class 4 (>50–75%); Class 5 (>75–95%), Class 6 (>95–100%). Cover values for the microplots were summarized for each species. Points located at the 4 corners of the 2×5 dm frame were used to estimate percent bare ground, litter, cryptogam, rock and vegetation. There were 80 points per transect, or 160 points per macroplot. Canopy cover of woody species was estimated using line intercept along the tape which defined each belt transect. Measurements were made to the nearest centimeter.

Analytical Methods

Ordination has been defined a the arrangement of stands in a multi-dimensional space such that similar stands are close and dissimilar stands far apart (Bray and Curtis 1957; Gauch 1982). One object of ordination is to aid in the interpretation of community relationships to environment. Studies of secondary succession reflect the type, degree and time since disturbance as axes of the ordination. The use of time since disturbance has been used as an axis by several authors (Huschle and Hironaka 1980; Peet and Christiansen 1980).

Principal component analysis (PCA) was conducted on cover estimates of the species to ordinate sampled sites (Legendre and Legendre 1983). PCA fits a line through the swarm of sample units, which accounts for most of the variation among sample units. Sample units were separated into 3 groups on the basis of soils. A PCA was run on 2 of the soil-derived groups; the third grouping consisted of 8 sample units and was not ordinated. Clusters of sample units were defined as community types, which were evaluated within each of the 2 ordinations, using a stepwise discriminant analysis procedure based on soil depth to a restrictive layer, aspect, elevation, slope, percent rockiness, bare ground, litter cover, type of disturbance, and severity of disturbance (Pielou 1977; Neff and Marcus, 1980). Species which added most to the first 3 principal components were examined for differences among community types for each PCA using an Analysis of Variance (Ott 1977). Least square means were used to compare groups if there were significant differences.

Table 2. Mulitple comparisons of the species percent cover for the groups from the third ordination, the *Pinus edulis-Juniperus monosperma/Muhlenbergia pauciflora* habitat type. Least square means were used for the comparisons.

	*Bouteloua curtipendula**	*Bouteloua gracilis**	*Muhlenbergia repens****	*Eriogonum hierac-ifolium****	*Gutierrezia sarothrae****	*Quercus undulata***	*Juniperus mono-sperma****	*Pinus edulis**
Group	Mean	Mean	Mean	Mean	Mean	Mean	Mean	Mean
1975 cable on deep soil	0.378 B[1]	26.188 A	1.408 AB	0.046 C	0.856 AB	2.060 C	2.711 B	0.640 C
1975 cable on normal soil	2.98 A	19.956 B	2.417 A	0.314 AB	1.078 A	2.020 C	2.640 B	4.296 B
1950 cablings with low amounts of pinyon	2.686 A	10.206 C	0.028 B	0.418 A	0.528 B	11.135 B	7.253 A	7.853 B
1950 cabling with high amounts of pinyon	2.194 A	5.238 D	0.889 B	0.290 AB	0.456 BC	16.944 A	1.922 B	24.036A
Uncabled	1.060 B	9.309 CD	0.071 B	0.131 BC	0.211 C	8.400 B	10.058 A	19.371 A

[1] Means followed by different letters are significantly different (*$P < .001$, **$P < .005$, ***$P < .05$).

Results and Discussion

Vegetational Analyses

Sample units were separated initially on the basis of soil and PCA was run on 2 of the groupings. The group with the fewest sample units occurred in the *Pinus edulis-Juniperus monosperma/-Bouteloua gracilis* habitat type (Kennedy 1983), which was found on a clayey, mixed, mesic Haplustalf soil (U.S. Forest Service ND). Because there were only 8 sample units in this habitat type, they were not ordinated. Four sample units were old growth stands near climax. The other sample units were from stands where the trees had been removed by bulldozing (push) in 1965.

Species were analyzed to determine if their cover values differed between 2 treatments. Six species were significantly different (P<.01). Blue grama (*Bouteloua gracilis* (H.B.K.) Lag.) in the old growth stands had an average cover estimate of 1.9%, while blue grama in the push stands had an average cover value of 32.9%. Removal of the trees resulted in a significant increase in blue grama. Denttooth (*Chenopodium incisum* Poir) had an average cover estimate value of 1.0% in the old growth stands, but was rarely sampled in the pushed sample units. Pinyon ricegrass (*Piptochaetium fimbriatum* (H.B.K.) Hitch.), like denttooth, was found only under tree canopies; thus, it did not occur on the pushed sites. Snakeweed (*Gutierrezia sarothrae* (Pursh) Britt & Rusby) did not occur in the old growth stands, but had an average cover estimate of 1.6% on the pushed sites. As expected, pinyon had greater canopy cover values in old growth stands than in the pushed stands, 28.3% and 0.01%, respectively. Few juvenile pinyons had become established since bulldozing. One-seed juniper (*Juniperus monosperma* (Engelm.) Sarg.) response was similar to that of pinyon, in that old growth sites had greater canopy cover than the pushed stands, 28.3 and 0.7%, respectively.

Blue grama was negatively correlated with denttooth (r = –.6042), one-seed juniper (r = –.7396), pinyon (r = –.7421) and pinyon ricegrass (r = –.8318). Both pinyon and juniper have a negative effect on blue grama by shading, litter accumulation, and interception of rain by their canopies (Johnsen 1962, Jameson 1967). One-seed juniper also appears to have an allelopathic effect on blue grama, and it competes for soil water (Jameson 1965, 1966). Both denttooth and pinyon ricegrass were positively correlated with both pinyon and juniper, r = –.49 and r = –.77, respectively for pinyon, and r = –.58 and r = –.74, respectively for juniper. Denttooth and pinyon ricegrass are positively correlated (r = –.68). These species appear to do well under the canopies of pinyon and one-seed junipers, while blue grama does not. This explains the negative correlation between these species and blue grama. Pinyon and one-seed junipers are strongly correlated in these stands (r = –.91).

A PCA was run on sample units from the dry phase of the *Pinus edulis-Juniperus deppeana/Muhlenbergia dubia* habitat type (Kennedy 1983) (Fig. 2). This habitat type occurs on a Tortugas, gravelly loam, rock outcrop complex, which was a loamy-skeletal, carbonatic, mesic, Lithic Haplustoll (Bailey et al. 1982). Four point clusters were produced by the ordination.

Sample units comprising 2 clusters are from areas which were two-way cabled in 1975. Each cabling forms its own cluster. Community structure before the cabling was probably different for the 2 areas, resulting in different community-types after cabling. Both

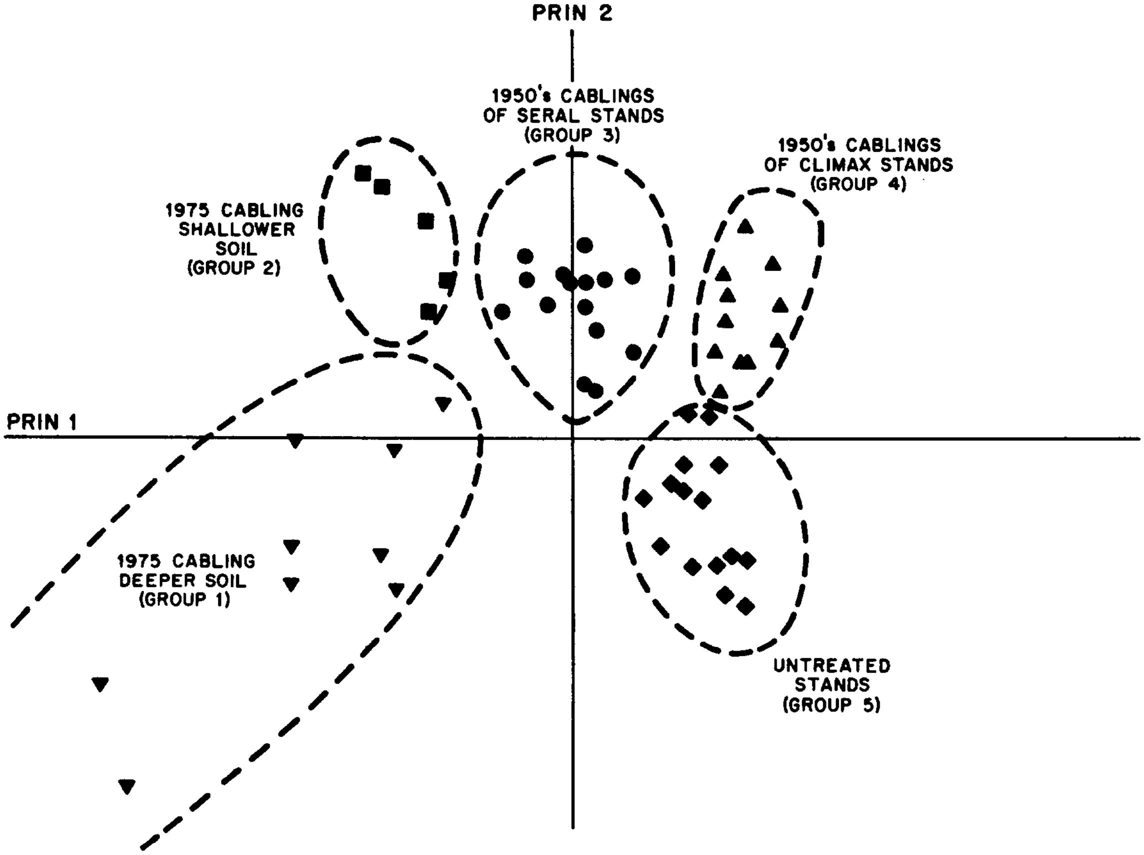

Fig. 3. *Ordination based on the first 2 principal componens of the sample units from the* Pinus edulis - Juniperus monosperma / Muhlenbergia pauciflora *habitat type. Sample units on deeper soils which were cabled in 1975 (group 1) are represented by* ▼. *The other-sample units cabled in 1975 (group 2) are represented by* ■. *Sample units which were not near climax prior to cabling in the 1950's (group 3) are represented by* ●. *sample units which were near climax prior to cabling in the 1950's (group 4) are represented by* ▲. *Untreated sample units (group 5) are repesented by* ◆ . *The ordination displays the similarity between groups 4 and 5. Also, it shows the direction of succession, from the upper left of the figure to the lower right. Successional direction is from left to right on principal component 1 and from high to low on principal component 2 with the expection of group 1 which is separated because of its deeper soil.*

areas showed evidence of firewood cutting around the turn of the century, but one area also had evidence of fire before the woodcutting. The other received more grazing pressure than the former. Another cluster was comprised from sample units which had been two-way cabled in 1954. The final cluster was largely comprised from sample units which had received minimal disturbance from firewood cutting or historic fire.

SDA selected only the degree of disturbance the sample unit received to discriminate between clusters, and its classification had a 42.3% agreement with the PCA clusters. One cluster had minimal disturbance, and the other 3 clusters had been severely disturbed. Thus, the SDA placed the 3 clusters which had received severe disturbance into 1 cluster. Sample units were selected to minimize differences attributable to environmental variables such as elevation, aspect, and slope, which is why the SDA was only able to select 1 variable.

Species which contributed the most to the first 3 principal components were analyzed for differences among clusters (Table 1). There were no differences in the cover estimates among clusters for blue grama, which is in contrast to the data from the sample units of the first PCA. The difference in response may be the result of differences in soils. On rocky soils, blue grama is prevented from spreading because it spreads by tillering, and rock interferes with formation of adventitious roots (Hyder et al. 1971).

Pine muhly (*Muhlenbergia dubia* Fourn.) has significantly greater coverage estimates on the burned 1975 cabling than most of the other clusters. The burn may have stimulated the pine muhly.

Wolftail (*Lycurus phleoides* H.B.K.) has the opposite response to grazing pressure; it appears to increase with disturbance. Its greatest coverage occurs on the other 1975 cabling. This cabling receives more grazing pressure than the first which, combined with the actual cabling, probably acted to release the wolftail.

Snakeweed, also a disturbance species, had greater coverage on the burned 1975 cabling than in the other clusters. Differences in these 3 species probably account for separation of the 2 clusters comprising the 1975 cablings. However, none of these species show strong correlation with each other.

There is little response by grass species following cabling on these rocky soils. Pine muhly and wolftail show slight increases on the 1975 cablings. They probably increased because of tree removal, but differences between the 2 groups appear to be caused by events before cabling.

Both one-seed juniper and alligator-juniper (*Juniperus deppeana* Steud.) had significantly greater cover estimates on uncabled sample units. There was no difference in canopy cover among the treated stands. Cover values of both juniper species on the cablings were contributed by plants which either survived the cabling or became established from seeds which were on the areas before cabling, or were brought in by animals from adjacent stands. One-seed juniper seeds are known to remain viable for 20 years (Johnsen 1959). With removal of the mature junipers, the only seed sources are those that were present under tree canopies before cabling and those brought in by animals (Salomonson 1978). Junipers seldom become established in the first few years following cabling. After establishment they grow slowly and can reach seed bearing age at 10 years, but the optimum is between 50–200 years (Tueller and Clark 1975). The combination of slow growth in junipers and limited seedling establishment helps explain why there is little difference in juniper cover between the 1954 cabling and the 1975 cabling.

Pinyon also has the greatest canopy coverage for the cluster of uncabled sample units, but the cluster of sample units cabled in 1954 exhibited greater canopy coverage than clusters comprised of sample units cabled in 1975. Compared to juniper, pinyon is faster growing and produces seed at an early age. Also, pinyon readily replaces itself in old growth stands more readily than junipers do. Thus, at the time of the cablings, there were probably a large number of young pinyons and only a few junipers. Cabling is not effective in removing young trees (Aro 1971; Springfield 1976). The faster growing rate, combined with greater densities of reproductive trees surviving cabling accounts for the greater canopy cover on the cluster comprised of sample units from 1954 cablings.

There were no difference in the coverage of either wavyleaf oak (*Quercus undulata* (Torr.)) or skunkbush (*Rhus trilobata* Nutt.) among any of the clusters. Canopy cover of wavyleaf oak averaged about 9.5% for the clusters. Firewood cutting before cabling may have released the oak, which would account for the amount of oak found in the uncabled sample units. Another possible explanation for the amount of oak on uncabled sites is that junipers in rocky broken soils do not compete as much with oak as on less broken soils. Juniper lateral root systems may be restricted by rocky soil, reducing the competition between oaks and junipers. Wavyleaf oak spreads by adventitious roots, and shallow soil and rock outcroppings may control the amount of oak as it does for blue grama (Tucker 1961). Skunkbush does not spread vegetatively, but it may have been released by firewood cutting, and was showing maximum expression before cabling.

The PCA (Fig. 2) illustrates the successional direction. The uncabled group is low on principal component 2, and near the center of the other principal component. The group cabled in 1975, and which received the grazing pressure, is found on the left side of principal component 1. The other group which was cabled in 1975, but had been burned, is placed high on principal component 2. As succession occurs, variation among sample units decreases and there is movement towards the untreated stands. The initial process is fairly rapid; the 1954 grouping is about half way between the uncabled group and the 1975 cabling groups, although there is only 21 years between the 1954 cabling group and the 1975 cabling groups.

Sample units of the second PCA were in the *PCA edulis-Juniperus monosperma/Muhlenbergia pauciflora* habitat type described by Kennedy (1983). This habitat type was found on the Tortugas soil series, where it was cobbly rather than gravelly and there were fewer rock outcroppings. Five clusters were delineated from the PCA (Fig. 3). Two clusters were comprised of sample units cabled in 1975, 2 were comprised of stands cabled in 1954 through 1959, and the last cluster was made up from uncabled stands.

New Mexican muhly (*Muhlenbergia pauciflora* Buckl.) is present on all the sample units, but often to a lesser degree than that reported by Kennedy. Grazing pressure may have caused a decrease in its cover, because an ungrazed plant was rarely observed during sampling.

SDA selected aspect, soil depth and percent bare ground as the basis for classification. Its classification had an 81% agreement with the clusters delineated from the PCA. One of the clusters comprised of sample units from a 1975 cabling is delineated by deeper soils and the SDA has a 100% agreement with the grouping. The other 1975 cluster is separated mainly on the basis of aspect. Stands in ths cluster faced east, while most of the other sample units faced N to NE. The SDA has a 100% agreement with this grouping (group 2). The 3 remaining groups appear to be separated on the basis of percent bare ground. As expected, the group comprised of uncabled stands has the least amount of bare ground, averaging 13.9%. The other group, comprised of stands cabled in 1954 through 1959, had about the same amount of bare ground as the groups comprised of stands cabled in 1975 averaging 33.8% bare ground. Those sample units of the 1951 and 59 cablings with high pinyon densities had an average of 18.0% bare ground, approaching that found of the uncabled group. SDA classification has a 58.8% agreement with this group. The SDA places 2 sample units of this group in the groups with low pinyon densities and 3 with the uncabled groups. Group 4 appears to grade into group 5, and is less clearly defined as would be expected since the main difference is related to pinyon density.

There were significant differences among the groups for 8 species: blue grama, sideoats grama (*Bouteloua curtipendula* Michx Torr.) creeping muhly (*Muhlenbergia repens* (Presl. Hitch.), wild buckwheat (*Eriogonum hieracifolium* Benth.), snakeweed, one-seed juniper, wavyleaf oak and pinyon (Table 2). Sample units on the 1975 cabled area with deep soil had the highest cover estimates for blue grama. Deeper soils and tree removal appear to account for the high cover values. Sample units with "normal" soils cabled in 1975 have less blue grama than the first, but more than those on sites cabled in the 1950's or the control. Soil depth accounts for the differences between the first 2 groups, and the more recent removal of the pinyon and one-seed junipers is the reason for the differences between the remaining groups. There is no difference in the amount of blue grama found on uncabled sample units and those cabled in the 1950's. However, those with low densities of pinyon had significantly more blue grama than those with high densities of pinyon. The relatively large cover of both pinyon and oak in this group may have caused a reduction in blue grama cover.

Sideoats grama cover on sample units with deep soil cabled in 1975 showed an opposite response to that of blue grama. This group and the uncabled sample units had the least amount of sideoats grama. The other groups had the most. Sideoats grama appears to increase with tree removal. Creeping muhly exhibited its highest coverage on those sample units cabled in 1975, reflecting the more recent disturbance of these groups; there was no difference in its coverage among the remaining groups. Wild buckwheat has the least coverage on the deeper soils of those sample groups with little difference in its coverage among the other groups. Snakeweed has the highest coverage on the 1975 cablings and the least on uncabled stands, which may reflect the response to the more recent cabling disturbance. Wavyleaf oak is the only shrub species which reflected differences among the groups. Wavyleaf oak had the greatest cover on sites cabled in the 1950's with high pinyon densities. Sample units cabled in 1975 had the least amount of oak. Most of the sample units in the uncabled areas have had some firewood cutting on them, which may account for relatively high cover of wavyleaf oak. Firewood cutting opened up the stand, which may have released the oak. Sample units on the older cablings have large values for wavyleaf oak cover. This oak species is known to increase after fire, and cabling has an effect similar to that of fire in removal of overstory. Low coverages of oak on those sample units cabled in 1975 were unexpected. There are 2 possible explanations for the low coverages. The areas might have had small amounts of oak present before cabling due to competition from the trees; or cabling directly or indirectly destroyed some of the oak.

One-seed juniper had the greatest canopy coverage in the uncabled sample units and those cabled in the 1950's with the low pinyon cover. There were no differences in pinyon cover among the other groups. The difference in the amount of juniper and pinyon between groups cabled in the 1950's with low and high amounts of pinyon may be a reflection of the age of the stand before cabling. Pinyon typically has the greater cover in old undisturbed stands and there are many small pinyons under the canopy. In contrast, young one-seed junipers are not common under the canopy of near climax stands (Salomonson 1978). Those sample units cabled in the 1950's with high cover of pinyon were probably near climax at the time of cabling, while the groups with low pinyon cover were probably from much younger stands at the time of cabling.

Successional Patterns

A general scenario of secondary succession following cabling on this soil is similar to what was reported by Tausch and Tueller (1977). The cabling removes most of the trees and some of the wavyleaf oak. Initially, grasses respond to the overstory removal, but somewhere between 8 and 28 years, grass cover declines. Snakeweed has a response similar to that of grasses, an initial increase following cabling followed by a deceases to the same level as the uncabled site after 28 years. Wavyleaf oak is at its lowest levels soon after cabling. It slowly increases for the first few years. Somewhere between 8 and 28 years, oak canopy coverages exceed or equal those of uncabled areas. Sometime, around 28 years, pinyons and junipers start suppressing the oak and become dominant. If the stand was near climax at the time of cabling, pinyon rapidly becomes dominant on the stand. However, if the stand was not nearly climax, there will be less pinyon and more junipers on the stand. This depends entirely on the number of young trees of each species found in the stand at the time of cabling.

Examining the second ordination (Fig. 3) groups 1 and 2 are placed to the left on Figure 3. The deeper soil of group 1 causes this group to be placed lower on the second axis than group 2. Both these groups display a large amount of variability among the sample units which comprise them. Group 3 is located in the upper center of the figure. Group 4 is to the upper right, and group 5 is in the right center of the figure. Distance between cabled and uncabled stands decreases as succession moves forward to the climax. Group 5, the uncabled sample units, still exhibits a large amount of distance among stands, but this is due to firewood cutting and fire disturbances these stands have received. This decrease in distance satisfies the cone model of Huschle and Hironaka (1981) where succession is directional, and there is less distance among sample units nearing climax than among early successional units. Group 4 is more similar to the uncabled groups. This is probably due to the character of the community before cabling. These sample units probably had many young pinyons under the canopy and cabling released these trees through the rapid succession towards climax.

Succession in this habitat type also appears to fit the general successional models of Arnold et al. (1964), Barney and Frischknecht (1974) and Erdman (1970) (Fig. 1). The rate of succession is faster than these authors found after fire, and these results are more similar to those Clary and Jameson (1981) found for succession following chaining in Arizona. Succession in the *Pinus edulis-Juniperus deppeana/Muhlenbergia dubia* h.t. does not appear to follow the model of Arnold et al. (1964) or that of Barney and Frischknecht (1974). The rocky soil limits the increase in grass cover following cabling and the shrub stage does not occur. The shrubs do not appear to spread beyond what is found in the uncabled stands. This may be due to the way wavyleaf oak spreads. This species does not appear to reproduce often from seed and, if it did, it is a poor disperser. Rather, this species spreads by adventitious suckers on its roots, and rocky soil may restrict the spread.

Conclusions

Succession after cabling pinyon-one-seed juniper communities may or may not follow the general successional models of Arnold et al. (1964), Barney and Frischknecht (1974) and Erdman (1970), depending on the soil they are found on. Rocky, shallow soils do not exhibit the grass or grass shrub stages after cabling. There is a small response by a few grass species after cabling, but if all the grasses are included, response is minimal. There proved to be no difference in shrub cover on 1975 cabling, 1954 cablings, and uncabled stands, which indicates shrubs failed to respond to the tree removal. Wavyleaf oak is the dominant shrub on these sites, and it spreads primarily by adventitious shoots from its roots. Rocky, broken soil may restrict the spread of the oak, which could account for the lack of response after cabling. Both alligator and one-seed juniper have the same coverage on both the 1954 and 1975 cablings. These species are slow growing and need time for maturation. Slow growth and low establishment of the junipers accounts for the lack of differences among the cablings. Young pinyons are common under the canopies of old growth stands, and their small size allows many of them to survive cabling. Pinyons have fast growth rates when compared to junipers, and also mature faster. Because of their faster growth rates and availability of a seed source, the 1954 cabling had a greater coverage of pinyon than the 1975 cablings.

Cablings on less rocky soils follow the generalized successional models of Arnold et al. (1964) and Barney and Frischknecht (1974). Coverages of the grass species and snakeweed increase after cabling. However, the increases have disappeared after 25 to 2 years. Wavyleaf oak appears to decline initially after cabling, but it gradually increases until it reaches maximum coverages 25 to 28 years after cabling. Pinyons and one-seed junipers start to become dominant 28 years after cabling. Which species becomes dominant depends on the structure of the stand before cabling. If the stand was near climax, pinyons became dominant after cabling. If the stand was at a lower seral stage, one-seed juniper became dominant.

Succession on both of these soils support the cone model of Huschle and Hironaka (1980) for secondary succession. Succession on both areas appears to directional, and variability within community types appears to decrease with succession. Community types represented by stands which had been cabled in 1975 had the greatest variability, while community types which were represented by uncabled stands had the least variability. Firewood cutting probably caused most of the variability found within these community types.

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Book Reviews

A Review of Wildlife Management. By James M. Peek. 1986. Prentice-Hall, Inc., Englewood Cliffs, NJ 07632. 486 p. $31.95.

The published literature on wildlife management has expanded greatly since Aldo Leopold wrote *Game Management* in 1933. This information is spread out among many books, journals, bulletins, and reports printed during the past 50 years. Peek attempts to review the more important highlights of this literature and condense them into a single volume. Major subject headings include food habits, habitat relationships, fire and wildlife, competition, predation, population exploitation, and waterfowl management. Additional chapters explore characteristics of conservationists, laws and treaties in wildlife management, snow and wildlife, pesticides and herbicides, and wildlife management in parks and wilderness areas. Over 1,000 literature citations are included in this review.

Peek defines wildlife management as "...the art of making the land produce wildlife." Although "science" is not incorporated as part of this definition, Peek stresses topical ecological concepts such as competition, optimal foraging, predation, and niche theory as important underlying foundations for understanding the abundance, distribution, and interactions of animals. Chapters are well organized, with a synthesizing summary following each one. The biology and management of deer, elk, and moose in North America is emphasized, along with most species of game birds. There is an admitted orientation toward species and management systems in the Northwest and upper Midwest. The impact of forestry and range management programs on wildlife receives more emphasis than the impact of urbanization and agriculture. Omissions include furbearer biology and management, wildlife damage prevention and control (except for deer, deer mouse, and waterfowl depredations to crops and forests), and endangered species management (except for whooping cranes and trumpeter swans).

A major annoyance in this book is the inconsistent use of both common and scientific names, and English and metric units. For example, in a discussion of tree and shrub productivity in response to prescribed burning, Table 6.5 lists the scientific names of plants and productivity values in units of lb/acre, while Table 6.6 lists common names of plants and productivity values in units of g/m^2! This lack of consistency makes rapid comparisons difficult.

Peek emphasizes realistic approaches to management, as is illustrated in the following three quotations. "Very frequently, wildlife management is conducted in a highly emotional setting where cool heads are few and far between" (p. 4). "It is imperative that we work with land managers and ranchers to arrive at accommodations that will benefit wildlife even if the accommodations are not immediately optimal. Thus, a knowledge of range management and grazing systems, plus a willingness to work with others, are attributes of the complete wildlife manager" (p. 185). "While efforts to retain old-growth stands are commendable in the short term, efforts to identify the components of the old-growth forest that are needed by each species and to actively recreate and manage for them is the challenge for the future" (p. 92-93). However, Peek is confusing when he states that "...competition plays an important, perhaps dominant, role in the dynamic process of habitat selection..." (p. 84), and later admits that "...the existing evidence for competition is largely circumstantial" (p. 177). The importance of competition in structuring communities is currently a controversial topic.

This attractive book contains excellent figures and tables, and is relatively free of errors. As a review book, it should prove valuable as a text for both undergraduate and graduate students, and as a reference book for wildlife professionals. Peek does not intend that this book replace current literature in wildlife management. I agree, and see the value in this book as a foundation upon which more current, and shifting, attitudes and management practices can be examined and evaluated. Range managers and foresters with an interest in wildlife management will find it especially useful.—*Robert H. Schmidt,* Natural Resources Specialist, University of California Cooperative Extension, Hopland Field Station, Hopland, California.

Management of Migratory Shore and Upland Game Birds in North America. Edited by Glen C. Sanderson. 1977. The International Association of Fish and Wildlife Agencies, Washington, D.C. 20036. 358 p. Price unknown.

This book is a direct result of the creation of a program in 1967 which addressed a variety of migratory bird problems which had received too little recognition in prior years. The program was organized by a "National Program Planning Committee" developed by the International Association of Fish and Wildlife Agencies. Accelerated research was stimulated in the 1950's by state, federal, and public interest groups, which resulted in the earmarking of special funding in 1967 to gather needed information for the management of these migratory species. This book reports results obtained.

Contents of what is actually a management oriented publication include information pertaining to Sandhill Cranes, Rails and Gallinules, American Coots, American Woodcock, Common Snipe, Band-tailed Pegeon, White-winged and Mourning Doves and a chapter relating generally to other shorebirds. Information presented includes descriptions of the species, life histories, a historical view, distribution and density, census procedures and population trends, harvest and hunting pressure, potential harvest, needs of the species, public management and research and recommendations based on identified problems. The text of each chapter is enhanced through tables, diagrams (distribution), photographs and drawings.

Almost any wildlife habitat manager, range manager, or biologist concerned with management of this migratory species will find this book useful. A large amount of information can be gained by perusing it, and many management-oriented ideas pertaining to each of the species may be found within its pages.—*Danny O. Stroud,* Yoder, Wyoming.

Soil Erosion and Crop Productivity. Edited by R.F. Follett and B.A. Stewart. 1985. American Society of Agronomy, Inc., Crop Science Society of America, Inc., and Soil Science Society of America, Inc., 677 S. Segoe Road, Madison, WI 53711. 533 p. $36.

Anyone with more than a casual interest in soil erosion can profit from this book. It is loaded with information. The book contains 28 chapters, contributions from 89 people knowledgeable about different aspects of agriculture, crop production, and soil erosion. One of the main strengths of the book is the broad range of disciplines and viewpoints represented. The book originated with a symposium by the same name held in Denver, Colo., in March, 1983. An excellent job was done of selecting and organizing the different subject matter areas. Despite the great complexity and diversity of subjects addressed, it has an unmistakable continuity of purpose and thought. I will try to give a flavor of the contents.

The first 8 chapters set the stage: a call for action, a world-wide perspective, an historical perspective, soil appraisal, erosion assessment, socioeconomic evaluation of soil-loss tolerance (T values), and a farmer's perspective on soil erosion. Chapter 3 by Miller et al. highlights this section and disproves the adage that scientific writing has to be dull, e.g.,

> "Human desires, motive, and emotions, including greed and drive for self-preservation, are as crucial to the cause of soil erosion as rainfall, erosivity, and soil erodibility."

Chapters 8-13 delve into the technical aspects of soil erosion. There are chapters on characterizing the mechanics of erosion, setting criteria for T values, and determining experimentally the effects of soil erosion on productivity. Chapter 13 by Meyer et al. should be useful to scientists and others working on erosion assessment. These authors provide lists of research needs, "minimal" parameters and measurements needed, and researchers and projects working to quantify effects of erosion on productivity.

The next six chapters (14-19) provide regional perspectives about the effects of erosion. From these chapters, one begins to appreciate the importance of soil organic matter as a nutrient reservoir and mediator of soil water relationships and other factors that make soils arable. Cheap fertilizers "mask" the loss of nutrients, but circumventing the effects of dense, clayey, or acidic subsoils is not so easy. In Chapter 18, Papendick et al. argue that erosion exacts a "double penalty", reducing not only current productivity but also future increases in productivity that might be forthcoming from technology. Renard et al. in Chapter 19 say, "Experimental data to illustrate how soil erosion might affect the productivity of the soil pedon are essentially nonexistent for rangeland areas of the Southwest." They could have said rangelands, period. They do point out, however, that models can be used to evaluate such erosional effects.

Preventing and ameliorating soil erosion are the subjects of Chapters 20-25. Excepting Chapter 23, which is devoted to structural control of erosion (terraces for example), the authors of these chapters emphasize again and again the importance of conserving crop residues and soil organic matter. As discussed by Allmaras et al. in Chapter 21, various kinds of conservation tillage systems, such as no-till, will be the technology of choice. They state, "...new tillage technology and a better understanding of the new field ecology ... will bring about a major technological change in agriculture."

The last three chapters deal with policy issues, and are well worth reading, particularly about the conflicts in national policy goals relating to soil conservation, balance of payments, farm income, food prices, crop surpluses, and others.

Between Calamity and Complacency, one of the subtitles in Chapter 2, in a phrase captures the essence of this book, and indeed the problem of soil erosion. We know we have a serious problem, but the evidence is fragmentary, yields of most crops continue to rise, we already have huge crop surpluses, and erosion is an insidious problem of greatest complexity.—*Albert R. Grable,* Agricultural Research Service, Fort Collins, Colorado.

Beef Cattle Production: An Integrated Approach. By Verl M. Thomas. 1986. Lea and Febiger, 600 Washington Square, Philadelphia, PA 19106-4198. 270 p. $29.75.

Beef Cattle Production: An Integrated Approach will serve as a very useful textbook or reference for college students or livestock producers. The book covers all aspects of beef cattle production from breeding through reproduction, nutrition and herd health as well as other management practices. Thomas handles management practices in much more detail than many of the other beef cattle production texts that are presently available. This is especially true in describing calving and calving difficulty in the cow as well as discussing methods of pulling calves. There are other instances where this text goes into more detail about actual production practices than many of the upper level textbooks currently available. Beef Cattle Production: An Integrated Approach will be expecially useful for junior colleges and universities that contain some hands-on management practices in laboratories to accompany lecture material in beef cattle production.

A definite strength of this text is the discussion of pasture and range management. This discussion is in much more detail than pasture and range beef cattle production are covered in most of the other beef cattle texts currently available. This is especially useful for the western United States where most beef cattle are managed under very extensive management systems. Range and grazing management are normally only covered minimally in most beef cattle production texts.

Beef Cattle Production: An Integrated Approach by Thomas also includes a glossary of terms as well as questions for study and discussion at the end of each chapter. There also are some general references given at the end of each chapter for review.

Beef Cattle Production: An Integrated Approach is a well written easy-to-read beef cattle production textbook. It covers all aspects of beef cattle management very thoroughly and does go into some detail on various management procedures. For those colleges and universities that are considering adoption of a beef cattle text, this is the text that certainly should be considered. This book will also serve as a very useful reference for beef cattle producers—*James R. Males,* Pullman, Washington.

Bear attacks: their causes and avoidance. By Stephen Herrero, 1985. Winchester Press, 220 Old New Brunswick Road, Piscataway, NJ 08854. $15.95 cloth. 287 p.

Reading this book gave me both chills and reassurance. The chills came from living through bear attacks so vividly described by the author, and the reassurance came later with his discussion of causes and avoidance. If you have a weak heart, perhaps you should begin at the back of the book and read forward.

Stephen Herrero, the author became interested in bear psychology soon after receiving his Ph.D. in animal behavior. Since then (1967) he has lived near the Canadian Rocky Mountains studying bear attacks and their causes. He is recognized as one of the world's foremost authorities on bears, and is noteably expert with a story.

The first six chapters describe examples of grizzly and black bear attacks, to establish situations which might be analyzed to shed light on the danger. Chapters seven through eleven generally describe bear characteristics and evolution, followed by six chapters devoted to avoiding injury.

This book is recommended reading for all who work, live in, or visit bear habitat. It is also useful as a supplementary text in university courses related to wildlife management or animal behavior.—*Grant A. Harris,* Pullman, WA.

INSTRUCTIONS FOR AUTHORS: This page is reproduced from the *Handbook and Style Manual for the Journal of Range Management.* Copies of the complete booklet (12 pages) are available for $1.25 (single copy) or $1.00 each for 2 or more copies from the Society for Range Management, 2760 West Fifth Avenue, Denver, CO 80204.

Preface

Although not intended as an exhaustive presentation on manuscript preparation, this *Handbook and Style Manual* was prepared with the less experienced author in mind. Points of style, however, must be followed by all authors. Manuscripts submitted after 30 June, 1984, and not conforming to *JRM* style as designated here, will be returned to authors for correction before being sent out for review.

From time to time, this manual will be revised. The inside back cover of the *Journal* will carry brief instructions for authors and will advise them of style changes or a new edition of the style manual.

Introduction

Eligibility

The *Journal of Range Management* is a publication for reporting and documenting results of original research. Previously published papers are unacceptable and will not be considered for publication. Exceptions to this criterion are research results that were originally published as Department Research Summaries, Field Station Reports, Abstracts of Presentations, and other obscure and nontechnical handout publications. Manuscripts submitted to the *JRM* are the property of the *Journal* until published or released back to the author(s). Manuscripts may not be submitted elsewhere while they are being considered for this journal. Papers not accepted for publication are automatically released to the authors.

Kinds of Manuscripts

Journal Articles report original findings in Plant Physiology, Animal Nutrition, Ecology, Economics, Hydrology, Wildlife Habitat, Methodology, Taxonomy, Grazing Management, Soils, Land Reclamation (reseeding), and Range Improvement (fire, mechanical, chemical). *Technical Notes* are short articles (usually less than two printed pages) reporting unique apparatus and experimental techniques. By invitation of the Editorial Board, a *Review Paper* may be printed in the journal. *Viewpoint* articles or *Research Observations* discussing opinion or philosophical concepts regarding topical material or observational data are acceptable. Such articles are identified by the word *viewpoint* or *observations* in the title.

Manuscript Submission

Contributions are addressed to the Editor, Journal of Range Management, 2760 West Fifth Avenue, Denver, Colorado 80204. Manuscripts are to be prepared according to the instructions in this handbook. If the manuscript is to be one of a series, the Editor must be notified. Four copies of the complete manuscript, typed on paper with numbered line spaces, are required. Authors may retain original tables and figures until the paper is accepted, and send good quality photocopies for the review process. Receipt of all manuscripts is acknowledged at once, and authors are informed about subsequent steps of review, approval or release, and publication.

Manuscripts that do not follow the directives and style in this handbook will be returned to the authors by the Editor. A manuscript number and submission date will be assigned when the paper is received in the appropriate format.

Manuscript Review

Manuscripts are forwarded to an Associate Editor, who usually obtains two or more additional reviews. Reviewers remain anonymous. Where reviewers disagree, the Associate Editor, at his discretion, may obtain additional reviews before accepting or rejecting a manuscript.

The Associate Editor sends the approved manuscript, with recommendation for publication, to the Editor, who notifies the author of a projected publication date. Manuscripts found inappropriate for the *JRM* are released to the author by the Associate Editor. Manuscripts returned to an author for revision are *returned to the Associate Editor* for final acceptability of the revision. Revisions not returned within 6 months, are considered terminated. Authors who consider that their manuscript has received an unsatisfactory review may file an appeal with the Editor. The Editor will then determine the seriousness of the situation, and may select another Associate Editor to review the appeal. The Associate Editor reviewing the appeal will be provided with copies of all correspondence relating to the original review of the manuscript. If the appeal is sustained, a new review of the manuscript may be implemented at the discretion of the Editor. Manuscripts will not be sent for second reviews merely on the possibility of finding Associate Editors more favorable to the manuscript.

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Basic Writing Style for Journal Articles

Every paper should be written accurately, clearly, and concisely. It should lead the reader from a clear statement of purpose through materials and methods, results, and to discussion. The data should be reported in coherent sequence, with a sufficient number of tables, drawings, and photographs to clarify the text and to reduce the amount of discussion. Tables, graphs and narrative should not duplicate each other.

Both authors and reviewers are responsible for insuring that the *Journal* manuscripts are clear, concise, and accurate. Editors encourage authors to have manuscripts thoroughly reviewed by colleagues in their own institution and elsewhere before being submitted. Peer review before submission insures that publications will present significant new information or interpretation of previous data,and will speed *JRM* review processes.