

Journal of Range Management

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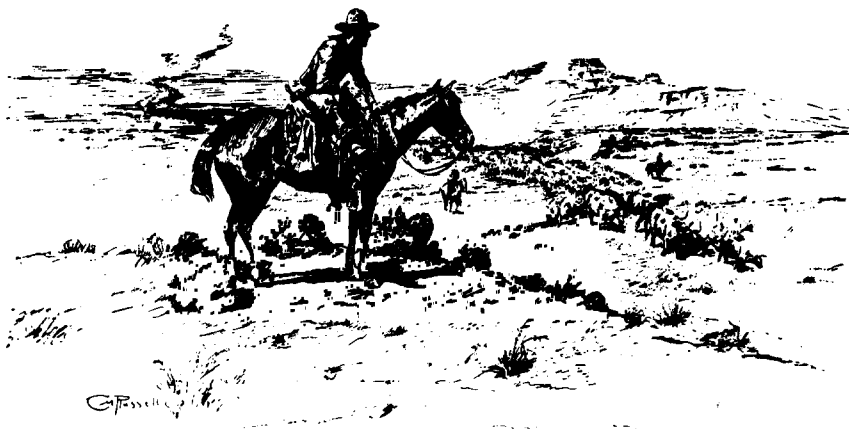
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Effects of Fire on Texas Wintergrass Communities

S.G. WHISENANT, D.N. UECKERT, AND C.J. SCIFRES

Abstract

The effect of season of burning on standing crop, point frequency, density, and reproductive vigor of Texas wintergrass (*Stipa leucotricha* Trin. & Rupr.) communities was measured in this study. Additional information on the effects of fire on Texas wintergrass will aid resource managers plan the use of fire in these communities. Burning or clipping Texas wintergrass did not significantly affect the number of reproductive culms per plant in the northern Edwards Plateau region of Texas. Burning, regardless of season, reduced standing crops for 1 year and burning in January or March reduced Texas wintergrass point frequency for 1 year. Burning where annual cool-season grasses were abundant in the southern Rolling Plains tended to increase Texas wintergrass density, point frequency, and standing crop, apparently a result of reduced competition from annual plants. Increases in Texas wintergrass point frequency and standing crop were greater following burning in the fall than following burning in the spring. Prescribed burning in Texas wintergrass communities generally killed annual grasses and forbs if burning occurred subsequent to seedling emergence. However, soil reserves of seed and/or subsequent seed immigration into burned areas appeared to be sufficient to reestablish populations of annual plants during the second year following burning. Annual grass populations consistently tended to be higher in the second year after burning than on unburned rangeland.

Texas wintergrass (*Stipa leucotricha* Trin. & Rupr.) is an erect, tufted, cool-season perennial that commonly occurs on fine-textured, calcareous soils in the Edwards Plateau, Rolling Plains, Cross Timbers and Prairies, and other land resource areas of Texas (Correll and Johnston 1970). On the western Edwards Plateau, Texas wintergrass is representative of sites with relatively deep soils (Smeins et al. 1976).

Texas wintergrass is one of the most important grasses in the diets of domestic livestock and wildlife in Texas (Drawe and Box 1968, Ramsey and Anderegg 1972, Sanders 1975, Bryant et al. 1979, Taylor et al. 1980). Texas wintergrass may contain green foliage at any time of the year, but usually provides an adequate forage supply from October through June in years with at least average rainfall and relatively warm winters. Texas wintergrass has some characteristics objectionable to sheep and hair-goat producers because the sharp-pointed, densely hairy callus of the floret, and the stout, twisted awn of the lemma enable the floret to easily penetrate the fleece and skin of sheep and hair-goats. This can result in decreased value of wool (Bell 1973) and mohair, loss of weight, decreased carcass quality, and occasional death losses.

Attitudes among resource managers are mixed relative to the values of Texas wintergrass. There is an abundance of cool-season forages in many areas and a corresponding shortage of warm-season forages so that producers are interested in shifting the forage balance toward the warm-season species. When cool-season

forage is limiting and warm-season forage is plentiful, a shift in vegetative composition toward the cool-season species may be desirable. Several species of warm-season grasses occur in many Texas wintergrass communities while cool-season, annual grasses are codominants in others.

Fire can change the species composition of plant stands. Burning in the fall minimizes potential damage to cool-season perennial plants (Wright 1974). Results of 17 years of burning research in the Kansas Flint Hills showed that cool-season species were reduced and warm-season species favored by spring burning (Anderson et al. 1970). Burns early in the growing season were lethal to more plants than burns late in the season. Similar results were obtained in Alberta with western porcupinegrass (*Stipa spartea* var. *curtiseta* Trin.) (Bailey and Anderson 1978). Texas wintergrass is reported to be severely harmed by intense fires (Dahl and Goen 1973) but it increased following spring fires of low intensity (Bean et al. 1975). Production of Texas wintergrass increased for 2 growing seasons after burning in late-winter in the southern Rolling Plains (Ueckert and Whisenant 1980). Box et al. (1967) reported that standing crop of Texas wintergrass was not affected by burning in the fall on the Coastal Prairie region of Texas.

Burning after seedling emergence is usually detrimental to annual plants (Daubenmire 1968, Wright 1974). Seeds of annual grasses are seldom damaged by the flames of grassland fires unless they are in the upper parts of the inflorescence. Seeds in or on the soil surface are seldom damaged by grassland fires (Daubenmire 1968, Vogl 1974).

Two distinctly different responses of annual grasses to litter removal have been reported. Most annual grasses are pioneers requiring bare ground and sunlight, conditions common on post-burn sites (Curtis and Partch 1950, Ehrenreich and Aikman 1957, Daubenmire 1968, Wright 1974). However, other annual grasses require a certain amount of mulch on the soil surface for their seeds to germinate. This requirement for mulched seedbeds has been demonstrated for prairie threeawn (*Aristida oligantha* Michx.) (Owensby and Launchbaugh 1977); soft brome (*Bromus mollis* L.); and downy brome (*Bromus tectorum* L.) (Heady 1956, Smith 1970).

The purpose of this study was to determine the effect that season of burning has on standing crop, point frequency, density, and reproductive vigor of Texas wintergrass and associated species in central and northcentral Texas. An appropriate burning prescription could potentially enable resource managers to manipulate the quantity of Texas wintergrass with fire as needed to achieve a more desirable balance in the yearlong forage base.

Study Areas and Methods

Research was conducted on 6.5 ha in McCulloch County and on 7.5 ha in Coleman County, Texas. These areas typically have dry winters and hot summers with precipitation peaks in April, May, September, and October. Mean annual precipitation is 59 and 69 cm for McCulloch and Coleman Counties, respectively (Bynum and Coker 1974, Botts et al. 1974). Study areas at both locations were fenced to exclude livestock.

The McCulloch County study area has Tobosa clay (fine, montmorillonitic, thermic, Typic Chromustert) on lower areas and

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Valera clay (fine, montmorillonitic, thermic, Petro Calciustoll) on higher areas. The Coleman County study area contains both Rowena clay loam (fine, mixed, thermic Vertic Calciustoll) and Kavett silty clay (clayey, montmorillonitic, thermic, shallow Petrocalcic Calciustoll).

The McCulloch County study area is located in the northcentral Edwards Plateau and is in the Oak Savannah floristic association of McCulloch County (Whisenant 1981). The Coleman County study area is located in the mesquite (*Prosopis glandulosa* Torr. var. *glandulosa*) grassland floristic association of the Rolling Plains.

Fine fuel loads and fuel-water contents were determined before each burn by clipping fifteen, 0.25-m² sampling areas to a 2.5-cm stubble height, drying at 60°C for 48 hr, and weighing. Air temperature, relative humidity, and instantaneous wind speed were measured with a mercury thermometer, sling psychrometer, and a hand-held wind meter immediately before, during, and after each burn.

One experiment at the McCulloch County location was designed as completely random and arranged as a split-plot (hereafter called small plots), with season of treatment as the main-plot effect and treatment as the sub-plot effect. Treatments and seasons were each replicated 4 times and applied to 3- by 3-m subplots. Treatments used were (1) burn, (2) clip and remove all vegetation and mulch, and (3) no treatment. Treatments were conducted during fall (September 28, 1979); winter (January 24, 1980); and spring (March 19, 1980). Each subplot was separated from the others by a 1-m buffer.

Plant density and numbers of reproductive culms per plant were determined on June 3, 1980, and June 4, 1981, in two, 13- by 192-cm (0.25-m²) quadrats placed on a permanently marked diagonal across each plot. Point frequency (hereafter referred to as frequency) was determined (based on foliar hits) on June 3, 1980, and June 2, 1981, using 10 placements of an inclined 10-point frame on each plot. Statistical comparisons of numbers of reproductive culms were conducted on a per plant basis.

The second experiment at the McCulloch County study site contained ten, 0.3-ha plots arranged as a randomized complete block design (hereafter called large plots). Soil type was used as the criterion for the 2 blocks. Two of these were not burned and 2 each were burned on September 27, 1979; January 24, 1980; March 19, 1980; and November 21, 1980.

Standing crops were determined using fifteen to twenty-five, 0.25-m² quadrats in each plot. Standing crops were determined on June 3, 1980; June 2, 1981; and October 23, 1981. Green herbaceous vegetation was clipped, by species, to a 2.5-cm stubble height

and oven-dried at 60°C for 48 hr before weighing. Frequency was determined on each 0.3-ha plot along 2 permanently marked 61-m lines with 200 points spaced 30.5-cm apart per line. Evaluation dates were June 3, 1980; October 10, 1980; June 2, 1981; and October 23, 1981.

The Coleman County experiment contained eight 0.8-ha plots arranged in a randomized complete block design. Soil type was used as criterion for the 2 blocks. Two of these were not burned, and two each were burned on October 9, 1979; January 25, 1980; and March 21, 1980.

Frequency was determined on each 0.8-ha plot along 2 permanently marked 91-m lines with 200 points spaced 45.7-cm apart per line. Evaluation dates were June 12, 1980; October 10, 1980; May 22, 1981; and November 6, 1981. Plant density was measured in four 13- by 192-cm (0.25-m²) quadrats at each of four, permanently marked sampling areas in each 0.8-ha plot. Standing crops were determined on June 12, 1980; May 22, 1981; and November 6, 1981, by harvesting to a 2.5-cm stubble height in 15 to 25, 0.25-m² quadrats in each plot.

Treatment effects on frequency, plant density, and the numbers of reproductive culms per plant were determined for the split-plot experiment using analyses of variance of plot means. Differences in frequency among treatments on the randomized complete block experiments were determined with analyses of variance using data from each transect as a subsample. Differences in standing crop among treatments with the randomized complete block experiments were determined with analysis of variance using quadrat data as subsamples. Treatment means from the large plot experiments were separated with Duncan's multiple range test ($P \leq 0.05$) when appropriate. Orthogonal comparisons were made of untreated vs. treated plots (clipped and burned) and clipped vs. burned plots on the small plot experiment.

Results and Discussion

Weather at Time of Burns

Environmental and fuel variables during fires installed in Texas wintergrass stands during 1979-1980, at both study sites, are listed in Table 1.

Texas Wintergrass

At the McCulloch County site in June 1980, Texas wintergrass densities on treated plots were significantly higher after September treatments and lower following January treatments compared to untreated plots (Table 2). In June 1981, Texas wintergrass densities were higher on plots treated in September, 1979, January 1980, or March 1980 when compared to untreated plots. No significant

Table 1. Environmental and fuel variables during fires installed in Texas wintergrass stands during 1979-1980, McCulloch County and Coleman County, Texas.

Date burned	Experiment ¹	Ambient temperature (°C)	Wind speed (km/hr)	Relative humidity (%)	Fuel water (%)	Fine fuel (kg/ha)
McCulloch County						
Sep. 1979	LP	32	1-5	19	14	2,700
	SP	35	10-13	18	16	2,680
Jan. 1980	LP	18	10-16	42	14	3,700
	SP	16	10-13	44	13	3,650
Mar. 1980	LP	20	18-24	30	18	3,000
	SP	22	13-23	33	18	3,000
Nov. 1980	LP	12	0-5	54	22	3,300
Coleman County						
Oct. 1979		23	8-16	24	13	3,000
Jan. 1980		18	10-14	35	12	3,100
Mar. 1980		21	14-18	23	9	2,500

¹LP = Large plots.
SP = Small plots.

Table 2. Live plant densities (no./m²) in June 1980 and 1981 after burning or clipping at several dates in 1979-1980, for small plots, McCulloch County, Texas.¹

Treatment	Treatment date				Treatment means
	September 1979	January 1980	March 1980		
Texas Wintergrass, June 1980					
No treatment vs Treated ²	170 * 224	133 * 78	122 111 NS		141 NS 138
Clipped vs. Burned	202 NS 247	87 NS 69	118 104 NS		135 NS 140
Texas Wintergrass, June 1981					
No treatment vs Treated	85 ** 114	75 ** 112	78 ** 141		79 ** 122
Clipped vs. Burned	114 NS 113	117 NS 106	142 140 NS		124 NS 120
Ozarkgrass, June 1980					
No treatment vs Treated	34 NS 27	10 NS 7	24 * 8		22 NS 35
Clipped vs. Burned	24 NS 30	12 * 3	16 * 1		17 NS 11

¹NS means the contrast is not significantly different, * means significant at the 5% error level, and ** means significant at the 1% error level using an F-test for comparison.
²Treated category includes both clipped and burned treatments.

differences in Texas wintergrass densities were found between burned and clipped plots regardless of treatment date or evaluation date. Comparison of densities on the untreated plots indicated decreases from June 1980 to June 1981. There were no obvious reasons for this apparent natural mortality on untreated plots; it may have been related to excessive litter accumulation on those plots. Untreated plots had not been grazed for almost 2 years before the June 1981 evaluation.

Texas wintergrass densities on the Coleman County site were not significantly affected ($P \leq 0.05$) during the first spring after burning, regardless of season of burning (Whisenant 1982). However, there was a strong (yet not significant) trend toward increased Texas wintergrass densities following burning, especially following burns installed in October or January. Plant densities on plots burned in October, January, or March increased by 66, 75, and 53%, respectively, by the first spring subsequent to burning compared to densities on adjacent unburned rangeland.

Average numbers of reproductive culms per Texas wintergrass plant were not affected by burning or clipping, regardless of season of treatment or location (Whisenant 1982). Frequencies of Texas wintergrass on the treated small plots in June 1980 were reduced

(Table 3), but did not differ at the end of the second growing season. No significant differences in Texas wintergrass frequency were found between burned or clipped plots, regardless of treatment date or evaluation date.

Reduction in Texas wintergrass frequency attributable to clipping or burning appeared to be related to the amount of green tissue removed. Treatments in September 1979 were applied when the Texas wintergrass plants were dormant. Extremely small amounts of green tissue were removed, and treatments did not reduce Texas wintergrass frequencies. Large amounts of green tissue were removed by burning or clipping during January or March.

The length of time between treatment and evaluation is another important consideration in assessing reduction of Texas wintergrass frequency. The September treatments had the longest post-treatment growth period and reflected the least treatment effect. The January and March treatments had shorter post-treatment growth periods prior to evaluation and relatively large reductions in Texas wintergrass frequencies.

Texas wintergrass frequencies on the large plots burned in October or January, had increased by June 1980 compared to

Table 3. Texas wintergrass frequencies (%) after burning or clipping at several dates in 1979-1980, for small plots, McCulloch County, Texas.¹

Treatment	Treatment date				Treatment means
	September 1979	January 1980	March 1980		
June 1980					
No treatment vs. Treated ²	56 NS 46	74 * 52	68 ** 44		66 ** 47
Clipped vs. Burned	45 NS 47	48 NS 55	48 41 NS		47 NS 48
June 1981					
No treatment vs. Treated	83 NS 79	81 NS 79	81 NS 78		82 NS 79
Clipped vs. Burned	78 NS 81	82 NS 75	72 NS 85		77 NS 80

¹NS means the contrast is not significantly different, * means significant at the 5% error level, and ** means significant at the 1% error level using an F test for comparison.
²Treated category includes both clipped and burned treatments.

Table 4. Frequencies (%) and standing crops (kg/ha) after burning in 1979-1980, Coleman County, Texas.¹

Date burned	Evaluation date			
	June 1980	October 1980	May 1981	November 1981
Texas Wintergrass Frequency (%)				
Unburned	24 c	22 a	30 a	38 a
Oct. 1979	48 a	26 a	44 a	42 a
Jan. 1980	44 ab	26 a	43 a	44 a
Mar. 1980	29 bc	19 a	37 a	40 a
Texas Wintergrass Standing Crop (kg/ha)				
Unburned	339 a	—	523 a	538 b
Oct. 1979	500 a	—	943 a	689 a
Jan. 1980	400 a	—	743 a	539 b
Mar. 1980	402 a	—	1264 a	545 b
Japanese Brome Standing Crop (kg/ha)				
Unburned	212 a	—	726 a	—
Oct. 1979	130 a	—	660 a	—
Jan. 1980	357 a	—	447 a	—
Mar. 1980	31 b	—	375 a	—

¹Means within a column within an evaluation date, followed by the same letter, are not significantly different ($P \leq 0.05$) according to Duncan's multiple range test.

the unburned plots at the Coleman County study site (Table 4). Texas wintergrass frequencies on plots burned in March 1980 were not different ($P \leq 0.05$) from frequencies on unburned plots when evaluated in June 1980. Although no differences in Texas wintergrass frequencies occurred in October 1980, May 1981, or November 1981, frequencies on untreated and on plots burned in March 1980 tended to be less than on plots burned in October or January. This trend is consistent with observations of Daubenmire (1968), Wright (1974), and Wright and Bailey (1982) that fall burns benefit cool-season plants.

Texas wintergrass standing crops on the McCulloch County study site were reduced during the first spring subsequent to burning in September 1979, January 1980, or March 1980 (Table 5). However, burning in November 1980 reduced standing crops during the first growing season. Texas wintergrass standing crops on burned rangeland were equal to those on unburned rangeland during the second growing season when rainfall was slightly below average (1980 evaluation) and during the first growing season when it was above average (see 1981 evaluations of November 1980 burn in Table 5).

Texas wintergrass standing crops demonstrated variable responses to fall burning in different years. Burns in September 1979 were conducted under relatively hot, dry conditions (Table 1); most of the ground mulch was consumed. Plots burned in November 1980 were burned under relatively cool and humid conditions (Table 1); little ground mulch was consumed and 3 to 6 cm of green leaf material was left relatively undamaged. Standing crop data indicated that "cool" fall burns followed by excellent

Table 5. Standing crops (kg/ha) after burning in 1979-1980, for large plots, McCulloch County, Texas.¹

Date burned	Evaluation date		
	June 1980	June 1981	October 1981
Texas Wintergrass			
Unburned	893 a	2028 a	1964 a
Sep. 1979	334 b	1206 a	1753 a
Jan. 1980	396 b	2268 a	1715 a
Mar. 1980	320 b	1492 a	1247 a
Nov. 1980	—	1736 a	1883 a
Ozarkgrass			
Unburned	36 b	251 a	—
Sep. 1979	138 a	433 a	—
Jan. 1980	6 b	257 a	—
Mar. 1980	2 b	51 b	—
Nov. 1980	—	122 a	—

¹Means within a column within an evaluation date, followed by the same letter, are not significantly different ($P \leq 0.05$) according to Duncan's multiple range test.

growing conditions did not hurt Texas wintergrass during the first growing season.

Texas wintergrass standing crops on the Coleman County study site during June 1980 and May 1981 did not differ significantly between burned and unburned plots (Table 4). However, there were trends toward greater standing crops on burned plots during both years. Standing crops of Texas wintergrass in May 1981 on plots burned in October, January, or March tended to be greater than on unburned plots. Standing crops of Texas wintergrass in November 1981 were significantly greater ($P \leq 0.05$) on plots burned in October 1979 than on unburned plots or on plots burned on other dates (Table 4).

Cool-season Annual Grasses

Ozarkgrass [*Limnodea arkansana* (Nutt.) Engelm.] plant density was significantly reduced during the first growing season at the McCulloch County study area by treatments conducted in March after seedling establishment (Table 2). However, ozarkgrass density on clipped plots was significantly greater than on plots burned in January or March, indicating that mortality resulted from heat damage and not simply from removal of above-ground vegetative material (Table 2).

Standing crops of ozarkgrass at the McCulloch County study area increased during the first growing season following burning in September (Table 5). At the Coleman County study area there were nonsignificant trends toward reductions in frequency of Japanese brome (*Bromus japonicus* Thun.) following March burns, and increases following burning in October or January (Whisenant 1982). Standing crops of Japanese brome were reduced ($P \leq 0.05$) for the first growing season following burning in March (Table 4). Plots burned in March 1980 supported only 52% of the unburned Japanese brome standing crop during the second growing season

Table 6. Reproductive culms per red threeawn plant in June 1980 after burning or clipping at several dates in 1979-1980, for small plots, McCulloch County, Texas.¹

Treatment	Treatment date			Treatment means
	September 1979	January 1980	March 1980	
No treatment vs. treated ²	10 NS	2 NS	7 *	6 NS
	16 NS	13 NS	19 *	16 NS
Clipped vs. burned	17 NS	7 NS	20 NS	15 NS
	15 NS	18 NS	18 NS	17 NS

¹NS means the contrast is not significantly different, * means significant at the 5% error level, and ** means significant at the 1% error level using an F test for comparison.
²Treated category includes both clipped and burned treatments.

after burning. However, this difference was not statistically significant.

Warm-season Perennial Grasses

Red threeawn (*Aristida longiseta* Steud.) density, frequencies and standing crop at the McCulloch County study area were not affected by burning or clipping, regardless of season (Whisenant 1982). However, the March treated plots had significantly more reproductive culms per plant than the untreated plots in June 1980 (Table 6). No significant differences in the number of reproductive culms were found between clipped and burned plots.

Conclusions

Response of Texas wintergrass to burning is largely a function of environmental conditions during the fire, growing conditions following burning, and interspecific competitive interactions. Grazing by domestic livestock may also be a critical regulatory influence, but was eliminated as a factor in this study. Responses of Texas wintergrass to burning or clipping were similar for all attributes measured in this study, indicating that most of the responses brought about by burning or clipping result from mulch removal and associated indirect influences rather than direct heat effects.

Burning Texas wintergrass in dense homogeneous stands during January or March reduced Texas wintergrass standing crops and frequencies. Low intensity fall burns that did not consume the surface mulch and were followed by several months of average or above-average rainfall allowed plants to recover from any potentially detrimental effects during the first growing season. Fire-induced changes in Texas wintergrass were relatively short-lived (<1 year).

The pattern of Texas wintergrass response to burning was different in plant communities in which cool-season, annual grasses were major components of the vegetation. Consistent trends indicated that Texas wintergrass density, frequency, and standing crop may increase following burning in these communities. Increases in Texas wintergrass were more pronounced following burning in the fall and less pronounced following burning in the spring. These increases in Texas wintergrass appear to be a result of reduced interspecific competition following removal of annual plants by fire.

Plant density is probably a better long-term indicator of community response to burning than frequency or standing crop. Using this assumption, Texas wintergrass was benefited by burning, particularly when burning reduced interspecific competition. Texas wintergrass may increase its density to partially fill the resulting void when competition is reduced. Some evidence suggested that excessive litter accumulation may reduce Texas wintergrass density on unburned rangeland. Grazing or periodic burning will probably prevent excess litter accumulation.

Cool-season, annual grasses and forbs were generally killed when burning occurred after emergence. However, seed reserves in the soil and/or subsequent seed immigration into burned areas allowed annual plant populations to reestablish in the second year. Seed immigration into large areas would probably be less than in the small plots treated in this experiment. Clipping did not reduce ozarkgrass frequency as much as burning, indicating that mortality resulted from heat damage and not simply from removal of above-ground vegetative material. Annual grass frequencies and standing crops on plots burned in September-October were greater than on unburned plots whereas burning in March decreased annual grass density, frequency, and standing crop. Burning in January was less detrimental to annual grasses, than burning in March. Annual grasses and forbs tended to be more abundant in the second year after burning than on unburned rangeland.

A fire designed to benefit Texas wintergrass at the expense of warm-season, perennial grasses should be applied in the fall before

growth of Texas wintergrass begins and while warm-season perennial grasses are still actively growing. If management objectives demand favoring warm-season, perennial grasses, and reducing Texas wintergrass, the Texas wintergrass should be burned when it is actively growing and before initiation of warm-season perennial grass growth. However, the detrimental effect of fire on Texas wintergrass may last only 1 year.

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Long-term Effects of Annual Burning at Different Dates in Ungrazed Kansas Tallgrass Prairie

GENE TOWNE AND CLENTON OWENSBY

Abstract

Ungrazed tallgrass prairie plots in the Kansas Flint Hills have been burned annually at 4 different dates since 1928. Time of burning markedly altered the physiognomy and was the crucial factor effecting vegetation change. Late-spring burning, coinciding with emergence of the warm-season perennial grasses, increased grass production and favored *Andropogon gerardii* and *Sorghastrum nutans*. Burning in winter, early-spring, or mid-spring reduced herbage production and shifted vegetational composition by differentially favoring other species. *Andropogon scoparius* increased with mid- and early-spring burning, while perennial forbs and sedges increased with early-spring and winter burning. *Amorpha canescens* was favored by all burning treatments. Mulch buildup in unburned, undisturbed plots increased *Poa pratensis* and tree species and eventually reduced grass production. The long-term effects of annual late-spring burning, even in dry years, was not detrimental to herbage production, species composition, or total basal cover in tallgrass prairie.

Tallgrass prairie is fire-derived and fire-maintained (Stewart 1951). Historically, fires were intermittent and occurred at nearly any time of the year (Jackson 1965). In the 1880's, cattlemen observed that transient steers gained more weight on burned than on unburned range, and as a result, grazing leases later mandated annual burning (Kollmorgen and Simonett 1965). Time of burning, however, was of little concern, and most pastures were burned in January or February to stimulate earlier greenup.

Although voluminous literature exists on vegetational effects from fire, few studies have acknowledged the importance of time of burning. Aldous (1934) initiated preliminary research on burning ungrazed tallgrass prairie at different dates. Subsequent reports on herbage production (McMurphy and Anderson 1963) and botanical composition (McMurphy and Anderson 1965) were nonreplicated, short-term studies in which the unburned control was mowed and raked annually, and included data from years when the plots were not burned. This paper compiles earlier research and adds recent data from undisturbed control plots to evaluate the importance of time of burning on herbage production and species composition in ungrazed tallgrass prairie over the past 56 years.

Study Area and Methods

The experimental site is located on a level ridge top in the Kansas Flint Hills north of Manhattan. From the early 1900's, the area had been moderately grazed by cattle and routinely burned in late winter. Soil at the site is a loessial-derived Smolan silt loam classified as a Pachic Argiustoll. It has a dark-gray surface layer about 20 cm thick overlying a deep silty clay loam subsoil. Vegetation at the beginning of the study was predominantly little bluestem

(*Andropogon scoparius* Michx.)¹, with prairie junegrass [*Koeleria pyramidata* (Lam.) Beauv.], big bluestem (*A. gerardii* Vitman), and indiagrass [*Sorghastrum nutans* (L.) Nash] also prevalent (Table 1). Mean annual precipitation for Manhattan since 1928 is

Table 1. Percent botanical composition based on actual stem numbers in 1926 on Kansas Flint Hills study site before date of burning treatments began.

	%
<i>Andropogon scoparius</i> Michx.	32.6
<i>Koeleria pyramidata</i> (Lam.) Beauv.	20.2
<i>Andropogon gerardii</i> Vitman	16.7
<i>Sorghastrum nutans</i> (L.) Nash	11.0
<i>Poa pratensis</i> L.	1.0
<i>Panicum virgatum</i> L.	0.2
Other perennial grasses	8.9
Annual grasses	0.0
Sedges	3.1
Perennial forbs	6.1
Annual and biennial forbs	0.2
Woody plants	0.0

82.8 cm, ranging from 39.2 cm in 1966 to 153.4 cm in 1951. Rainfall generally is highest in spring and then declines through the summer. Average frost-free period is 178 days, extending from April 22 to October 17.

To study the effects of burning tallgrass prairie on different dates, a 0.4-ha area was fenced in 1926. Surrounding pasture land has been continuously grazed and annually supports dense stands of Japanese brome (*Bromus japonicus* Thunb.), common ragweed (*Ambrosia artemisiifolia* L.), woolly verbena (*Verbena stricta* Vent.), and numerous other forbs, but no trees are in close proximity. The enclosed site was partitioned into ten 20 × 10-m plots separated by 0.9-m alleys. Treatments were winter burn (December 1), early-spring burn (March 20), mid-spring burn (April 10), late-spring burn (May 1), and unburned. Actual dates of burning varied throughout the years depending upon seasonal weather conditions. Initially, 1 set of 4 plots was burned annually beginning in December 1926, and another set biennially burned. Starting in 1950, however, the plots formerly burned in alternate years were burned yearly to provide 2 replications for each treatment. Burning was discontinued from 1935–1937 and from 1945–1949. But for 48 of the past 56 years the research plots have been burned, representing, to our knowledge, the longest extent of burning studies in existence.

Initially, unburned control plots were mowed and the cut material removed every year before spring growth to prevent excess mulch accumulations. That practice, however, obscured differences between burned and unburned treatments and was stopped in 1968. Both unburned plots were accidentally burned by wildfires in January 1951 and again in March 1966.

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Additional graphs of yearly fluctuations for the major plant species under different burning treatments are available from the authors on request.

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¹Scientific names follow McGregor and Barkley (1977).

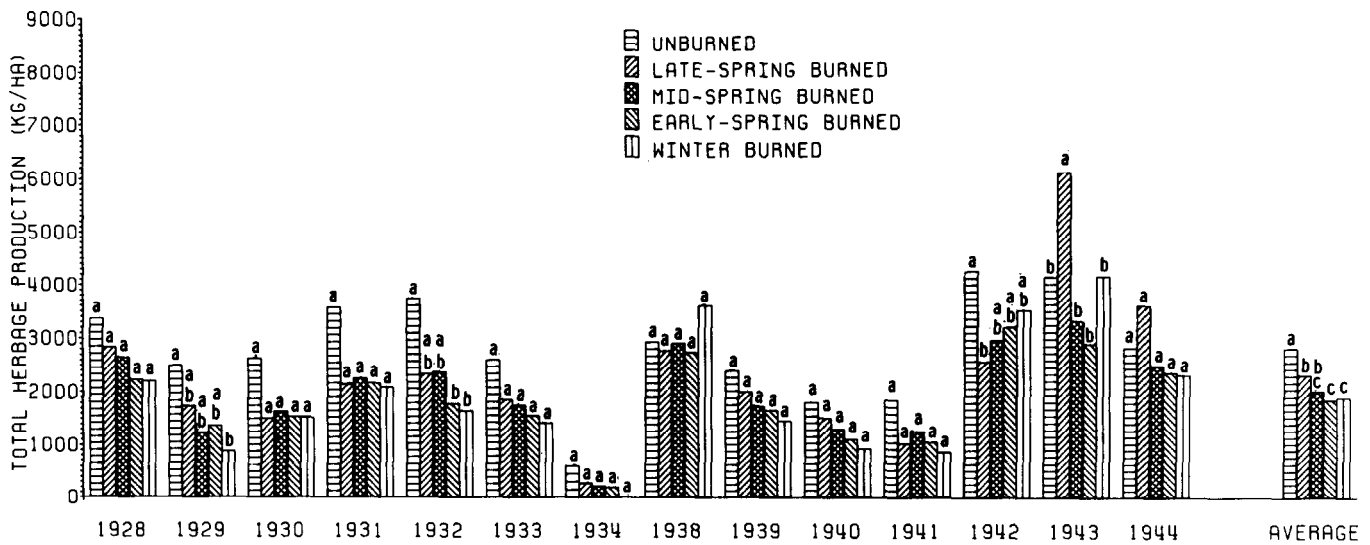


Fig. 1. Total annual herbage production (kg/ha oven-dry weight) from 1928-1944 under different burning dates. One replication per treatment. Unburned plots were mowed and raked annually in late-spring. Means within each year having the same letter are not significantly different ($P > .05$).

Total herbage production for each plot was measured annually at the end of the growing season, normally in early-October. Current year's biomass was harvested by mowing swaths to a 5-cm stubble height from 1928-1971, and by clipping four 0.4-m² quadrats per plot to ground level beginning in 1972. Prior to 1965, yields had been on an air-dry basis and were converted to approximate oven-dry weights by reducing the yields 10%. Plots were not harvested from 1945-1952. Yearly herbage yields were excluded from statistical analysis when plots were not burned (1935-1937), when all plots accidentally burned (1966), and in 1971, when erroneous sampling inflated production. Beginning in 1973, clipped herbage was segregated into grasses (including sedges) and forbs (including woody species). Mulch and old standing dead in unburned plots were removed from each quadrat prior to clipping and were not included in herbage production data.

Botanical composition was usually estimated by mid-June. From 1928-1942, actual stem numbers of plant species were

counted in 2 permanent meter-square quadrats in each plot. No plant census was taken from 1943-1949. From 1950-1974, basal cover and species composition were estimated by randomized line transects (Anderson 1942). Beginning in 1975, relative percentages of plant species and basal cover were determined by the modified step-point technique (Owensby 1973). To analyze the vegetational response from date of burning treatments, we segregated out 5 primary perennial grass species, and grouped other grasses, forbs, and woody species into appropriate categories.

All data were statistically analyzed by standard analysis of variance and treatment means separated by Duncan's multiple range test ($P < .05$). Because of variations in data collection, herbage yields were analyzed separately for 3 time periods: (1) from 1928-1944 when there was only one treatment replication and thus no interaction variability; (2) from 1950-1967 when unburned plots were annually mowed and raked; (3) from 1968-1982 when mulch was allowed to accumulate on the unburned plots. Herbage

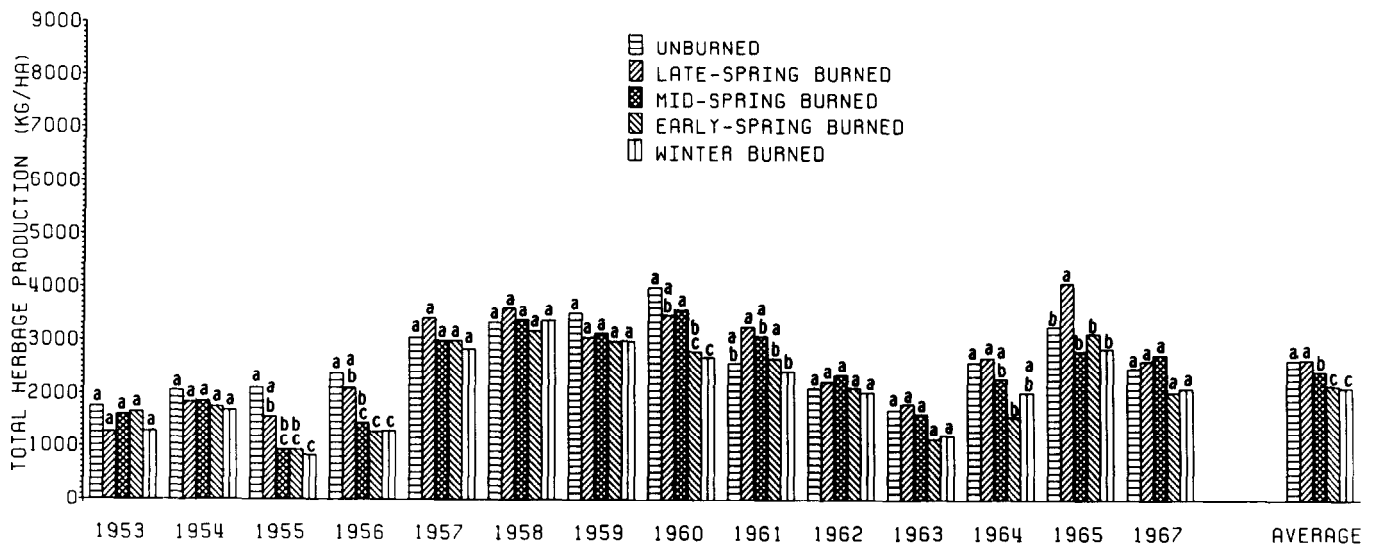


Fig. 2. Total annual herbage production (kg/ha oven-dry weight) from 1953-1967 under different burning dates. Two replications per treatment. Unburned plots were mowed and raked annually in late-spring. Means within each year having the same letter are not significantly different ($P > .05$).

Table 2. Correlation coefficients (r) of total herbage yields from 1928–1982 for date of burning treatments and independent precipitation variables.

Precipitation	Unburned	Late-spring burn	Mid-spring burn	Early-spring burn	Winter burn
Yearly total	.28*	.37*	.32*	.35*	.36*
Previous years total	.31*	.23	.23	.29*	.26*
January–April	.03	.24*	.19	.24	.17
May–June	.17	.30*	.25*	.29*	.36*
May–September	.24	.28*	.23	.26*	.31*

* $P < .05$

production and species composition from the burning treatments were correlated with 5 selected combinations of precipitation: yearly total; previous year's total; amount prior to growing season (January–April); amount during early portion of growing season (May–June); and amount during entire growing season (May–September).

Results and Discussion

Herbage Production

Herbage yields fluctuated greatly throughout the years, ranging from 8,455 kg/ha in 1981 mid-spring burned plots to 0 kg/ha in 1934 winter burned plots. Total herbage production in all burning treatments was highest in 1981 and second highest the following year, indicating that long-term annual burning does not decrease prairie productivity.

In the first phase of the study, average herbage production was significantly reduced by burning at any time compared to not burning (Fig. 1). However, the effects were not uniform over time. In only 3 of the 14 years did unburned plots produce significantly more biomass than any burned plot.

A significant interaction between burning and year of treatment in both the second and third phase of the study indicated total herbage yields were affected by date of burning more in some years than in others (Fig. 2 and 3). McMurphy and Anderson (1963) speculated that the greatest reduction in herbage yields from burning occurred in the driest seasons. However, correlation coefficients disclosed a weak relationship between herbage yields and time of burning over all precipitation variables (Table 2). Although most of the independent variables were significant, the low coefficient values indicate that only a small portion of the variation in herbage yields can be attributed to precipitation factors. In years with annual precipitation at least 10% below normal, late-spring

burning never significantly reduced herbage production compared to unburned plots. Thus, contrary to rumored opinion, burning tallgrass prairie at the proper time, even in dry years, does not adversely affect herbage yields.

In other geographic regions, studies of vegetational response to wildfires or prescribed burns occurring at inopportune times often have neglected to take into account the time of burning. Although fire intensity, fuel source, and soil moisture are all potentially important in influencing vegetational response to fire, time of burning is the proxy for these factors, and in this study was the crucial factor ultimately affecting herbage production. Since 1928, burning in winter and early-spring has reduced total herbage yields an average of 15% and 16%, respectively, over plots burned in late-spring. Anderson (1965) attributed that to a reduction in soil moisture due to decreased infiltration and increased evaporation. Bieber and Anderson (1961) found progressively lower soil moisture the earlier an area was burned in relation to initiation of spring growth; however, there was no significant difference between unburned and late-spring burned plots. Burning at a time to minimize surface exposure will thus curtail soil moisture loss and prevent concomitant herbage reduction.

Differences in herbage yields between burned and unburned plots prior to 1968 are misleading because the unburned plots were mowed and raked annually. Mechanical mulch removal increases total biomass production in tallgrass prairie (Penfound 1964). Higher soil temperatures on areas denuded early in the growing season by either clipping or burning are responsible for the increased productivity (Hulbert 1969, Rice and Parenti 1978, Adams and Anderson 1978). Mulch accumulations in undisturbed prairie eventually depress herbage yields and reduce the number of plant species (Weaver and Rowland 1952). After mulch removal was halted in 1968, unburned plots continued to yield more her-

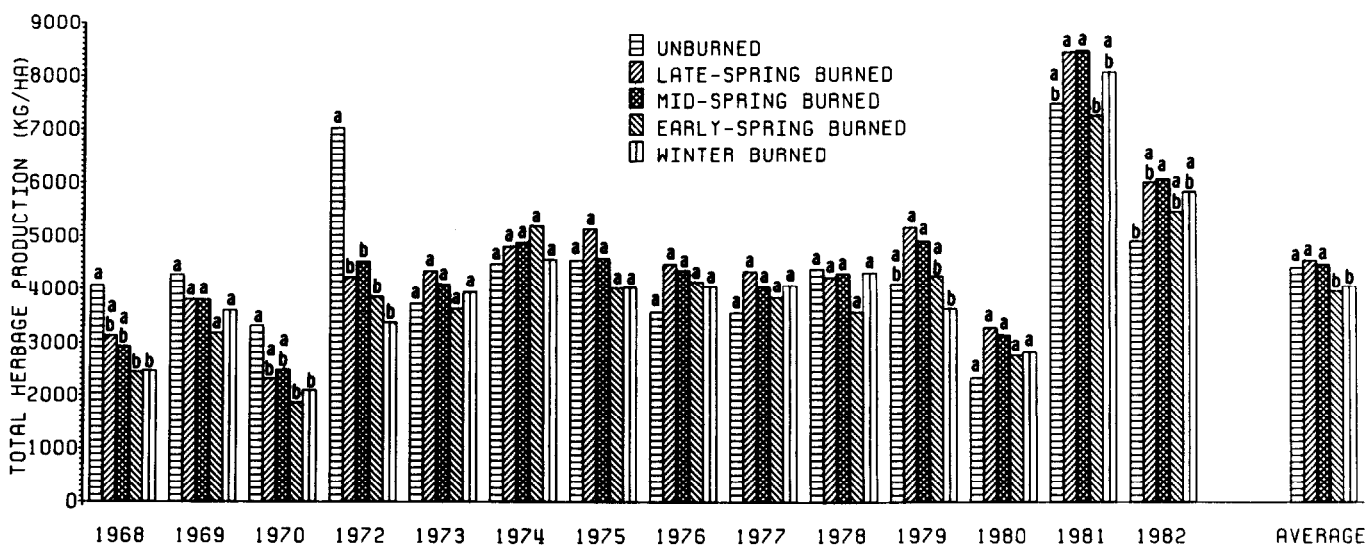


Fig. 3. Total annual herbage production (kg/ha oven-dry weight) from 1968–1982 under different burning dates. Two replications per treatment. Mulch allowed to accumulate on unburned plots, but was excluded from yearly production data. Means within each year having the same letter are not significantly different ($P > .05$).

bage than burned plots for another 4 years (Fig. 3), but biomass from unburned plots undoubtedly was inflated in some years due to inadvertent harvesting of litter and old standing dead.

Total herbage production, however, may not be the most important criterion in assessing benefits from burning. Analysis of individual herbage components from 1973-1982 indicated that late-spring burning significantly increased grass production and lowered forb production compared to any other treatment (Fig. 4).

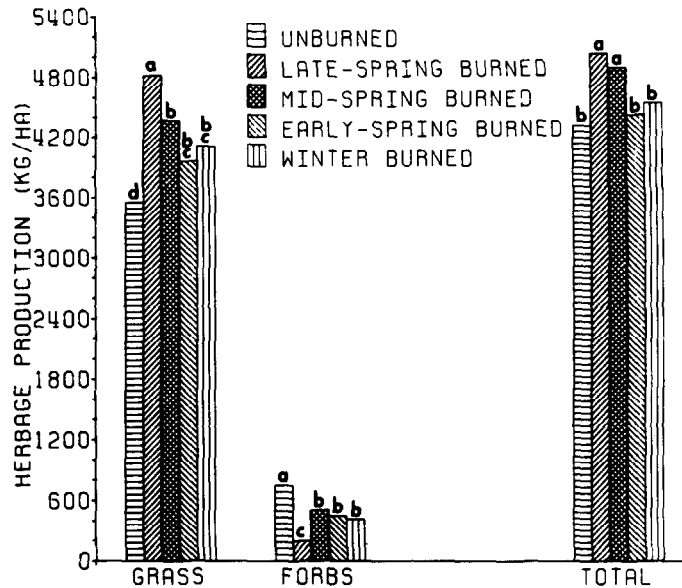


Fig. 4. Average grass, forb, and total production (kg/ha oven-dry weight) from 1973-1982 under different burning dates. Litter and old standing dead in unburned plots were excluded from production data. Means within each component having the same letter are not significantly different ($P > .05$).

Unburned plots had the lowest grass and highest forb yields of any treatment. Burning in late-spring reduced forb production because most species were actively growing and at a low point in their carbohydrate reserves (Anderson et al. 1970). Grass yields increased from late-spring burning because fire at that time coincided with emergence of the dominant warm-season perennial grasses (Owensby and Anderson 1967).

Botanical Census

Long-term annual burning at various dates differentially affected plant species and shifted botanical composition from that prior to initiation of the study. Phenological development of a species at the time of burning largely determines its response to fire. Plants actively growing when burning occurs are more susceptible to fire injury than dormant species or those just initiating growth (Anderson et al. 1970).

Andropogon gerardii Vitman

Late-spring burning significantly increased big bluestem amounts compared to other treatments (Fig. 5). Since 1961, big bluestem consistently accounted for over 50% of the total vegetation in late-spring burned plots, indicating that it responds favorably to fire, particularly when burning occurs at the onset of spring growth. Unburned plots prior to 1968 contained lower amounts of big bluestem than other treatments; however, once yearly mulch removal was halted, relative density of big bluestem began increasing. Nearly pure stands of big bluestem eventually develop in ungrazed, heavily mulched prairie (Weaver and Rowland 1952, Hulbert 1969). Apparently, big bluestem is not adversely affected by fire exclusion when mulch accumulations inhibit competition from other species.

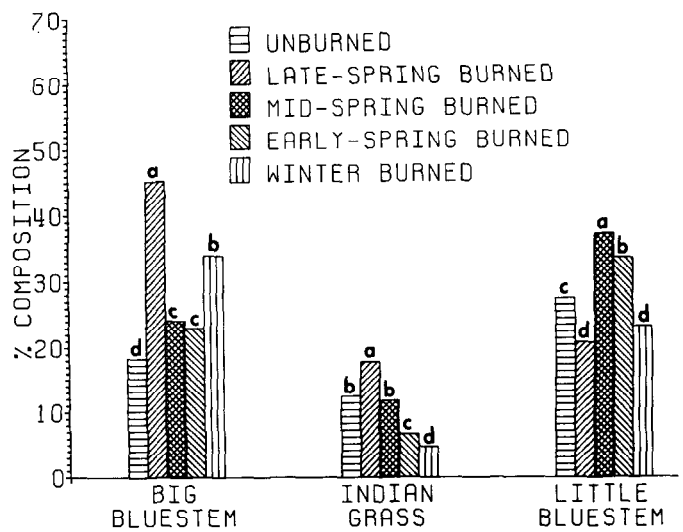


Fig. 5. Average % composition of big bluestem, indiagrass, and little bluestem from 1928-1982 under different burning dates. Means within each year having the same letter are not significantly different ($P > .05$).

Sorghastrum nutans (L.) Nash

Late-spring burning significantly increased indiagrass, while winter and early-spring burning reduced amounts compared to those of unburned plots (Fig. 5). Since 1976, big bluestem and indiagrass together have comprised over 90% of the total vegetation in late-spring burned plots. In unburned plots, indiagrass density began declining after 1973. Because indiagrass, unlike big bluestem, has indeterminate tillering (McKendrick et al. 1975), mulch accumulations likely inhibited tiller development.

Andropogon scoparius Michx.

Winter and late-spring burning adversely affected little bluestem, but mid- and early-spring burning significantly increased amounts compared to not burning (Fig. 5). Hensel (1923) and Aldous (1934) also noted that little bluestem was favored by early-spring burning. In grazed pastures, however, Anderson et al. (1970) reported that little bluestem was reduced by early-spring, but not by late-spring burning. McMurphy and Anderson (1965) concluded that burning at any time was detrimental. Because little bluestem is a bunchgrass, the plant crown is susceptible to fire injury unless conditions are moist. Thus, discrepancies in the response of little bluestem to time of burning may reflect short-term fluctuations in prevailing environmental conditions at ignition time.

Little bluestem often accounted for over 50% of the total vegetation, culminating at 75.8% in 1974 mid-spring burned plots. But the average percentage for all treatments fell from 43.6% in 1974 to 14.3% in 1975. At that time, the randomized line transect method for determining vegetation composition was abandoned in favor of the modified step-point. Increased amounts of big bluestem, indiagrass, sedges, and perennial forbs offset little bluestem reduction in winter, early- and mid-spring burned plots. However, in unburned and late-spring burned plots, no species increases were associated with the changeover in sampling technique.

Poa pratensis L.

Kentucky bluegrass, a cool-season perennial with low drought tolerance and inherently low productive capacity in Kansas, was effectively reduced by burning on all dates (Fig. 6). Fire essentially eliminated bluegrass because the plant was actively growing and susceptible to injury.

Fluctuation of Kentucky bluegrass in unburned plots was responsible for a significant interaction among years. That effect, however, was not correlated with precipitation ($r < .12$ for all inde-

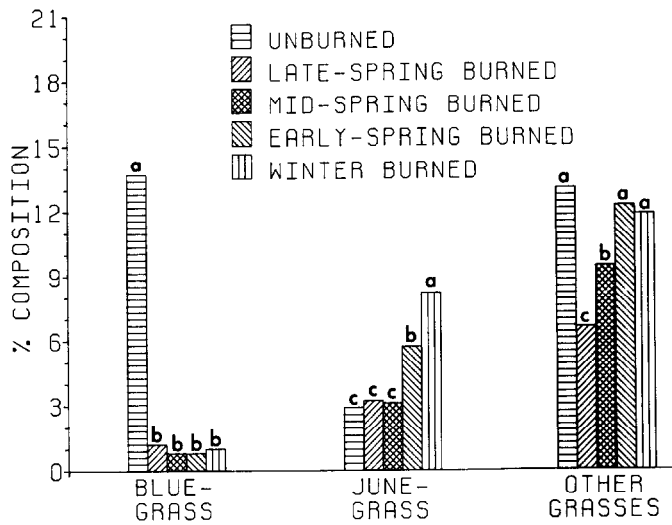


Fig. 6. Average % composition of Kentucky bluegrass, prairie junegrass, and other perennial grasses from 1928-1982 under different burning dates. Means within each block having the same letter are not significantly different ($P > .05$).

pendent variables). Apparently, there was an interaction with mulch thickness because bluegrass began increasing in unburned plots 3 years after annual top growth removal ceased. Bluegrass peaked in 1979 at 34.8% of the total vegetation and then began progressively declining, probably because of dense mulch accumulations. Weaver and Rowland (1952) observed an absence of Kentucky bluegrass in heavily mulched tallgrass prairie undisturbed by fire, grazing, or mowing.

Koeleria pyramidata (Lam.) Beauv.

Prairie junegrass, another cool-season perennial, is not a dominant species in the tallgrass prairie, but was segregated out because it accounted for 20-30% of the total vegetation in the 1920's. Unlike bluegrass, prairie junegrass was adversely affected by protection from fire but was favored by winter and early-spring burning (Fig. 6). That explains the high amount of junegrass present at the beginning of the study when it was common practice to burn in January or February.

Other Perennial Grasses

The remaining aggregate of perennial grass species decreased under late- and mid-spring burning (Fig. 6). Fire at that time favored big bluestem and indiagrass, which displaced other perennial grass species. Predominant recurring species in all plots included sideoats grama [*Bouteloua curtipendula* (Michx.) Torr.], tall dropseed [*Sporobolus asper* (Michx.) Kunth var. *asper*], prairie dropseed [*S. heterolepis* (Gray) Gray] and Scribner's panicum [*Panicum oligosanthos* Schult. var. *scribnerianum* (Nash) Fern.]. Following the 1930's and 1950's drought, sideoats grama significantly increased, particularly in plots burned in winter, early-, and mid-spring. Otherwise, average composition of all the species remained relatively stable throughout the years, indicating their persistence as subdominants in the tallgrass prairie.

Switchgrass (*Panicum virgatum* L.), considered a dominant in many parts of the tallgrass prairie, was not abundant enough for statistical evaluation and was analyzed with the other perennial grasses. Highest amounts of switchgrass were in unburned plots that were mowed and raked annually. However, after mulch removal was stopped, switchgrass stands declined. Under all burning treatments, switchgrass generally maintained a relative composition of less than 1%.

Sedges

Early-spring and winter burning significantly increased the

amount of sedges compared to not burning (Fig. 7). Late-spring burning essentially eliminated sedges, because growing season of the dominant genus, *Carex*, began in late March, making it susceptible to fire injury.

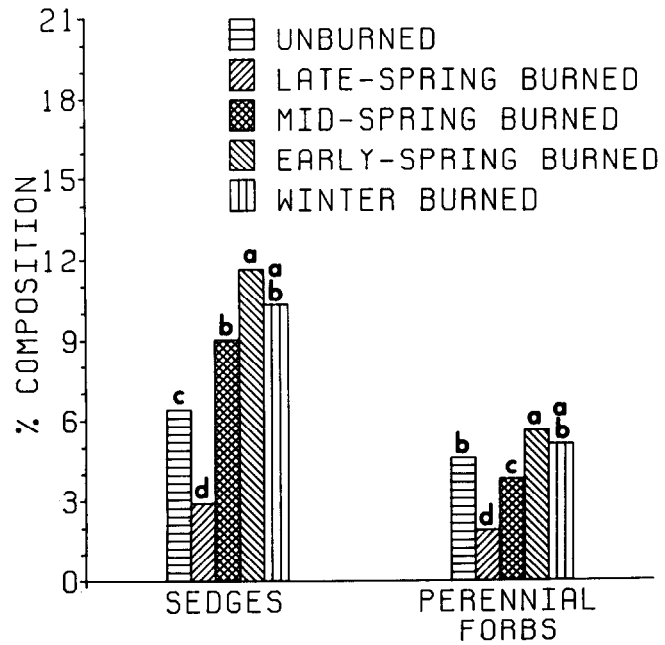


Fig. 7. Average % composition of sedges and perennial forbs from 1928-1982 under different burning dates. Means within each block having the same letter are not significantly different ($P > .05$).

Annual Grasses and Annual Forbs

Annual grasses have been virtually nonexistent in any treatment since inception of the study. Although they never exceeded trace amounts, average percentage of annual grasses was highest in unburned plots and lowest in plots burned in late-spring. Sporadically appearing species included common witchgrass (*Panicum capillare* L.) and poverty dropseed [*Sporobolus vaginiflorus* (Torr.) Wood].

Annual forb populations also were insignificant, accounting for less than 1% of the vegetation in any treatment since 1950. There was no significant difference among treatments ($P > .14$). During the drought of the 1930's, however, a few species, primarily daisy fleabane (*Erigeron strigosus* Muhl.) and rough ffalsepennyroyal (*Hedeoma hispida* Pursh), flourished for a short period in all burned plots. Small amounts of snow-on-the-mountain (*Euphorbia marginata* Pursh) have occurred most years in unburned plots.

Perennial Forbs

Compared to other treatments, late-spring burning significantly reduced perennial forbs while burning in winter and early-spring favored them (Fig. 7). Throughout the years, perennial forb populations have remained relatively stable in each of the respective treatments. Predominant species that have survived repeated burnings include heath aster (*Aster ericoides* L.), showy goldenrod (*Solidago speciosa* Nutt.), and pitcher sage (*Salvia pitcherii* Torr.). In unburned plots, the dominant perennial forbs included Louisiana sagewort (*Artemisia ludoviciana* Nutt. var. *ludoviciana*) and western ragweed (*Ambrosia psilostachya* DC.).

Woody Species

Burning had a diverse effect on woody species, but composition in any treatment rarely exceeded 1% of the total vegetation. Plots burned in winter, early-, and mid-spring contained significantly higher amounts of woody plants than late-spring or unburned plots. That was because leadplant (*Amorpha canescens* Pursh), the

only woody species occurring in burned plots, was favored by fire. Unburned plots, however, support thick stands of dogwood (*Cornus drummondii* Mey.), interspersed with Eastern redcedar (*Juniperus virginiana* L.) and American elm (*Ulmus americana* L.). All trees in the unburned plots are saplings because annual mowing prior to 1968 prevented them from becoming established. In the absence of fire, tree species progressively invade and will eventually dominate tallgrass prairie (Bragg and Hulbert 1976).

Buckbrush (*Symphoricarpos orbiculatus* Moench), a shrub species normally infesting unburned prairie, has not yet invaded the experimental area. Previous mowing of unburned plots in late-spring coincided with the low point in buckbrush carbohydrate reserve cycle and would effectively control it (Aldous 1934).

Total Basal Cover

Total basal cover was highest in plots burned in mid- and early-spring (Fig. 8). Burning at that time favors little bluestem, a bunchgrass, which would account for the increased basal coverage.

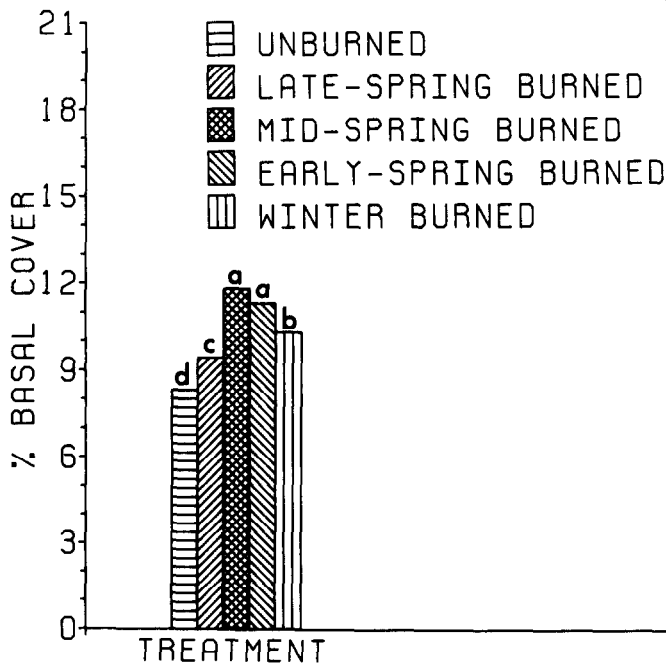


Fig. 8. Average % of total basal cover from 1950-1982 under different burning dates. Means having the same letter are not significantly different ($P > .05$).

Unburned plots had significantly lower basal cover than any other treatment, particularly after mowing stopped, indicating that accumulated mulch reduced plant basal cover. Total basal cover was lowest in 1956 following a prolonged drought, but there were no significant differences among burning treatments. There was also no year by treatment interaction, indicating that despite opinions to the contrary, burning tallgrass prairie in dry years does not adversely affect total basal cover compared to not burning.

Conclusions

Time of burning has a profound effect on the vegetational response to fire. The closer time of burning is to initiation of spring

growth, the more favorable the response. Our data indicate that only 3 weeks difference in time of spring burning has a dramatic long-term influence on the vegetation. Yet most studies have not addressed the importance of when a burn occurred. Reported discrepancies in the effects of fire on herbage yield and species composition in tallgrass vegetation likely are due to differences in time of burning.

Differential response of plant species to time of burning allows for manipulation of vegetation. In Kansas tallgrass prairie, annual burning in late-spring will maximize yield and composition of big bluestem and indiangrass. Burning earlier in spring will reduce herbage yields, but will increase species diversity and benefit perennial forbs. Unburned, prairie deteriorates in both grass production and species composition.

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Burning of Northern Mixed Prairie During Drought

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Abstract

Standing crop of current year's growth and response of key management species were evaluated following burning in mid-May (before emergence of warm-season grasses) and mid-June (after emergence of warm-season grasses). The study was conducted during 2 dry years in a mesic Mixed Prairie in South Dakota. Cool-season precipitation was 33% below average in both years of the study, while warm-season precipitation was only slightly below average both years. Standing crop of current year's growth was increased by burning on overflow range sites, but not on silty range sites. Big bluestem (*Andropogon gerardi*) standing crop was greatest with mid-May burning. Kentucky bluegrass (*Poa pratensis*) standing crop and leaf length were reduced with burning on both dates. Leaf length, basal area and number of inflorescences of native cool-season grasses were also reduced. Mid-May burning in drought years may be recommended for the reduction of Kentucky bluegrass. However, reductions in production of native cool-season vegetation can be expected on silty range sites. In contrast, mid-June burning in dry years is not recommended.

Burning has been widely recommended on the subhumid and humid grasslands of the Great Plains and the Midwestern prairie peninsula for manipulating botanical composition, increasing herbage production, and providing more nutritious forage for livestock. The True Prairie in the Flint Hills of eastern Kansas (McMurphy and Anderson 1965, Anderson et al. 1970) and the humid grasslands of the Midwest (Curtis and Partch 1948, Ehrenreich 1959, Kucera and Ehrenreich 1962, and Ehrenreich and Aikman 1963) can be effectively managed with fire. In the Northern Great Plains, fires have resulted in varying vegetation responses.

In the semiarid Mixed Prairie of the Northern Great Plains, fire has resulted in critical reductions in litter (Dix 1960) and decreased herbage yields (Gartner et al. 1978), although effects appear to be dependent on season of the burn and on precipitation. In the mesic (dry subhumid) Mixed Prairie (Kirsch and Kruse 1972) and the True Prairie (Kaiser et al. 1979), fire may benefit the warm-season tall grasses and result in a reduction of undesirable cool-season species. Before fire can be judiciously prescribed as a management tool in the mesic Mixed Prairie, data must be available for burning under a variety of environmental conditions. Series of dry years are common in the Northern Great Plains (Schumacher 1974) and this may limit the application of prescribed burning in these areas during extended drought periods.

Studies reviewed by Daubenmire (1968) as well as studies in the Kansas Flint Hills (Anderson et al. 1970, Owensby and Smith 1979) indicate that spring burning reduces Kentucky bluegrass

(*Poa pratensis*).¹ Smith and Owensby (1972) concluded that actively growing Kentucky bluegrass is more susceptible to injury than the warm-season native grasses that are dormant or just beginning to grow when spring burned. In this study, burning was timed during the latter part of the active growth stage of Kentucky bluegrass, both before and after the emergence of warm-season native grasses. Comparisons were made for 2 burning dates on 2 range sites during a period of below-average precipitation in the prairie pothole region of the mesic Mixed Prairie.

Methods and Materials

The study was conducted on the Samuel H. Ordway Memorial Prairie in north-central South Dakota. The study area is part of the prairie pothole region of the northern Mixed Prairie (Kuchler 1964). Average annual precipitation from 1940 to 1970 at Leola, S. Dak., about 10 km east of the study area, was 50.2 cm.

Soils of the study area are Williams loams (silty range site) and Bowbells loams (overflow range site). The Williams soils are fine-loamy, mixed Typic Argiborolls. The Bowbells soils are fine-loamy, mixed Pachic Argiborolls. Silty range sites in excellent range condition are dominated by western wheatgrass (*Agropyron smithii*), needleandthread (*Stipa comata*), and green needlegrass (*Stipa viridula*). Overflow range sites in excellent condition are dominated by big bluestem (*Andropogon gerardi*). Both range sites become progressively dominated by Kentucky bluegrass as range condition declines. At the time the study was initiated, Kentucky bluegrass was a major component on both the silty and overflow range sites, partly in response to repeated midsummer haying.

Treatment plots (25 × 50 m) were established in 1980 on native range neither grazed nor hayed for 3 years. A randomized block design with 3 replications was used in the experiment. Treatments consisted of 2 1980 burning dates and a control nested within 2 range sites (silty and overflow). The early burning date, applied before emergence of warm-season grasses, and the late burning date, applied after warm-season grasses had emerged to a height of 5 to 10 cm, were in mid-May and mid-June, respectively. In a normal year these growth stages would be expected to occur earlier in the season, but were later in 1980 because of late frosts and below normal precipitation. Plots were burned with a headfire after a base control line was established with a backfire. Weather conditions during the burns were monitored and appear in Table 1.

¹Common and scientific names after Beetle (1970).

Table 1. Weather conditions for May and June 1980 burning treatments at Ordway Prairie.

Burn dates	Wind speed (km/h)	Air temperature (°C)	Relative humidity (%)
May 13-16	3-13	4-19	23-45
June 16	0-24	20-23	42-66

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Table 2. Least squares means of leaf length, number of inflorescences and basal area of dominant species at Ordway Prairie, as estimated on August 8-11, 1980.

Site	Species	Plant characteristic	1980 Burning Date			
			May 15 ¹	June 16	Control	
Silty	<i>Stipa viridula</i>	Leaf length (cm)	24.7 b ²	23.3 b	41.1 a	
		Inflorescences/m ²	2.8 b	0 b	16.8 a	
		Basal area (cm ²)	10.3 b	6.9 b	20.8 a	
Overflow	<i>Agropyron smithii</i>	Leaf length (cm)	11.7 b	9.3 c	13.5 a	
		<i>Poa pratensis</i>	Leaf length (cm)	13.7 b	10.3 b	30.9 a
			<i>Andropogon gerardi</i>	Leaf length (cm)	21.3 b	16.8 b
	Inflorescences/m ²	132.4 a		95.2 a	2.0 b	
		<i>Poa pratensis</i>	Leaf length (cm)	17.7 b	13.5 b	38.7 a

¹May burns were applied May 13, 14, and 16.

²Means in the same row followed by different letters are significantly different.

Ten, 0.25 m² circular quadrats on each treatment plot were randomly located and herbage was clipped to ground level between July 28 and August 1, 1980. Three 1.0 m² quadrats per treatment plot were clipped between July 27 and August 3 in 1981. Standing crop of current year's growth of hand separated species and vegetation classes was bagged and allowed to air dry before weighing. Species and vegetation classes were Kentucky bluegrass, big bluestem, needlegrasses (*Stipa* spp.), western wheatgrass, sedges (*Carex* spp.), other grasses, and forbs. Standing litter and mulch were also included in the harvest data in 1981. Fire effects on green needlegrass, western wheatgrass, Kentucky bluegrass (cool-season grasses) and big bluestem (a warm-season grass) were also evaluated by randomly selecting 2 plants in 5 randomly located quadrats (0.25 m²) within each treatment plot. Leaf length was measured as the average of the longest leaf of 2 plants of each species. Basal area (length × width) of 2 green needlegrass plants was measured and the number of seedheads per quadrat was counted for green needlegrass and big bluestem. Analysis of variance was performed on these measurements for species and vegetation class components by the General Linear Model Procedure in the Statistical Analysis System (Barr et al. 1979). Treatment means were separated using Tukey's w-procedure at the 0.05 level of probability (Steel and Torrie 1960).

Results and Discussion

Precipitation for the 1980 vegetation year (September 1979–August 1980) was 26% below average and 20% below average in 1981 (Fig. 1). A reduction in cool-season (September–May) precipitation may be more important than a reduction in annual precipi-

tation to the production of cool-season species. In both years cool-season precipitation was 33% below average, whereas warm-season (June–August) precipitation was only 17 and 6% below average for 1980 and 1981, respectively.

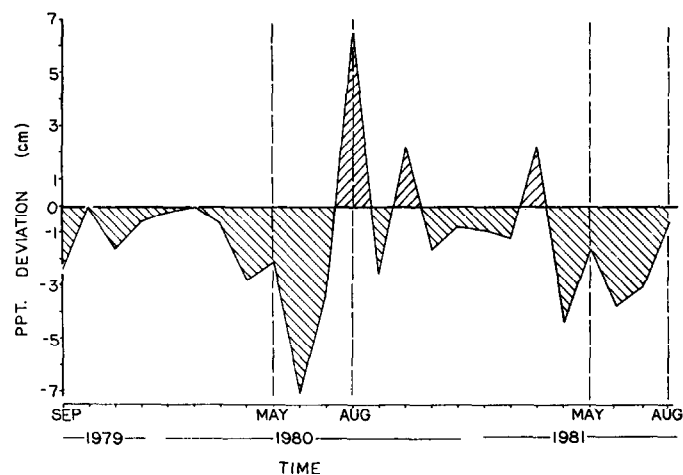


Fig. 1. Deviation (cm) in precipitation from 30-year monthly average, September 1979 to August 1981, Leola, S. Dak. Vertical hatch lines separate months of cool-season (September through May) and warm-season (June through August) precipitation.

Leaf length of cool-season species and the number of inflorescences and basal area of green needlegrass were reduced by burning

Table 3. Least squares means of leaf length, number of inflorescences and basal area of dominant species at Ordway Prairie, as estimated on August 10-11, 1981.

Site	Species	Plant characteristic	1980 Burning Date			
			May 15 ¹	June 16	Control	
Silty	<i>Stipa viridula</i>	Leaf length (cm)	38.9 b ²	37.3 b	57.5 a	
		Inflorescences/m ²	32.9 a	34.0 a	19.7 b	
		Basal area (cm ²)	12.3 a	7.8 b	6.5 b	
Overflow	<i>Agropyron smithii</i>	Leaf length (cm)	11.5 b	12.1 b	15.6 a	
		<i>Poa pratensis</i>	Leaf length (cm)	23.1 b	24.3 b	33.0 a
			<i>Andropogon gerardi</i>	Leaf length (cm)	45.2 a	37.0 b
	Inflorescences/m ²	69.8 a		53.8 a	15.1 b	
		<i>Poa pratensis</i>	Leaf length (cm)	43.7 c	49.2 b	53.0 a

¹May burns were applied May 13, 14, and 16.

²Means in the same row followed by different letters are significantly different.

(Tables 2 and 3). These effects were more pronounced on the June burn than on the May burn. Leaf length of big bluestem on overflow sites was reduced by burning although the number of inflorescences increased similarly to that reported in more humid grasslands (Kucera and Ehrenreich 1962). The burning treatment effects on most species were still evident the year following the burning treatments, especially on the June burned plots.

Standing crop of current year's growth of big bluestem on overflow sites was greater in 1980 and 1981 on plots burned in May but not on plots burned in June (Tables 4 and 5). In 1980, needlegrasses produced less growth on burned than on unburned plots on both sites. In 1981, however, needlegrasses produced as much growth on burned plots as on control plots. Kentucky bluegrass standing crop was decreased by burning on both sites, but the effect was greater and was still evident in the second year of the study on silty range sites burned in May.

Burning did not reduce standing crop of other species and vegetation classes. Only in the second year following burning was total current year's growth on overflow sites higher on burned plots than on control plots. However, burned plots on silty sites had lower standing crops than control plots in both years. The June burn plots on silty sites had less than 30% of the total standing crop of control plots in 1980. Mulch and litter levels were generally reduced by burning.

A portion of observed decreases in standing crops of cool-season species in the burned treatments may be attributed to consumption of spring growth, especially of Kentucky bluegrass, by the fires. Peak standing crops of green biomass on 2 communities in 1977 at Ordway Prairie were measured between June 16 and June 30, a year in which precipitation was 30% above average (Ode et al. 1980). Therefore, burning in either mid-May or mid-June of 1977 would have consumed substantial amounts of the current year's growth. Burning in mid-May or mid-June in years of below average cool-season precipitation would also be expected to result in a direct reduction of current year's growth.

In the True Prairie and prairie peninsula, herbage yields can generally be expected to increase or remain the same after spring burning (Curtis and Partch 1948, Kucera and Ehrenreich 1962,

Anderson et al. 1970). However, in xeric portions of the northern Mixed Prairie, herbage yields have generally been reported to decline following spring burning (Clarke et al. 1943, Dix 1960, Coupland 1973), although herbage yield increases have been reported with burning under favorable soil water conditions (White and Currie 1983). In considering the usefulness of fire in the central grasslands of North America, Launchbaugh (1973) concluded that burning will result in increased yields when mulch accumulations are excessive and reduced yields when mulch is at lower levels. Under drought stress, even with excessive mulch accumulations, herbage yields were not increased by burning in our study. Considering that our treatments were applied at later calendar dates than are reported elsewhere in the literature it appears that in drought years mesic northern Mixed Prairie responds to spring burning more like xeric Mixed Prairie than True Prairie. However, the response is site dependent in that the reduction in herbage yield will be greater and of longer duration on the xeric sites than on mesic sites. Even so, these grasslands were capable of making a substantial recovery in the second year following a severe fire event. This is indicative of a fire tolerant system.

Kentucky bluegrass, the dominant introduced species, and green needlegrass, a desirable cool-season native species, were harmed with spring burning in a drought year. Green needlegrass, with accumulations of mulch and litter, may have been negatively impacted by fire in much the same manner as needleandthread (Wright 1971). Therefore, desirable decreases of Kentucky bluegrass may be offset by undesirable decreases in green needlegrass. We observed a number of green needlegrass plants on the silty sites that were killed by the fires. However, individual green needlegrass plants that survived the burn appeared to gain additional vigor the year after burning and were producing as much or more total growth as those on control plots. The authors observed that most desirable species, including green needlegrass, were in a depressed state of vigor prior to burning probably as a result of excessive mulch and litter accumulations. On silty sites the usual first year benefits of burning to remove excessive mulch and litter were probably offset by accentuating the existing drought.

Table 4. Least squares means of standing crops (air dry weight) of current year's growth (g/m²) (July 28–August 5, 1980) on plots burned in 1980 on two range sites.

Species	Site	1980 Burning Date		
		May 15 ¹	June 16	Control
<i>Poa pratensis</i>	Silty	20.2 b ²	10.8 b	94.4 a
	Overflow	7.2 b	7.8 b	77.2 a
<i>Andropogon gerardi</i>	Silty	0 a	0 a	0 a
	Overflow	128.8 a	71.4 ab	23.0 b
<i>Stipa</i> spp.	Silty	15.0 b	10.5 b	35.7 a
	Overflow	5.3 b	6.5 b	16.8 a
<i>Agropyron smithii</i>	Silty	8.0 a	6.0 ab	1.5 b
	Overflow	12.0 a	6.0 b	8.8 ab
<i>Carex</i> spp.	Silty	13.3 a	4.3 a	13.9 a
	Overflow	14.9 a	4.4 a	26.9 a
Other grasses	Silty	5.7 a	0.2 a	0.6 a
	Overflow	5.4 a	1.4 a	0.2 a
Forbs	Silty	44.1 a	10.5 b	6.0 b
	Overflow	55.5 a	25.9 b	20.8 b
Total grasses and grasslikes	Silty	62.1 b	31.8 b	146.1 a
	Overflow	174.3 a	98.6 b	152.9 ab
Total current year's growth	Silty	106.2 ab	42.4 b	152.0 a
	Overflow	230.9 a	124.5 b	173.7 ab

¹May burns were applied on May 13, 14, and 16.

²Means in the same row followed by different letters are significantly different.

Table 5. Least squares means of standing crops (air dry weight) of current year's growth standing litter and mulch (g/m²) (July 27–August 3, 1980) on plots burned in 1980 on two range sites.

Species	Site	1980 Burning Date		
		May 15 ¹	June 16	Control
<i>Poa pratensis</i>	Silty	62.5 c ²	100.9 b	135.9 a
	Overflow	53.4 b	80.1 a	89.4 a
<i>Andropogon gerardi</i>	Silty	0	0	0
	Overflow	313.3 a	279.7 ab	232.8 b
<i>Stipa</i> spp.	Silty	43.4 a	51.7 a	63.8 a
	Overflow	32.6 a	23.5 a	25.2 a
<i>Agropyron smithii</i>	Silty	17.0 b	39.0 a	3.6 c
	Overflow	18.2 a	9.6 a	10.1 a
<i>Carex</i> spp.	Silty	38.4 a	26.5 b	13.7 c
	Overflow	31.0 a	12.4 b	5.0 b
Other grasses	Silty	24.2 a	8.5 b	4.5 b
	Overflow	9.4 ab	15.4 a	4.0 b
Forbs	Silty	58.1 a	7.6 b	18.7 b
	Overflow	30.9 a	33.1 a	20.4 a
Total grasses and grasslikes	Silty	185.6 a	226.6 a	221.6 a
	Overflow	457.7 a	420.7 ab	366.5 b
Total current year's growth	Silty	244.3 a	233.9 a	240.2 a
	Overflow	488.6 a	454.3 a	386.9 b
Standing litter	Silty	11.0 b	3.0 b	230.6 a
	Overflow	90.0 b	57.3 b	476.2 a
Mulch	Silty	22.7 b	21.6 b	182.7 a
	Overflow	124.4 ab	60.8 b	193.7 a

May burns were applied on May 13, 14, and 16.

²Means in the same row followed by different letters are significantly different.

Conclusions

Burning in a dry year in a mesic northern Mixed Prairie provided some reduction of Kentucky bluegrass on both silty and overflow range sites and an increase in current year's growth on overflow sites. However, burning did not increase standing crop on silty sites and resulted in a period of reduced vigor of green needlegrass. If a primary objective of management is to control Kentucky bluegrass, mid-May burning (immediately prior to warm-season tall grass emergence) in dry years may be recommended. However, if increasing forage production is a major management objective on pastures where there is a mixture of both xeric and mesic sites, mid-May burning is not recommended in years of below average cool-season precipitation. Burning in mid-June (after emergence of warm-season grasses) in years of below average precipitation is not recommended.

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Fire Effects on Nitrogen Mineralization and Fixation in Mountain Shrub and Grassland Communities

N. THOMPSON HOBBS AND DAVID S. SCHIMEL

Abstract

Prescribed burns were carried out in mountain shrub and grassland communities in the montane zone of the Rocky Mountains in Colorado. Nitrogen mineralization rate was increased 1 year after the burn in both communities. This increase persisted for 1 year in the grassland and for 2 years in the shrub community. Total mineralized soil-N was greater in the burned than unburned areas of both communities during the first growing season after fire. An acetylene reduction assay for nitrogenase activity showed depressed activity 1 year after the burn. We suggest that elevated inorganic N levels caused the reduction in nitrogenase activity.

The influence of fire on the nitrogen economy of ecosystems has been widely studied. Fire acts as a potent mineralizing agent, causing the rapid transformation of organic nitrogen to inorganic forms (Christensen 1973, St. John and Rundel 1976, Dunn et al. 1979). Fire results in alterations of the abiotic environment, which in turn lead to changes in biotic processes (reviewed by Viro 1974, Raison 1979). Elevated soil temperatures that result when the plant canopy is removed and the release of cations in ash improve conditions for microbial growth in the soil environment (Christensen and Muller 1975, Tiwari and Bharat 1977, Raison and McGarity 1980). It follows that nitrogen transformations mediated by microbial populations should be similarly altered by burning.

Despite the scrutiny that ecosystem effects of fire have received, few studies have examined the influence of fire on biotic transformations of nitrogen. Dunn et al. (1979) reported that nitrogen mineralization was stimulated following fire, but Schimel (1982) found that repeated burning reduced potentially mineralizable N. Although Jorgensen and Wells (1971), Youngberg and Wollum (1976), and Grove et al. (1980) observed that fire increased rates of nitrogen fixation in forest ecosystems, no work to date has examined these effects in mountain grassland or shrub communities. Prescribed burning is widely used in these communities to improve range conditions for wild and domestic animals; however, the ecosystem effects of such application are poorly understood. Here, we report experiments on the influence of fire on nitrogen mineralization, nitrogenase activity, and soil inorganic N in mountain shrub and grassland communities during 2 years following burning.

Materials and Methods

We conducted our studies in a south-facing mountain valley at 2,500 m in elevation 2 km NE of the town of Rustic, Colo. Vegetation on the study area is typical of the upper-montane climax region (Marr 1967); dry meadows, dominated by *Agropyron spicatum* (bluebunch wheatgrass) and *Stipa comata* (needle and thread),

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spread across the valley floor and merge with dense stands of shrubs, predominantly *Artemisia tridentata* (big sagebrush) and *Purshia tridentata* (antelope bitterbrush), on steeper slopes. Soils are composed of decomposed granite and mica-schists and are classified as Dystric Eutrochrepts. Organic matter content of soils in the surface 5 cm averaged 8% in mountain shrub and 11% in grassland and was unaffected by burn treatments.

We chose 3 pairs of plots in each plant community, the members of each pair being similar in slope, aspect, vegetative cover, and soil moisture. Plots were 0.3 ha in size in grassland and 1.0 ha in mountain shrub. Treatment was randomly assigned to 1 member of each pair of plots.

Treatment plots were burned on September 29 and 30, 1979. Treatment was not uniform across all plots because of differences among plots in fuel loadings, time of ignition, and thus fire intensity. Energy release by fire measured by water can analogs (Beaufait 1966) was substantially greater in mountain shrub ($\bar{x} = 32$ kcal, SE = 8 kcal) than in grassland ($\bar{x} = 8$ kcal, SE = 0.3 kcal). Plots in mountain shrub burned more completely and intensely than plots in grassland. Pretreatment fuel loads and detailed fire behavior measurements have been described previously (Hobbs and Spewart 1984).

During the following 2 growing seasons, we estimated soil concentrations of $\text{NO}_2^- + \text{NO}_3^-$ and NH_4^+ and the rates of nitrogen mineralization and fixation (nitrogenase activity) on burned and unburned plots. Mineralization was estimated by the buried bag technique of Eno (1969). On June 4, 1980 and 1981, 20 soil cores (5 cm \times 5 cm) were taken at random locations on each plot. Each core was split longitudinally and sieved through a 2-mm mesh screen to remove large roots and rocks. Half of each core was placed in a polyethylene bag and replaced in the ground at depth similar to the original core and covered with 1 cm litter and/or surface soil. The remaining portion was immediately taken to the laboratory for analysis.

Within 10 hours of taking samples, we extracted a 3-g subsample of each core with 2 M KCl containing 5 ppm phenyl-mecuric acetate added to inhibit microbial activity. Moisture content of a separate 5-g subsample was determined gravimetrically; organic matter was determined by loss on ignition. Ammonium content was determined by a colorimetric ammonium reaction with salicylate nitroprusside at pH 13; $\text{NO}_3^- + \text{NO}_2^-$ was determined by a cadmium reduction using a continuously copperized reduction column. Six weeks later, we retrieved the buried polyethylene bags and treated those samples the same as described for the initial samples. Net mineralization was estimated as the increment in total inorganic nitrogen (NH_4^+ , NO_2^- , + NO_3^-) between 2 sample dates.

Potential heterotrophic nitrogenase activity was estimated with the acetylene reduction procedure as described by Hersman and Klein (1979). Thirty 5-cm soil cores were taken from random locations on each plot on June 10, 1980, and June 12, 1981, and analyzed within 2 days of sampling. For each plot, cores were composited into 3 samples of 10 cores each, placed in plastic bags, and immediately cooled to approximately 5° C in a portable ice

chest. Upon returning it to the laboratory, each composite was sieved through a 2-mm screen and mixed. Twenty subsamples were selected from different locations within each composite and were mixed to form a 10-g sample for analysis; these samples were stored in plastic bags at 10° C. Immediately prior to analysis, samples were wetted to field capacity with distilled water. We expressed nitrogenase activity as p moles ethylene produced.

Responses were analyzed with an analysis of variance for a split plot design with plant community type forming the whole plot, and burn vs. control contributing the split plot. Differences among individual means were established with Tukey's Q simultaneous comparisons at $P = 0.10$. Years and replicates were considered random effects.

Results and Discussion

We observed that fire resulted in significant ($P < 0.10$) increases in NH_4^+ and $\text{NO}_2^- + \text{NO}_3^-$ contents of grassland and mountain shrub soils 10 months after the burn (Fig. 1). This effect, however,

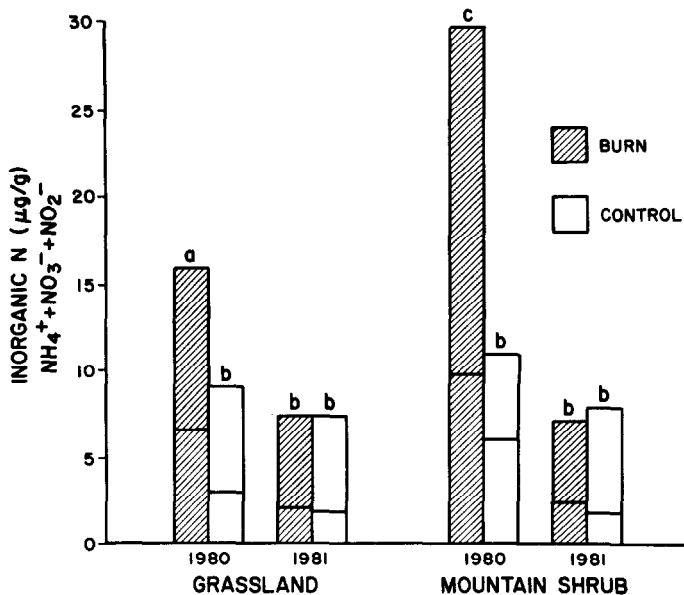


Fig. 1. Soil concentrations of inorganic nitrogen ($\text{NH}_4^+ + \text{NO}_2^- + \text{NO}_3^-$) in mountain shrub and grassland communities on June 4, one and two years after prescribed burning. Different letters indicate differences in means at $P = 0.10$. Upper portion of bars shows contribution of NH_4^+ , lower portion shows $\text{NO}_2^- + \text{NO}_3^-$.

disappeared in the second year (year \times treatment interaction $P = 0.05$); soil mineral N values were significantly higher on burns during Year 1, but returned to control levels during Year 2. We attribute this return to uptake of N by the recovery plant community; above-ground plant biomass on burned plots was almost 3 times greater during Year 2 compared with Year 1 (Hobbs unpublished data). Reduced levels of inorganic N may have been due to increased microbial uptake, denitrification, or leaching. Surface soils were probably temporarily sterilized. The winter following the burn was exceptionally severe; microbial populations had little opportunity to recover prior to the first sample.

Effects of fire on soil mineral N also depended on plant community (community \times treatment interaction $P = 0.12$). The larger increases in NH_4^+ in mountain shrub relative to grassland likely resulted from the more even nature of the burn. The patchy distribution of burned areas within grasslands resulted in some treatment plots being similar to controls while in the mountain shrub practically all the area was burned.

Net mineralization of soil N was significantly greater ($P = 0.10$) on burned grassland plots during Year 1, and on burned mountain shrub plots during both years (Fig. 2). Dunn et al. (1979) and Sharrow and Wright (1977) also found that rates of nitrogen

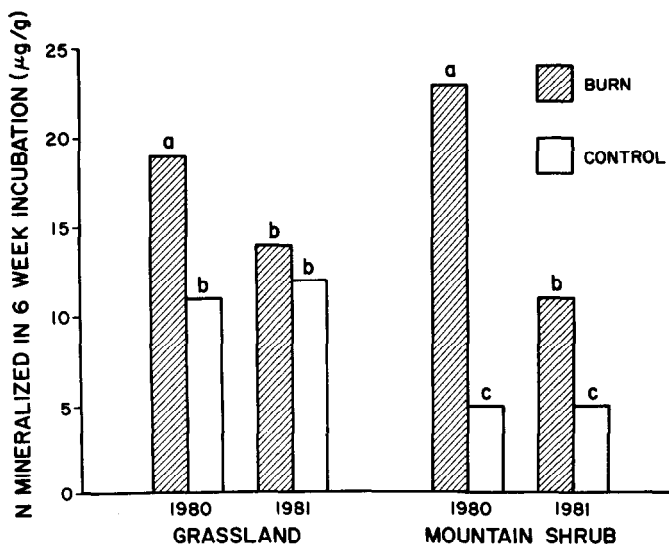


Fig. 2. Net mineralization rate in mountain shrub and grassland communities during the 6-week growing season, one and two years after treatment. Different letters indicate differences in mean values at $P = 0.10$.

mineralization were increased by burning. However, although a single fire may increase amount of N mineralized, the cumulative result of several fires inhibit it. Schimel (1982) and Biederbeck et al. (1980) suggested frequent fires led to decreased mineralization as a result of reductions in pools of readily decomposable C and N and resultant decreases in microbial biomass.

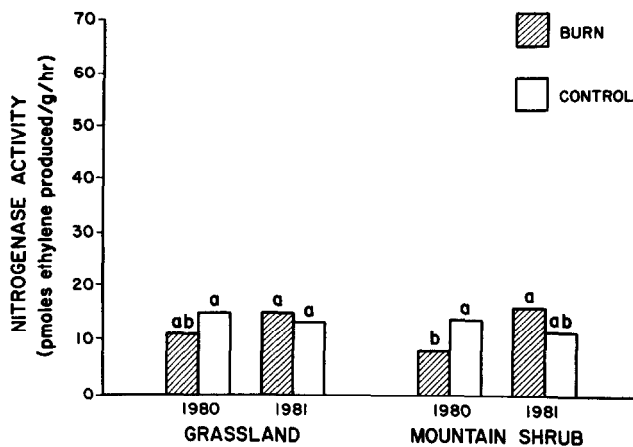


Fig. 3. Nitrogenase activity (acetylene reduction) in mountain shrub and grassland communities, one and two years after treatment. Different letters indicate differences in means at $P = 0.10$.

The magnitude of fire effects on net mineralization depended on year (year \times treatment interaction $P = 0.11$) and vegetation type (community \times treatment interaction $P = 0.005$); treatment effects were greater in mountain shrub than grassland, and declined in magnitude during Year 2. Main effects and interactions can be explained by changes in the soil environment. Soils in burned grasslands are typically 3–16° C warmer than similar unburned sites (Weaver and Rowland 1952, Kucera and Ehrenreich 1962, Scotter 1963, Old 1969, Lloyd 1972, Peet et al. 1975). This increase results primarily from absorption of solar radiation on blackened

soils unshaded by litter and plants (Woodmansee and Wallach 1981). Nitrogen mineralization rate increases with increasing temperature (Stanford et al. 1973, Campbell et al. 1981). The effect of increased soil temperatures on N mineralization may have resulted in the elevated mineralization rates we observed. Immobilization of N into remaining litter may also have been a factor. Both of these explanations are consistent with the temporal and spatial interactions in treatment effects. Plant biomass on the burned plots of grassland was equal to the control by June of the second year; the difference in soil temperatures and the consequent divergence in N mineralization disappeared by Year 2 in that community. In contrast, total aboveground biomass in the mountain shrub community had not recovered to control levels by Year 2 and large areas of bare soil remained. As a result, we surmise that elevated soil temperatures would have persisted into Year 2. A similar pattern existed with respect to the immobilization potential of remaining litter. The mountain shrub community was burned intensely enough to remove all litter, while in the grassland some litter remained. Thus, the prolongation of increased N mineralization in the mountain shrub community is attributable to the greater intensity of the burn which occurred there, the slower recovery of the plant canopy, and the complete removal of the litter layer. The effect of fire on N mineralization in grassland was more brief because the fire was more heterogeneous and less intense. As a result, the recovery of plant canopy was more rapid and some litter remained.

Potential nitrogenase activity was lower on burned plots than controls during Year 1; however, this effect was significant only in mountain shrub ($P = 0.10$) (Fig. 4). Magnitude of treatment effects

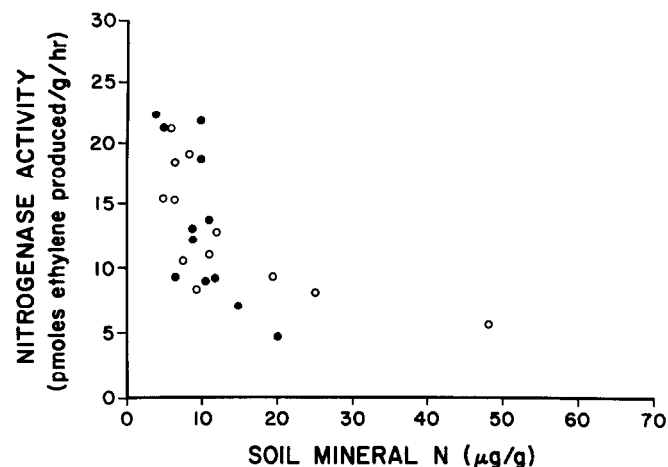


Fig. 4. Relationship between potential nitrogenase activity (acetylene reduction) and soil mineral N in mountain shrub (open circles) and grassland communities (closed circles). Equation is given by $Y = 39.6X^{-.53}$, $P = 0.0004$, $R^2 = 0.42$.

depended on year (year \times treatment interaction $P = 0.07$) but not on plant community (community \times treatment interaction $P = 0.74$). The reduction in nitrogenase activity may have resulted from sterilizing effects of fire. However, the inhibition of nitrogenase activity on burned plots during Year 1 and the return to control levels the following year appeared to be related to the concentration of mineral N in soils. Mineral N (NH_4^+ , $\text{NO}_3^- + \text{NO}_2^-$) was increased in soils of burned plots during Year 1 but not in Year 2. The reduction in potential nitrogenase activity was greatest in the mountain shrub community and the increase in soil inorganic N was also greatest there. Soil mineral N levels accounted for 42% of the variation in potential nitrogenase activity (Fig. 4); free-living and symbiotic nitrogen fixers decrease fixation when mineral N is elevated (Oghoghorie and Pate 1971, Manhart and Wong 1979, Wong 1980).

Our observation of a curvilinear relationship between nitrogenase activity and soil mineral N suggests that fixation responds in a threshold manner with respect to mineral N and that nitrogenase

activity is reduced drastically at soil mineral N concentrations $>10\text{--}20 \mu\text{g/g}$ dry soil. These findings are at odds with reports that fire increases rates of nitrogen fixation (Jorgensen and Wells 1971, Youngberg and Wollum 1976, Grove et al. 1980). However, we cannot exclude the possibility that N fixation may become significant after 2 or more years, that inorganic N would not have been elevated had the burn been followed by a more normal winter, or that previous studies involved soils with lower levels of mineral N. A better understanding of the controls of N-fixing organisms is required to better predict post-fire responses.

Conclusions

Fire caused increased rates of N mineralization for 1 year in a mountain grassland, and for 2 years in a mountain shrub community. The rapid recovery of the vegetation in the grassland caused rapid convergence of burned to unburned conditions. The shrub community burned more evenly and more severely, and so required longer to return to control conditions. We attribute most of the increase in N mineralization to increased soil temperatures.

Nitrogenase activity was depressed by fire 1 year after the burn in the mountain shrub community. This may have resulted from partial sterilization of the soil. In addition, soil inorganic N levels were elevated in burn relative to control plots and this probably contributed to the depression in nitrogenase activity.

The effect of fire was to increase the rate of N mineralization, and presumably, the availability of N to vegetation. Nitrogen losses doubtlessly occurred from the burned vegetation, and these may not have been rapidly compensated for by N-fixation. Consequently, we recommend that prescribed burns for range improvement in montane communities not be repeated frequently on the same sites until fire effects on N budgets in these communities are better understood.

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Shoot Growth and Development of Alamo Switchgrass as Influenced by Mowing and Fertilization

M.R. HAFERKAMP AND T.D. COPELAND

Abstract

The response of shoot development and forage yield of a 2-year old 'Alamo' switchgrass stand to mowing and fertilization was evaluated to provide information needed for effective management of this variety. Mowing to a 20-cm stubble height in mid-spring removed only a few apical meristems and had little impact on shoot development. Late spring and early summer mowing were done when apical meristems of primary compound shoots were elevated to near the 20-cm cutting height in May and over 20 cm in June. Secondary nonrooted shoot and aerial shoot numbers were increased and plant vigor, measured by spring growth in 1980, was decreased slightly the following spring. Mowing in mid-summer removed apical meristems from essentially all primary compound shoots and many secondary compound shoots. Regrowth was slight during the remainder of the summer, but the number of secondary and tertiary nonrooted shoots and aerial shoots increased. The number of proaxis buds decreased, and plant vigor was severely decreased the following spring. Mowing twice including early fall, removed apical meristems from secondary compound shoots and some primary and secondary nonrooted shoots. Numbers of secondary, tertiary, and quarternary nonrooted shoots increased, but proaxis bud numbers were reduced. Plant vigor was very low the following spring, possibly due to exposure of mowed plants to cold winter temperatures. Fertilization increased the rate of development of compound and nonrooted shoots, the number of secondary and compound shoots in spring, the number of proaxis buds in fall and the weight of primary and secondary compound shoots. Fertilized stands mowed during summer and early fall were more productive than all other mowed stands. Fertilized plants mowed in mid-summer were vigorous and productive the following spring. However, fertilization did not overcome the loss of vigor caused by fall mowing.

Alamo switchgrass (*Panicum virgatum* L.) was released by the United States Department of Agriculture, Soil Conservation Service and the Texas Agricultural Experiment Station in 1979 as a commercial variety for use in pasture and range seedings (Anonymous 1979). The variety has proven superior to other switchgrass varieties for forage production in central and southern Texas. However, little information is available concerning the effects of clipping and fertilization on forage yield and shoot development of Alamo switchgrass.

Defoliation of grasses may increase tillering and reduce the high

proportion of senescent leaves and shoots (Hyder 1974). Frequent defoliation, or clipping to a short stubble, however, can cause stand reduction and reduce forage production with many switchgrass varieties (Branson 1953, Neiland and Curtis 1956, Dwyer et al. 1963, Dwyer and Elder 1964, Beaty and Powell 1976).

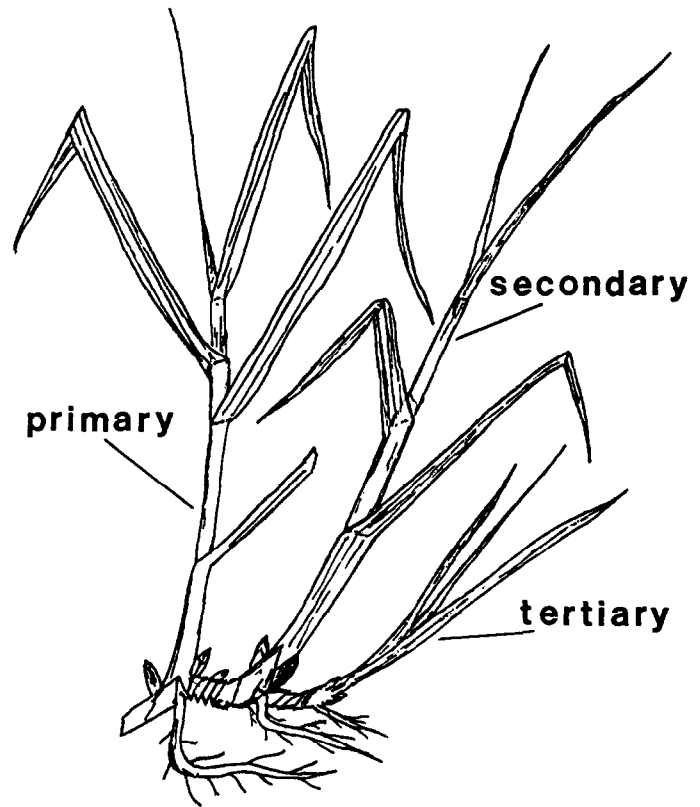


Fig. 1. Example of a shoot system of Alamo switchgrass with primary, secondary, and tertiary compound shoots.

Switchgrass elevates shoot apices early and produces a high ratio of reproductive to vegetative shoots, making it sensitive to clipping (Branson 1953). Switchgrass produces one crop of tillers in the spring and early removal can seriously reduce herbage production (Hyder 1974). According to Beaty and Powell (1976), switchgrass will tolerate a single defoliation almost anytime with no year to year reduction in vegetative vigor; however, 2 or more clippings per year reduce plant and crown survival. Dwyer and Elder (1964) found that moderate grazing of switchgrass reduced animal gains in August and September. Reduction in gain occurred because plants were producing inflorescences and leaves

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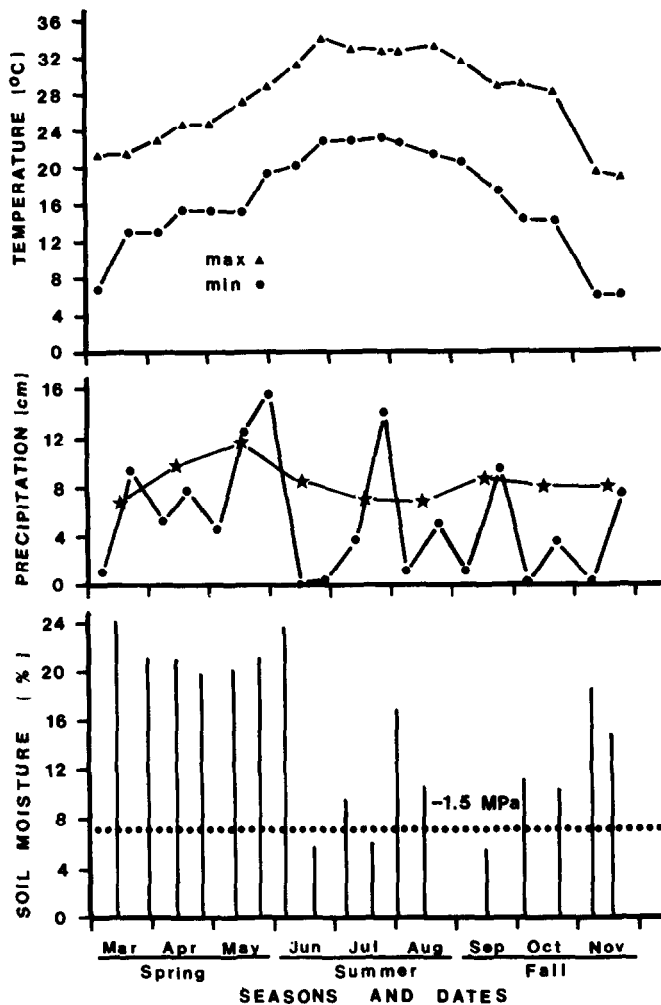


Fig. 2. Soil moisture (%) 0–30 cm depth, precipitation (cm) annual (●) and 99 year average (★), and air temperature (°C) maximum (Δ) and minimum (●) occurring near College Station, Texas, during March–November 1979.

were dying or dead. When switchgrass plants were grazed at a heavier rate (74% utilization), plants were maintained in an immature state, but shoot vigor was reduced by the close defoliation. Time of defoliation also influences regrowth of switchgrass. Sims et al. (1971) found that defoliating switchgrass plants prior to June 26 induced rhizomes to produce aerial shoots and inflorescences before the end of the growing season. Plants defoliated after June 26 produced small shoots that quickly went dormant. Holt (unpublished data) reported that shoot apices of several accessions of switchgrass growing near College Station, Texas, were evaluated above a 20-cm grazing and cutting height by late spring. If shoot apices were not removed with early spring defoliation a marked decrease in forage production resulted.

Effective management of switchgrass is tied closely to shoot growth (stem elongation) of plants. The objective of this study was to evaluate the effect of fertilization and mowing on growth, shoot density and shoot growth of Alamo switchgrass.

Materials and Methods

The investigation was conducted on a 2-year-old stand of Alamo switchgrass, located on the Texas A&M Range Research Area near College Station. The soil, a Lufkin fine sandy loam, in the taxonomic class of Fine, montmorillonitic, thermic Vertic Albaqualls with a hard restrictive layer of clay 20–30 cm below the soil

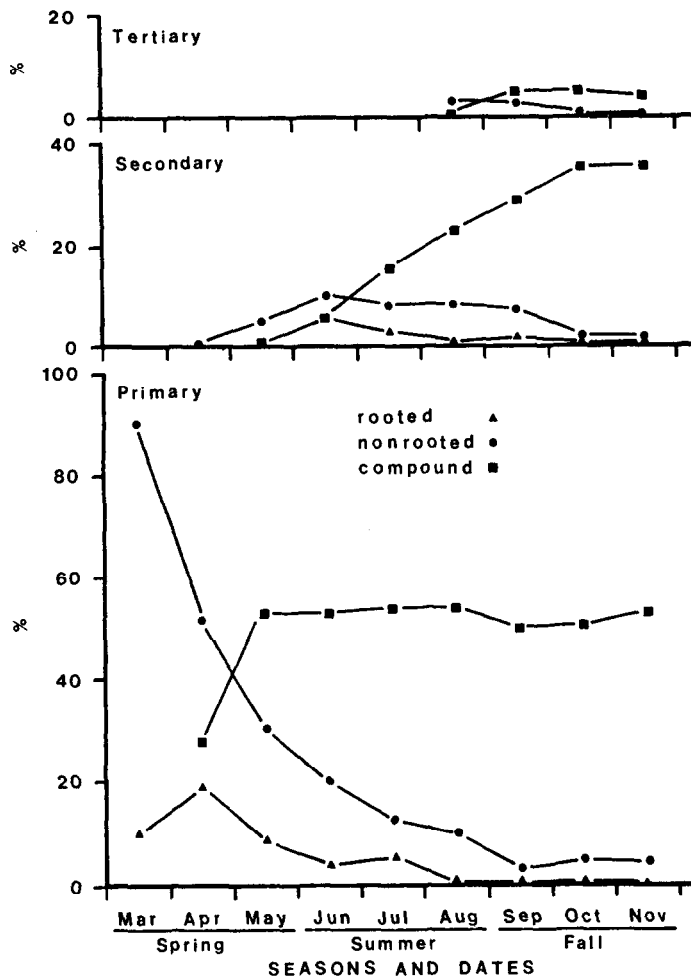


Fig. 3. Percent of nonrooted, rooted and compound shoots per plant within primary, secondary or tertiary shoot categories for untreated Alamo switchgrass plants growing near College Station, Texas. Values are the means of 3 replicates.

surface occurs within the Post Oak Savannah resource area (Gould 1975). Mean annual rainfall at the site is 100 cm with a peak in May.

Main plots 5 × 32 m in size were either untreated; fertilized in early spring (March) with 45–45–45 kg/ha of N, P₂O₅ and K₂O; or mowed to a 20-cm stubble height in mid-spring (April 15), late spring (May 15), early summer (June 15), and mid-summer (July 15). The main plots were arranged in a randomized block design with 3 replications. One-half of each fertilized plot was mowed in mid-summer (July 15) and one-half of all mowed plots were mowed again in early fall (September 15).

Beginning in early spring (March) and continuing through late fall (November), 5 plants were excavated from each plot at 2 to 4 week intervals. Whole plants from mowed plots were excavated prior to or just after mowing and soil was removed from root systems before storing. Collected plants were frozen or oven-dried at 70°C. Frozen samples were stored at 0°C until examined in the laboratory, and oven-dried samples were stored at room temperature.

Shoot numbers and weights were determined for each plant. Shoots and axillary buds were sorted by a system similar to those used by Stubbendieck and Burzlaff (1970), Dewald and Louthan (1979), and Nieland and Curtis (1956). Shoots with no roots were classified as nonrooted. Those with at least one root but without basal (proaxis) bud formation or secondary shoots were classified as rooted shoots; and shoots with secondary shoots or proaxis buds were classified as compound shoots. In early growth, proaxis

buds and rhizomes, were difficult to distinguish and were grouped together as proaxis buds. Axillary buds with green leaf elongation and located on elevated nodes were classified as aerial shoots. Shoots were further classified as primary (arising from buds formed the preceding year); secondary (arising from buds of primary compound shoots); or tertiary (arising from secondary compound shoots) (Fig. 1). The expanded leaves were counted and height of apical meristems was measured on only the unmowed-fertilized and untreated plants. All shoots were dried for 48 hours at 60°C and weighed.

Standing crop (kg/ha) above a 20-cm stubble height was determined by clipping prior to mowing in April, May, June, July, or September 1979. These samples represented the amount of forage harvested with the mowing treatments. Plants within each of 5 randomly placed 0.5-m² sample quadrats per replication were counted and clipped to a height of 20 cm, oven-dried at 60°C for at least 48 hours and weighed. Standing crop to ground level was also calculated by multiplying average number of plants per m² by average weight per excavated plant determined by summation of the weight of shoots in each category in the shoot development phase. On March 5, 1980, stands were burned to about a 5-cm stubble height to remove the standing dead forage from plots. Axillary buds had begun to swell, but no growth had occurred at this time. Thus, the burn was not considered detrimental to the switchgrass plants. Plants were allowed to grow, and standing crop was sampled by clipping plants to ground level on May 15, 1980. Plants within 4 randomly placed 0.5-m² areas per replication were clipped and dried at 60°C for 48 hours and weighed. Data were used to determine effects of fertilization and mowing treatments upon plant growth in spring following treatment.

Soil temperatures at depths of 7.5, 15, and 30 cm, air temperatures, and precipitation were measured continuously during the study. Soil moisture was determined gravimetrically on samples collected from the 0-7.5 cm, 7.5-15 cm, 15-30 cm, and 30-45 cm depths. These soil samples were taken within the untreated plot of each replication at approximately 2-week intervals.

Analysis of variance was conducted to compare treatment effects on shoot type, shoot weights, and plant weights across time. Treatment means were separated and significant differences were calculated at the 10% level.

Results and Discussion

Growth and Development

Growth of untreated Alamo switchgrass plants was monitored during a year with above-average total rainfall but with a drier than usual early summer and early fall (Fig. 2). Plants began growth in early spring with development of primary nonrooted shoots from proaxis buds formed the previous growing season. Adventitious roots began to form when shoots were in the three-to four-leaf stage. With development of roots, percent of primary nonrooted shoots decreased from 90% in early March to 3% by September (Fig. 3). Primary rooted shoots increased to 20% of the shoot component in mid-spring but decreased as proaxis buds formed and primary compound shoots developed. Percentage of primary compound shoots rapidly increased to 50% of the shoot component and remained stable for the remainder of the growing season. Primary compound shoots attained the six-leaf stage by early July, when flowering was also first observed. Anthesis occurred in late July and early August.

Secondary shoots developed in mid-spring from proaxis buds of primary compound shoots (Fig. 3). Percentages of secondary shoots in all categories were less than percentages of primary shoots. Secondary shoots formed about 25% of the shoot complex by early summer. Nonrooted shoots decreased from 10% of the shoot complex in early summer to 2% in mid-fall. Secondary rooted shoots were transient in nature, in that the percentage increased with root initiation in late spring, but decreased with increased development of proaxis buds in summer. Secondary

compound shoots increased from 0% during mid-spring to 35% by late fall. A third generation of shoots began to form from proaxis buds in late summer. By early fall tertiary shoots comprised about 5% of the shoot complex and remained at this level during the remainder of the season. The nonrooted shoot component was never greater than 3%, and tertiary compound shoots reached a maximum of 5% in early fall. Compound shoots comprised over 90% of the shoot complex by the end of the growing season (Fig. 3), and proaxis buds located at the base of compound shoots numbered 40 per plant by late fall (Table 1).

Mid-spring Mowed

Mowing in mid-spring had little impact on the shoot complex, but the total weight of primary compound shoots was reduced during fall (Table 2). Mowing removed less than 150 kg/ha forage (Table 3) and only a few apical meristems, but the treatment reduced plant vigor (1980 spring regrowth) by 30% (Table 4). April mowed plants regrew relatively slowly during the period from late-spring to mid-summer 1979 (Fig. 4).

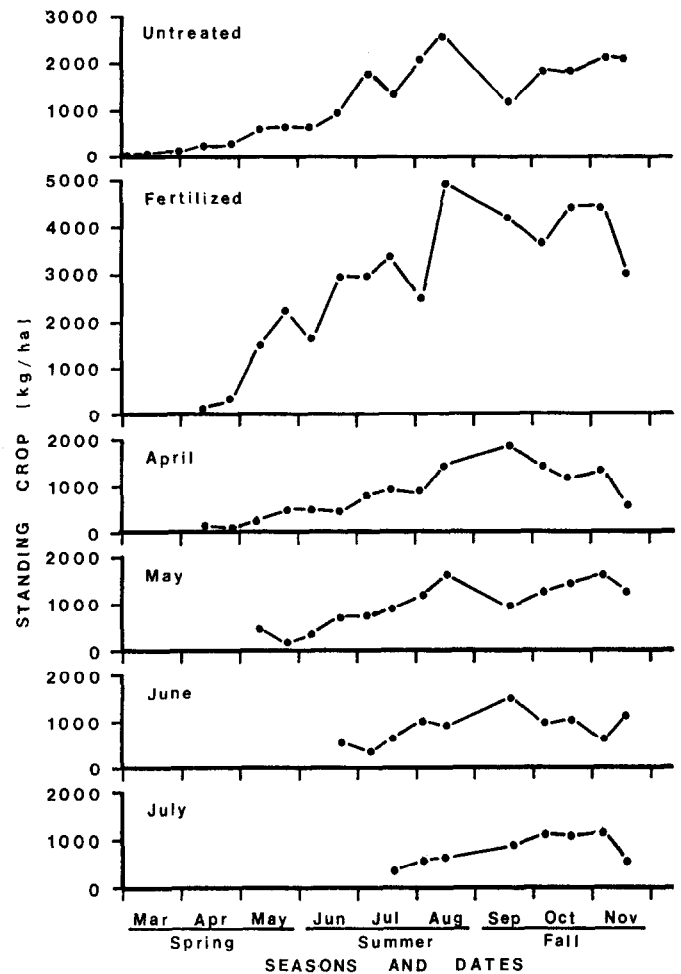


Fig. 4. Standing crop (kg/ha) of Alamo switchgrass growing near College Station, Texas, during 1979. Estimates equaled the average weight of excavated plants \times average number of plants per hectare.

Several factors may have been active in effectively reducing regrowth of April mowed plants in 1979. Brownseed paspalum (*Paspalum plicatulum* Michx.) plants were actively growing in April defoliated plots and may have competed for moisture. Beatty and Powell (1976) reported that clipping switchgrass plots in spring and summer allowed invasion of weeds into switchgrass stands in Georgia. Harvests later in the year reduced invasion. Temperatures in mid-spring (Fig. 2) were also below the 32°C day/26°C night temperatures reported optimum for switchgrass

Table 1. The average number of proaxis buds per plant for untreated, fertilized or mowed treatments of Alamo switchgrass growing near College Station, Texas, during 1979. Values are the means of three replicates.

Treatment	Season and date of harvest								
	Spring			Summer			Fall		
	April	May	June	July	August	Sept.	Oct.	Nov.	
	12	26	24	20	19	16	20	20	17
Unmowed									
Unfertilized	5a ¹	10ab	15b	27ab	24a	48a	29bc	34ab	40ab
Fertilized ²	7a	17a	33a	31a	28a	37b	41a	42a	52a
Mowed once									
April	2a	7b	14bc	15c	20ab	26c	25cd	38ab	32bc
May			8c	18c	12bc	27c	25cd	33ab	29bc
June				20bc	7c	23c	39ab	36ab	42ab
July					20ab	5d	16de	37ab	25c
Fertilized ² /July					27a	3d	8e	30b	30bc
Mowed twice									
April/September								4c	3d
May/September								4c	4d
June/September								5c	6d
July/September								4c	3d
Fertilized ² /July/September								5c	6d

¹Means within a column followed by the same letter are not significantly different at the 0.90 level according to Duncan's multiple range test.
²Fertilized March 1979 with 45-45-45 kg/ha N,P₂O₅,K₂O.

Table 2. Average weight (g) of primary compound shoots per plant for untreated, fertilized or mowed treatments of Alamo switchgrass growing near College Station, Texas, during 1979. Each value is the mean of three replicates.

Treatment	Season and date of harvest								
	Spring			Summer			Fall		
	April	May	June	July	August	Sept.	Oct.	Nov.	
	12	26	24	20	19	16	20	20	17
Unmowed									
Unfertilized	2a ¹	4a	11b	17b	21b	42b	19bc	23b	27b
Fertilized ²	4a	14a	35a	54a	46a	73a	60a	56a	56a
Mowed once									
April	2a	9a	8bc	8b	15c	20bc	22b	13cd	14c
May			3c	9b	9c	16cd	15bcd	17bc	11bcd
June				9b	9c	9e	10de	8de	9cd
July					6c	7e	6e	6de	6cd
Fertilized ² /July					12bc	12de	13bcd	8de	13cd
Mowed twice									
April/September								5e	5cd
May/September								4e	5cd
June/September								6de	4cd
July/September								3e	2d
Fertilized ² /July/September								5e	8cd

¹Means within a column followed by the same letter are not significantly different at the 0.90 level according to Duncan's multiple range test.
²Fertilized March 1979 with 45-45-45 kg/ha N,P₂O₅,K₂O.

Table 3. Standing crop (kg/ha) of fertilized and mowed stands of Alamo switchgrass growing near College Station, Texas, clipped to a 20 cm stubble height during 1979. Values are the means of three replicates.

Treatments	Harvests		
	First	Second	Total
April/September	133	1608	1741
May/September	526	1623	2149
June/September	1294	1523	2817
July/September	1152	602	1754
Fertilized ¹ /July/September	4015	1122	5137

¹Fertilized March 1979 with 45-45-45 kg/ha N,P₂O₅,K₂O.

growth by Balasko and Smith (1971). The regrowth potential of Alamo switchgrass plants, determined by the number of proaxis buds associated with compound shoots, was also lowest in April and increased as the growing season progressed (Table 1). Thus, mowing in April could possibly have delayed the allocation of carbon compounds for the formation of new proaxis buds. The cause for reduced plant vigor during spring 1980 is not clear because plants should have had adequate time for herbage production and carbohydrate storage.

Late-spring and Early-summer Mowed

Plants mowed in late spring and early summer responded similarly. Secondary nonrooted shoots increased in number following

Table 4. Standing crop (kg/ha) of untreated, fertilized or mowed Alamo switchgrass stands harvested to ground level on May 15, 1980 near College Station, Texas. Table values represent spring regrowth following a uniform burn in March 1980 and are the means of three replicates.

Treatment	Standing Crop
Unmowed	
Unfertilized	3022b ¹
Fertilized ²	4790a
Mowed once	
April	2118cd
May	2278bc
June	2482bc
July	1374de
Fertilized ² /July	2654bc
Mowed twice	
April/September	1216e
May/September	1068e
June/September	1272e
July/September	642e
Fertilized ² /July/September	1310e

¹Numbers followed by the by the same letter are not significantly different at the 0.90 level according to Duncan's multiple range test.

²Fertilized March 1979 with 45-45-45 kg/ha N,P₂O₅,K₂O.

mowing of primary compound shoots (Table 5). Aerial shoots also developed from axillary buds (Table 6). The number of proaxis buds decreased slightly during the summer as new shoots were formed (Table 1). Possibly, defoliation reduced apical dominance during the summer when proaxis buds were adequately developed to produce new shoots. Apical meristems of primary compound shoots were elevated to near 20 cm in May and over 20 cm in June. Weights of secondary nonrooted and aerial shoots increased three and six fold, respectively, compared to those of untreated plants, and weights of compound shoots were reduced 60% by mowing (Table 2). A single defoliation in early summer yielded about 1,200 kg/ha forage, twice the amount harvested in late spring (Table 3). Plant vigor in stands defoliated in May and June decreased 18 to 25% during spring 1980 relative to untreated plants (Table 4).

Table 5. Average number of secondary nonrooted shoots per plant for untreated, fertilized or mowed treatments of Alamo switchgrass growing near College Station, Texas during 1979. Values represent the means of three replicates.

Treatment	Season and date of harvest							
	Spring		Summer			Fall		
	April	May	June	July	August	Sept.	Oct.	Nov.
	26	24	20	19	16	20	20	17
Unmowed								
Unfertilized	0.4b ¹	1.2b	2.0b	2.0c	2.0d	1.6cd	0.3e	0.6de
Fertilized ²	2.6a	2.8b	2.6b	2.3c	0.9d	1.0d	0.6e	0.0e
Mowed once								
April	0.1b	3.0b	2.4b	2.8c	1.5d	0.9d	0.0e	0.2e
May		7.0a	14.0a	7.4b	4.7cd	2.2bcd	1.1e	0.8e
June			3.6b	11.6a	7.4bc	5.7abc	2.7d	2.0de
July				5.7bc	9.5b	6.2ab	2.7d	2.5de
Fertilized ² /July				3.0c	18.3a	9.4a	3.5bcd	4.8a
Mowed twice								
April/September							5.3a	3.9ab
May/September							4.6abc	3.5abc
June/September							3.4cd	1.8cde
July/September							3.2cd	1.4de
Fertilized ² /July/September							4.9ab	3.8abc

¹Means within a column followed by the same letter are not significantly different at the 0.90 level according to Duncan's multiple range test.

²Fertilized March 1979 with 45-45-45 kg/ha N,P₂O₅,K₂O.

Table 6. The average number of aerial shoots per plant for untreated, fertilized or mowed treatments of Alamo switchgrass growing near College Station, Texas during fall 1979. Values represent the means of three replicates.

Treatment	Date	
	October 20	November 17
Unmowed		
Unfertilized	0d ¹	0d
Fertilized ³	0d	0d
Mowed once		
April	1d	T ²
May	2cd	3cd
June	5abc	6bc
July	5abc	4bc
Fertilized ³ /July	8ab	10a
Mowed twice		
April/September	7ab	6bc
May/September	7ab	7b
June/September	9a	5bc
July/September	5bc	4bc
Fertilized ³ /July/September	5bc	4bc

¹Means within a column followed by the same letter are not significantly different at the 0.90 level according to Duncan's multiple range test.

²Average 0.5 or less.

³Fertilized March 1979 with 45-45-45 kg/ha N,P₂O₅,K₂O.

Mid-summer Mowed

Mowing in mid-summer increased the number of secondary and tertiary nonrooted shoots and aerial shoots (Table 5, 6 and 7). Proaxis bud numbers decreased and remained low through late summer and then increased in fall (Table 1). Forage yields were similar to those of early summer defoliated plants (Table 3), but this treatment caused a severe decline in plant vigor the following spring (Table 4). We can only speculate that growing conditions during late summer and fall were not adequate for growth and subsequent carbohydrate replenishment (Fig. 2). Apical meristems were removed from essentially all of the primary compound shoots and many of the secondary compound shoots, and regrowth was slight during the remainder of the summer (Table 3).

Mowed Twice

A similar pattern of shoot development occurred in stands mowed twice, with the second mowing

Table 7. Average number of tertiary nonrooted shoots and quaternary nonrooted shoots per plant for untreated, fertilized or mowed treatments of Alamo switchgrass growing near College Station, Texas, during fall 1979. Values represent the means of three replicates.

Treatment	Tertiary		Quaternary	
	October 20	November 17	October 20	November 17
Unmowed				
Unfertilized	0.1b ¹	0.0f	0.0c	0.0a
Fertilized ²	0.2b	0.2f	0.0c	0.0a
Mowed once				
April	0.0b	0.2f	0.0c	0.0a
May	0.0b	0.2f	0.0c	0.0a
June	0.3b	0.2f	0.0c	0.0a
July	1.0b	1.3ef	0.0c	0.0a
Fertilized ² /July	2.8b	3.0def	0.1bc	0.0a
Mowed twice				
April/September	11.1a	8.0b	1.0ab	0.2a
May/September	10.6a	12.3a	0.5abc	0.6a
June/September	8.5a	4.0cd	0.3bc	0.3a
July/September	8.9a	5.4cd	1.3a	1.0a
Fertilized ²	8.6a	7.0bc	1.0ab	0.3a

¹Means within a column followed by the same letter are not significantly different at the 0.90 level according to Duncan's multiple range test.

²Fertilized March 1979 with 45-45-45 kg/ha N,P₂O₅,K₂O.

occurring in early fall. Apical meristems were removed from most secondary compound shoots and some primary and secondary nonrooted shoots. Numbers of secondary, tertiary and quaternary nonrooted shoots increased as they developed from the proaxis buds (Tables 5 and 7). Nonrooted shoots became dormant after frost in late fall and resumed growth the following spring. Weights of the nonrooted shoot component increased (data not shown), but weights of rooted and compound shoot components decreased (Table 2). Total forage yields ranged from 1,700 to 2,800 kg/ha with maximum yields produced by an initial harvest in late spring and early summer (Table 3). Vigor of these plants, based on plant weight in spring 1980, was low relative to untreated plants or those mowed once in spring or early summer (Table 4).

Exposure of fall mowed plants to winter temperatures during 1979-80 (Fig. 2) that were .8 to 3°C below the long term average in November, December, February, March, and April may have reduced plant growth in spring 1980. Fall mowed big sacaton (*Sporobolus wrightii* Munro) plants also grew slowly the next spring (Haferkamp 1982). Switchgrass plants mowed in fall produced many small nonrooted shoots that became dormant and resumed growth the following spring (Tables 5 and 7), and these shoots may have been damaged by cold temperatures, thus reducing spring growth of fall mowed plants. Beaty and Powell (1976) also reported that 2 clippings per year on switchgrass reduced plant survival as well as the number of shoots per plant, but a single clipping was not detrimental.

Fertilization

Fertilization in early spring increased rate of development of compound shoots from nonrooted and rooted shoots (data not shown). Numbers of secondary nonrooted shoots and secondary compound shoots (data not shown) were significantly higher in fertilized plants in April and a trend toward a greater number of proaxis buds was apparent for the fall (Tables 5 and 1). Fertilization did not influence numbers of primary compound shoots (data not shown), but increased weights of primary and secondary compound shoots (Table 2). Fertilized plots were also the most productive during the growing season and the spring following treatment (Tables 3 and 4). Increases in forage production from fertilization have been reported for switchgrass by other researchers (Warnes and Newell 1969, Balasko and Smith 1971).

Fertilization and Mowing

Plants fertilized in spring and mowed in mid-summer yielded the most forage (Table 3), and these plants were almost as vigorous as

untreated plants the following spring (Table 4). Mowing removed apical meristems from both primary and secondary compound shoots. Fertilization apparently overcame the detrimental effects of mid-summer mowing. Fertilized plants contained significantly more secondary nonrooted shoots (Table 5) and aerial shoots (Table 6) and produced 500 kg/ha more regrowth than nonfertilized plants by fall (Table 3). However, numbers of proaxis buds were similar (Table 1). The enhanced growth response during spring of 1980 may have been due to a residual fertilizer effect.

Management Implications

These data indicate that deferment or light defoliation of Alamo switchgrass in early spring would allow development of compound shoots and an increased potential for plant regrowth in areas climatically similar to the Post Oak Savannah of Texas. Severe defoliation during this period could reduce vigor of plants by allowing invasion of weeds and subsequently reduce the growth rate of new shoots. Excessive defoliation in the fall could decrease the potential for early spring growth by reducing numbers of proaxis buds and by allowing damage due to low temperature.

Fertilization with a mid-summer defoliation was the most productive in terms of amount of forage harvested and plant vigor. The forage quality during mid-summer, however, would be lower than in spring or early summer.

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Chemically Thinning Blue Grama Range For Increased Forage and Seed Production

WILLIAM J. MCGINNIES

Abstract

Forage and seed production of blue grama rangeland can be increased by chemically thinning the native grass stand. Thinning of native blue grama range was accomplished by spraying strips 30 cm wide with glyphosate [N-(phosphonomethyl) glycine] and leaving alternating 15 cm wide strips of undisturbed vegetation. This reduced the stand to one-third of its original ground cover. Forage production was increased an average of 37% over the untreated pastures during a 7-year period. Plants in the thinned area were taller and had a more upright growth form which made the herbage more readily available to livestock. When plants were grazed during the winter, 67% more animal days of grazing were obtained from the thinned pastures than from the untreated pastures. For the 5 years when seed was harvested, production of clean seed averaged 5.6 kg/ha on the untreated pastures and 13.0 kg/ha on the thinned pastures.

In northern Wyoming, Rauzi (1980) reported that spraying strips of native range 36 cm wide with a heavy rate of atrazine [2-chloro-4-ethylamino-6-isopropyl amino-1,3,5-triazine] and leaving alternating bands of undisturbed vegetation 20 cm wide increased blue grama (*Bouteloua gracilis*) forage production. Production of blue grama during the first 5 years following treatment averaged 168% more than the untreated pastures and in the eleventh year was still 43% more.

In a study that evaluated the effects of growing space on individual plants of blue grama, as space per plant increased, the height of seed stalks, number of seed stalks per plant, and weight per plant increased (McGinnies 1971). Those plants with the most growing space had a more upright growth form than those with less growing space. When growing space was reduced to only 81 cm² per plant, there was no mortality even in drought years, which indicated that blue grama can persist when severely crowded.

It was assumed that if a dense stand of native blue grama range could be thinned so that the remaining plants had more growing space and thus more water available, it might be possible to increase plant height and seed yield. Increasing plant height would make the forage more readily available to grazing livestock. Taller stems would also make seed easier to harvest with a combine.

In a preliminary small-plot study (unpublished) native blue

grama range was thinned by chemically killing strips 15, 30, or 45 cm wide while leaving strips of living grass 15 cm wide between the killed strips. The treatment containing the 30-cm killed strip appeared to produce more blue grama forage than the 15-cm or 45-cm treatments or the undisturbed range. Nitrogen fertilizer increased annual forbs but did not affect the yield of blue grama. Controlling annual forbs with a pre-emergence spray of atrazine in the year following thinning appeared to increase the effectiveness of the strip-sprayed treatment.

This study was initiated to evaluate the effects of chemically thinning blue grama range on forage and seed production. Increased carrying capacity would result from increasing forage yield and plant height to produce a more upright growth form which would make the herbage more readily available to livestock. McGinnies (1978) previously reported results from the first 2 years of this study.

Methods

In 1975, six 3.65-ha pastures were established on native blue grama range at the Central Plains Experimental Range 20 km north of Nunn in northcentral Colorado. The native shortgrass vegetation was predominately grasses and blue grama comprised approximately 90% of the grass and grass-like component of the vegetation. Associated grass and sedge species included threadleaf sedge (*Carex filifolia*), sand dropseed (*Sporobolus cryptandrus*), and bottlebrush squirreltail (*Sitanion hystrix*). Elevation was 1,650 m and average annual precipitation was 31 cm with 66% falling May through August. Soil was an Ascalon fine sandy loam (Aridic Argiustoll). The area had been moderately grazed since 1939.

During July 1975, vegetation in 3 of the 6 pastures was thinned by killing the plants in strips 30 cm wide by spraying glyphosate at a rate of 4.5 kg/ha in 280 liter/ha of water onto the strips. Alternating strips of unsprayed native vegetation 15 cm wide were left between the sprayed strips (Fig. 1). The final configuration consisted of strips of undisturbed native vegetation 15 cm wide separated by strips of killed vegetation 30 cm wide. The spray rate of 4.5 kg/ha is the per ha rate for the treated strips. Because the sprayed strips occupy only 2/3 of the surface area treated, the overall rate was 3.0 kg glyphosate per treated hectare. The 3 check treatment pastures received no spray treatment.

In early April, 1976, before any growth started, the thinned pastures were sprayed with atrazine at a rate of 1.1 kg/ha to control annual forbs. Because annual forbs were abundant in 1977, 1981,

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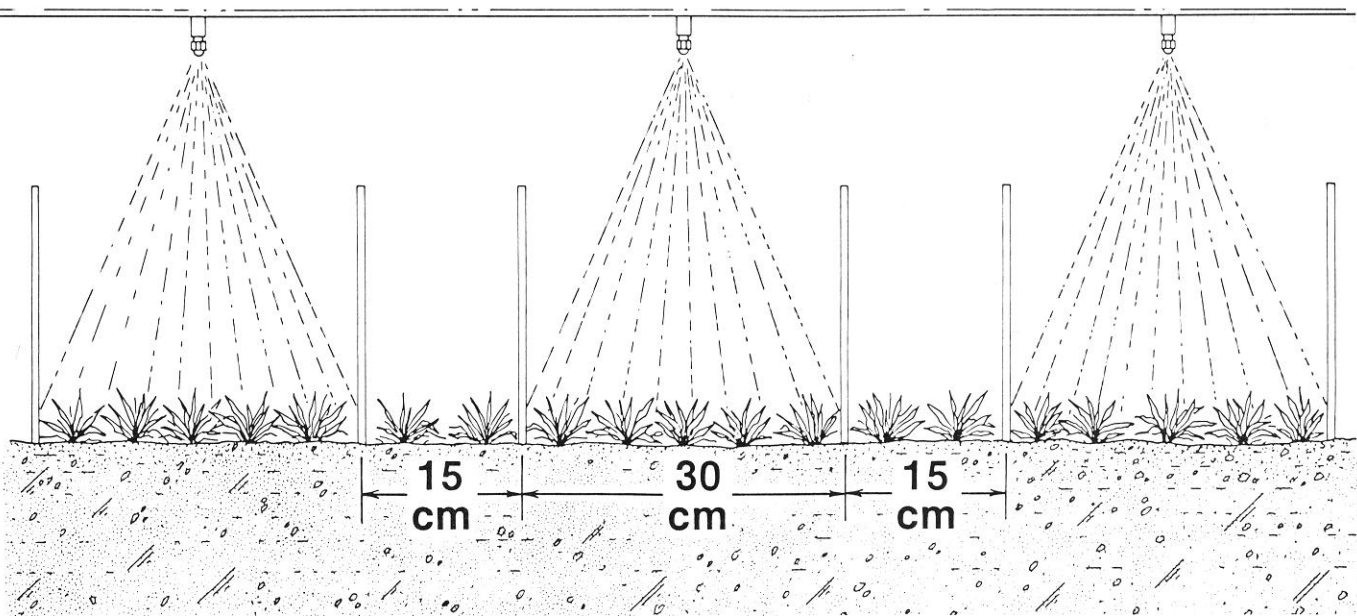


Fig. 1. Method of applying strip-spray thinning treatment. Metal shields confine spray to 30-cm wide killed strip while protecting 15-cm wide unsprayed native vegetation.

and 1982 on the thinned pastures, they were broadcast sprayed with 2,4-D [(2,4-dichlorophenoxy)acetic acid] in June. Annual forbs were never abundant enough to be considered a problem on the untreated pastures, and so were not sprayed with atrazine or 2,4-D.

Herbage yields were estimated on fifty 0.21-m² (2.25 ft²) plots in each pasture at the end of each growing season. Every fifth plot was both estimated and clipped, and the herbage sample was oven-dried in order to adjust herbage estimates to an oven-dry basis.

Seed yield was measured by clipping the seed heads on twenty-five 0.21-m² plots in each pasture. Seed heads (spikes) were counted, and the seed threshed and weighed to obtain an estimate of clean seed per ha.

The pastures were grazed during January, February or March with yearling heifers at a ratio of 5 heifers for thinned pastures to 3 heifers for untreated check pastures. Pastures were usually grazed until approximately 325 kg/ha of herbage remained. In years when less than 325 kg/ha were produced, heifers were allowed to graze until it appeared that they could not easily obtain enough to eat.

To determine how much the blue grama had invaded the sprayed strips, 150 measurements of the width of the bare strips between the strips of native vegetation were made in the late fall of 1982.

There were 3 replications in a randomized complete block design. Differences in treatment means were evaluated by analysis of variance. Other relationships were evaluated by linear correlation.

Results and Discussion

The average kill of blue grama in the sprayed strips was estimated to be 80 to 90%, but ranged from about 75 to 100%. Lack of rainfall in the period preceding spraying resulted in unfavorable growing conditions and reduced plant vigor, which resulted in the blue grama kill of less than 100%. Early growing species such as threadleaf sedge and bottlebrush squirreltail had largely completed their growth for the season and were little affected by the glyphosate.

The 1976 application of atrazine almost completely eliminated the annual forbs in the strip sprayed pastures. Those few annual forbs that escaped the spray, mostly Russianthistle (*Salsola kali*), were very large (Fig. 2). Because of the competition from the dense stand of blue grama, few annual forbs grew on the untreated

pastures and those that did grow were generally small. Hyder et al. (1976) and Houston (1977) reported that atrazine had little or no effect on blue grama. In this study, the atrazine was applied in early

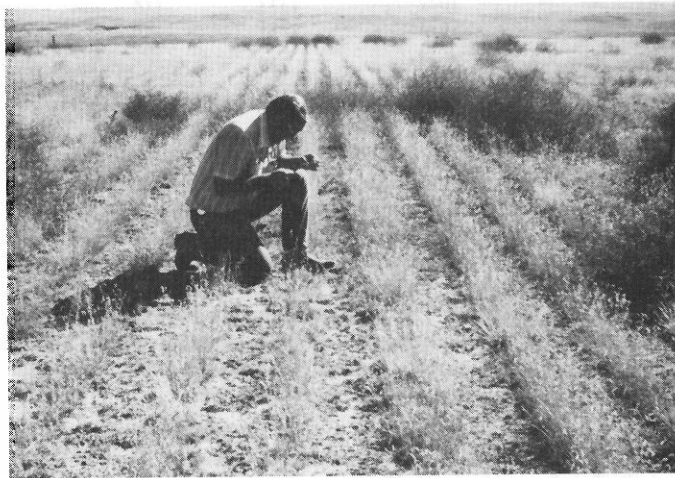


Fig. 2. Strip spray treatment in late summer, 1976, showing upright growth form and abundant seedheads. Killed plants in sprayed strips remain and protect soil surface from erosion. Large dark weeds in picture are individual plants of Russian thistle that escaped pre-emergence atrazine spray.

April, which is well before blue grama starts to green up. There were no observable effects of this early atrazine application on the blue grama.

The 2,4-D was much less effective than atrazine for controlling annual forb growth. The 2,4-D was not applied until it was felt that the annual forbs presented a problem, and by then the annual forbs were under a moisture stress which reduced the effectiveness of the 2,4-D. In spite of this, it was felt that the 2,4-D was effective in reducing competition from annual forbs during July and August. Annual forbs were never abundant in the untreated pastures and were not considered to be a problem.

The blue grama plants were much taller (both leaves and stems) and appeared more vigorous on the strip-sprayed pastures than in

the untreated pastures. During periods when the soil dried out during the summer, the plants in the strip sprayed pastures usually remained green and showed no signs of stress, but the plants in the check pastures appeared to be dry and severely stressed. Thus, moisture was available to the plants in the strip-sprayed pastures for longer periods than for the plants in the check pastures.

During 1978, the third of 3 consecutive dry years, considerable die-off of blue grama occurred in the untreated pastures. Most of the die-off resulted from parts of individual grass clumps dying while the remainder survived. In the strip-sprayed pastures, no die-off was observed, and plants stayed green most of the summer. Reducing the number of plants by two-thirds created a situation where those plants that remained apparently had adequate soil moisture to stay green during a severe drought, but in the untreated pastures where the grass had not been thinned the soil moisture was inadequate to support the much higher plant density.

Strip-sprayed pastures produced significantly more herbage than the untreated pastures in all years. During the 7 years of this study, herbage production on the thinned pastures averaged 37% greater than in the check pastures (Table 1), and ranged from a low

Table 1. Yield (kg/ha) by years for thinned and untreated pastures, 1976-1982.

Year	Untreated pastures	Strip spray	Significance of differences
1976	306	445	*** ¹
1977	297	333	***
1978	121	249	***
1979	633	897	***
1980	900	1059	***
1981	1072	1333	***
1982	623	711	**
Mean	565	718	

¹ * = $p < .05$.
 ** = $p < .01$.
 *** = $p < .005$.

of 12% greater in 1977 to a high of 105% in 1978. In terms of actual yield, the increase due to thinning ranged from a low of 36 kg/ha in 1977 to more than 260 kg/ha in both 1979 and 1981, and averaged 153 kg/ha for the 7-year period. There were no significant correlations between herbage yield and annual, seasonal, or monthly recorded precipitation. The poor relationship between precipitation and forage production may, in part, result from the highly localized nature of storms during the growing season and the nearest rain gauge being 2 km from the pastures.

Both treatments were grazed in mid- to late-winter (January, February, or March). It was found that the number of cattle used, usually 5 or less, was not sufficient to provide meaningful carrying capacity data because animal response could not be measured with a suitable level of statistical probability. In spite of this problem, in most years the pastures were grazed at a ratio of 5 animals on the strip-sprayed pastures to 3 animals on the untreated check pastures, or 67% more animal-days use on the strip-sprayed pastures. Animals were moved when it appeared that they had consumed the readily available herbage. Thinning produced a more upright growth form which made a higher proportion of the herbage available for grazing. This relationship produced an apparent increase in carrying capacity that was greater than expected from the increase in herbage weight alone. The effect of thinning on carrying capacity will be evaluated more thoroughly in a future study where pastures will be large enough to permit a satisfactory statistical analysis of animal production data.

Clean seed yields of blue grama in this section of the Great Plains are low even in favorable years. Clean seed yields averaged 5.6 kg/ha in the check treatment and 13.0 kg/ha in the thinned pastures for the 5 years that seed production was sampled (Table 2). In

Table 2. Yield of clean seed in kg/ha and number of seed stalks/m² for thinned and untreated pastures.

Item	Year	Untreated pastures	Thinned	Significance of differences
Seed yield	1976	4.0	24.2	*** ¹
	1977	0.9	5.4	***
	1980 ²	4.9	20.4	***
	1981	5.8	7.7	NS
	1982	4.5	7.1	*
Seed stalks	1976	44	211	***
	1977	16	73	***
	1978	56	84	*
	1979	140	208	***
	1980	187	265	**
	1981	126	170	*
	1982	95	145	***

¹ * = $p < .05$.
 ** = $p < .01$.
 *** = $p < .005$.

²Seed not harvested in 1978 or 1979.

1981 and 1982 there was considerable mid- to late-summer precipitation, and more than one crop of seed heads was produced. At the time the seed samples were collected, some seedheads were still green while others had already shattered. In 1976 and 1980, the seedheads all matured at approximately the same time.

Number of seed stalks per m² averaged 95 in the untreated pastures and 165 in the strip-sprayed areas for the 7-year period. The number of seed stalks was correlated with herbage yield ($r = .55$ for thinned treatment and $r = .78$ for the check treatment, both $p < .01$). The number of seed stalks also was related to seed yields ($r = .81$ for the thinned treatment, $p < .01$; and $r = .51$ for the untreated check pastures, $p < .05$). There was poor correlation between number of seed stalks and total, seasonal, or monthly recorded precipitation.

In 1982, the widths of the killed strips were measured. Blue grama reinvaded the bare areas in varying degrees; the amount of reinvasion appears to be related to characteristics of individual patches of blue grama. In some patches, the sprayed strip was completely revegetated, but in adjacent patches there had been almost no reinvasion. Although the rate of reinvasion appeared to be related to genetic differences among plants, it may have been influenced by minor soil or micro-relief differences (differences among plants are currently being investigated). The width of the killed strips, which was 30 cm in 1975, averaged 16 cm in 1982. When the strips become so narrow that they no longer increase herbage yield or cause a more upright growth form, re-treatment of the area will need to be considered.

Although there was some slight hummocking of the strips of unsprayed vegetation, there was no evidence of accelerated erosion from the sprayed strips. The plants killed by glyphosate remained to protect the site from erosion; dead root crowns were still visible in the sprayed strips in 1982. Spraying probably resulted in less soil erosion than would be expected with a mechanical thinning of the stand because spraying did not disturb the soil. Spraying on the contour should reduce any tendency for water to channel down the bare sprayed rows.

Conclusions

Herbage production and carrying capacity of blue grama rangeland can be increased by chemically thinning dense grass stands such as those in this study. Thinning results in fewer plants competing for available supplies of soil moisture and plant nutrients, and this in turn means that these fewer plants growing under more favorable moisture conditions will be able to grow and reproduce. This is in contrast to the many plants in the undisturbed areas where the individual plants must use most of the available water,

particularly in dry years, just to survive, and there is little water left over for growth. The more upright growth form and taller plants observed in the strip-sprayed pastures agrees with previous observations made on individual plants where growing space per plant was controlled to simulate the effects of plant spacing (McGinnies 1971). This, again, may represent a response to more water being made available to the individual plants.

Determination of the economic feasibility of thinning must await more extensive grazing trials where any increase in carrying capacity can be measured. Other economic considerations will include the cost of treatment and the rate of reinvasion which, in turn, will determine how soon retreatment will be needed. Improved spraying techniques are now being developed which will reduce the amount of herbicide required and increase the percentage kill in the sprayed strips. Chemical treatment is to be preferred over lower-

cost mechanical renovation techniques because of reduced erosion potential.

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Some Aspects of Rangeland Improvement In a Derived Savanna Ecosystem

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Abstract

Natural rangelands carry the bulk of ruminant livestock in the tropics of Nigeria. However, the productivity of such ecosystems is low. Some improvement of the rangelands' productivity is, therefore, needed and in this experiment the effects of fertilizers, legume oversowing, and harvesting management were evaluated. Dry matter yield increased from 3,400 kg/ha with zero fertilizer to 6,600 kg/ha with a combination of 200kg N, 44kg P, and 83kg K per hectare. NPK \times 6 weeks cutting interval gave the highest dry matter yield. Crude protein concentration and botanical composition of the herbage as well as the site's soil chemistry were altered by the treatments. Application of NPK fertilizers and harvesting every 6 weeks were, at least for this ecological zone, the best way of improving the rangeland and sustaining the improvement for long-term productivity.

Nigeria has about 57 million hectares of rangelands (McKell and Agboola 1966). The types vary from the derived savanna (a transitional zone between the rain forests and the true grasslands with its tall and tufted grass species mixed with forest tree species) to the low-producing scrublands of the Sahel savanna. The vegetation is similar in all of West Africa. In this region and elsewhere in the tropical world, much of the ruminant livestock is produced on natural rangelands of this type. Apart from a few established pastures aimed at supplementing the range, there has been very little improvement of this natural rangeland.

Fertilizers have been utilized to improve both rangelands and established pastures elsewhere (Henzel 1962, Smith 1964, Saleem and Chheda 1972). Nitrogen fertilizer indicated highly significant herbage yield increases along with changes in botanical composition of rangelands (Rogler and Lorenze 1957). Phosphorus fertilizer, especially in combination with nitrogen fertilizer, also im-

proved forage yield particularly when applied to soils inherently low in phosphorus. Additional improvement in the herbage yield and quality was obtained in the Northern Great Plains of the United States, where potassium fertilizer along with nitrogenous fertilizer was applied (Rogler and Lorenze 1957).

Further improvement has been obtained both by adopting more suitable management practices and by variations in the botanical composition of the sward. Garden et al. (1978) reported increases in yield, but not in quality, of an Australian native pasture as the harvesting increased from 2 to 8 weeks. Similar effects have been reported even in sown pastures (Oyenuga 1959, Omaliko 1980). Alteration of the botanical composition, through oversowing with productive species, especially the legumes, has helped to improve range productivity. For instance, improvement in a *Hyparrhenia* dominant grassland oversown with *Stylosanthes guyanensis* has been reported (Hagger 1971). The added advantage of this is the low cost of improvement, as use of N-fertilizer is minimized.

The objective of this study was to assess the effects of fertilizer application, legume oversowing, and harvesting frequency on the rangeland site, forage yield, and quality.

Materials and Methods

The experimental site was the Faculty of Agriculture farm, University of Nigeria, Nsukka. The location is a humid tropical site on a fine sandy loam (an oxisol). Soil properties are shown in Table 1. Ten-year average precipitation for the farm site is 1,547 mm, of which 1,455 mm is recorded between April and October, the rainy season. The rangeland has not been cropped for the past 15 years and was randomly grazed by livestock in addition to occasional burning. The botanical composition of the sward at the beginning of the study is shown in Table 2. *Panicum maximum* and *Anthephora ampulacea* accounted for about 67% of the herbage yield.

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Table 1. Soil properties of the experimental site¹.

Profile depth (cm)	Fine sand	Coarse sand (%)	Silt	Clay	pH	CEC (meq 100g ⁻¹)	Ca	Mg (g kg ⁻¹)	K	Na
0 - 15	21	58	3	18	4.8	6.4	0.48	0.12	0.36	0.18
15 - 30	18	64	1	17	5.0	6.8	0.30	0.10	0.10	0.35
30 - 45	18	60	2	20	4.9	4.3	0.20	0.00	0.10	0.30

¹Source: Soils of the University of Nigeria, Nsukka Farm. Mimeograph, Department of Soil Science, University of Nigeria, Nsukka.

Table 2. Pre-treatment frequency of occurrence and composition of plant species on the experimental site.

Species	Frequency of occurrence ¹	Composition ²
	%	%
<i>Panicum maximum</i>	100	47
<i>Antheplora ampulacea</i>	70	20
<i>Sporobolus pyramidalis</i>	40	10
<i>Loudetia simplex</i>	40	7
<i>Cynodon nlemfuensis</i>	60	4
<i>Andropogon gayanus</i>	20	4
<i>Digitaria horizontalis</i>	50	3
<i>Hyparrhenia rufa</i>	10	3
<i>Eupatorium odoratum</i>	10	1
<i>Centrosema pubescens</i>	10	1

¹Values are based on 40 quadrats (50 × 50 cm)

²Values are on dry-matter basis.

The legume species contributed 1% of the total herbage, similar to the findings by Ezedinma et al. (1979) in which only 1% of the herbage was legumes.

In July 1978, the site was mowed and plots (6.1 × 1.5m) marked out in a randomized complete block design and replicated 4 times. In 1979 and 1980, initial harvests were on May 7 of each year. The treatments consisted of all possible combinations of 3 harvesting intervals, 4 improvement methods, and a control. The harvesting was done every 4, 6, or 8 weeks. Improvement methods were nitrogen fertilizer only (N); nitrogen and phosphorus fertilizers in combination (NP); nitrogen, phosphorus, and potassium fertilizers in combination (NPK); phosphorus and potassium fertilizers plus legume oversowing (PKL); and finally a control that received neither fertilizer nor the legume oversowing. The fertilizer rates were 200kg N/ha, 44 kg/ha phosphorus, and 83 kg/ha potassium

applied as ammonium sulphate, triple superphosphate, and muriate of potash, respectively. One-half of the nitrogen and all of the phosphate and potash fertilizers were applied at the beginning of the experiment in May of 1979 and 1980. Fifty kgN/ha was applied after 6 and 12 weeks of starting the annual harvesting. *Stylosanthes hamata* cultivar Verano was the legume used.

Harvesting lasted between July and November in 1978 and between May and November in both 1979 and 1980. At each harvest date, the entire plot was harvested and total fresh weight taken soon after the cutting. Two representative samples (600g each) were taken. One was dried at 65° C for 48 hours for dry matter determination. The second sample was used for determination of botanical composition. Each sample was sorted into (a) *Panicum maximum*, (b) *Antheplora ampulacea*, (c) *Stylosanthes hamata*, and (d) all other species. These samples were dried as in dry matter determination.

After weighing, the first samples were ground in a laboratory mill and preserved for crude protein (N × 6.25) determination. In March 1981, soil samples were collected from each plot at 15-cm intervals to a maximum depth of 45 cm using a 5-cm diameter corer. Soil samples were air dried before being analysed for N, P, and Ca percentages. Nitrogen concentration was determined by kjeldahl method (Jackson 1962); phosphorus photocolometrically by the Bray No. 1 Method (Bray and Kurtz 1945); and calcium by flame photometry (Black 1965). Data were statistically analysed and differences between treatments were tested for significance with least significant difference at 5% level of probability (Steel and Torrie 1960).

Results and Discussion

Herbage Yield

The first year's as well as the second and third years' average dry matter yields are shown in Table 3. Harvesting either every 4 or 6 weeks significantly improved the dry matter yield when compared to the 8-week interval. These findings contradict the results

Table 3. Total dry matter (1000 kg/ha) of swards as influenced by harvesting intervals and improvement methods.

Harvesting intervals (weeks)	Improvement methods ¹					Mean ²
	N	NP	NPK	PKL	Control	
	1st year					
4	6.65	7.83	8.66	5.46	5.92	6.90 ^c
6	7.20	7.25	7.81	4.79	3.99	6.21 ^b
8	4.70	7.08	6.14	4.00	2.84	4.95 ^a
Mean ⁺	6.19 ^c	7.39 ^d	4.75 ^b	4.25 ^a		
	2nd and 3rd years' average					
4	5.25	5.95	6.88	5.29	4.09	5.49 ^b
6	5.40	5.54	6.92	4.71	3.39	5.19 ^b
8	4.28	5.57	5.91	4.99	2.79	4.78 ^a
Mean ⁺	4.98 ^b	5.69 ^c	6.57 ^d	5.00 ^b	3.42 ^a	

¹N = nitrogen only applied

NP = nitrogen plus phosphorus applied

NPK = nitrogen, phosphorus and potassium applied

PKL = phosphorus and potassium applied in addition to legume oversowing

Control = received neither nutrient nor legume - oversowing.

²Improvement methods means or harvesting interval means followed by the same letter are not significantly different at 5% level of probability.

Table 4. Crude protein concentration (g per kg dry matter) of herbage, as influenced by harvesting intervals and improvement methods.

Harvesting intervals (weeks)	Improvement methods ¹					
	N	NP	NPK	PKL	Control	Mean ²
4	119.3	113.7	105.4	79.1	83.4	100.2 ^c
6	98.4	101.8	92.0	74.4	76.1	88.5 ^b
8	88.4	76.6	79.8	80.3	66.2	78.3 ^a
Mean ²	102. ^e	97.4 ^d	92.4 ^c	77.9 ^b	75.2 ^a	

¹N = nitrogen only applied

NP = nitrogen plus phosphorus applied

NPK = nitrogen, phosphorus and potassium applied

PKL = phosphorus and potassium applied in addition to legume oversowing

Control = received neither nutrient nor legume - oversowing.

²Improvement methods means or harvesting interval means followed by the same letter are not significantly different at 5% level of probability.

reported by Garden et al. (1978) from a study in Wales, Australia, in which increasing the harvesting interval from 2 to 8 weeks apparently increased the herbage dry matter yield. In an earlier study in the same ecosystem, the more frequent 4-week harvesting interval was superior to the 8-week interval at the second half of the year (Omaliko 1980). These reduced yields of the longer intervals compared to those of shorter intervals was attributed to reduced floral development in this season and, therefore, more dry matter accumulation by the more frequently cut sward. In this study, the major portion of the harvesting was carried out between June and November, thus this may account for the apparent superiority of the 4-week over the 8-week interval.

Dry matter production was highest in the plots receiving N, P, and K fertilizers in combination and lowest in those receiving neither fertilizers nor legume oversowing. Furthermore, each treatment effect was superior to the control. However, the inability of the oversown sward to yield as much as the fertilized plots 3 years after initiating the treatment is of concern. The legume species, especially *Stylosanthes guyanensis*, are often used to improve both the yield and quality of similar rangelands (Foster 1961), as well as to reduce rangeland improvement costs, especially in a developing agricultural system where fertilizers are both scarce and expensive. Further improvement in the performance of legume oversown plots may be attained through the use of more productive legume species. There is a need to screen the adapted species for ability to improve dry matter yield at least to levels attainable with NPK treatments.

Individual P and K fertilizer effects were not assessed but the results demonstrate that the addition of P fertilizer, either alone or in combination with K, improved herbage yield more than N alone. Additional 15% increase in dry matter yield was obtained by using NPK combination instead of NP combination. Applying the N fertilizer alone significantly increased dry matter production compared to control but had the same effect as oversowing with legume in addition to P and K fertilizer application. Significant fertilizer ×

harvesting interval interactions existed (LSD 0.05 = 0.61 and 0.44 for the 1st year and 2nd/3rd year averages, respectively). Applying NPK fertilizers and cutting every 6 weeks resulted in the highest dry matter yield and agrees with similar results reported in the manipulation of this ecosystem (Omaliko 1980). However, the nitrogen rate to be used requires further investigation as the apparent nitrogen fertilizer recovery from the NPK treatment was 30% indicating that 200kg N/ha was too high. The lowest yields were from the control plots under the 8-weeks harvesting interval. Increasing the interval from 6 to 8 weeks also depressed the yield of swards receiving NPK treatment, while this is a contraindication on those under PKL treatment. This due to the increased regrowth capability of legumes, which results in greater dry matter yield of the sward. Therefore, different harvesting schemes need to be adopted for different improvement programmes if such an improvement is to be sustained over time.

Herbage Quality

Each fertilizer regime significantly improved the crude protein (CP) content of the herbage compared to the control (Table 4). The CP content of herbage from sward oversown with legume was also significantly lower than each of those receiving fertilizer. A higher increase in herbage CP content than the values presented was expected from the PKL treatment. The possible atmospheric nitrogen fixed by the legume may not have been available to the grass at the same quantity as for swards receiving fertilizer N, hence a lower N content. Therefore, the possible effects of initial application of N (at a rate to be determined) to plots receiving legume oversowing need further investigations.

Botanical Composition of Herbage

The botanical compositions of herbage from the improved swards in the first and third years of the study are shown in Tables 5 and 6. *Panicum maximum* remained the dominant species at the conclusion of the 3-year study except in swards oversown with legume. Proportionately (averaged over all improvement methods)

Table 5. Fertilizer treatment and harvesting interval effects on botanical composition (%) of the sward in the first and third years of improvement.

	<i>Panicum maximum</i>		<i>Anthephora anthephora</i>		Other species	
	Year 1	Year 3	Year 1	Year 3	Year 1	Year 3
Fertilizer treatment						
N	65	52	7	17	28	31
NP	69	38	5	22	26	40
NPK	68	31	9	35	24	33
Control	52	49	12	9	36	42
L.S.D. (0.05)		7.1		3.2		5.4
Harvesting interval (weeks)						
4	63	54	9	16	27	31
6	55	52	10	20	35	38
8	65	29	12	27	22	55
L.S.D. (0.05)	8.5		3.9		8.4	

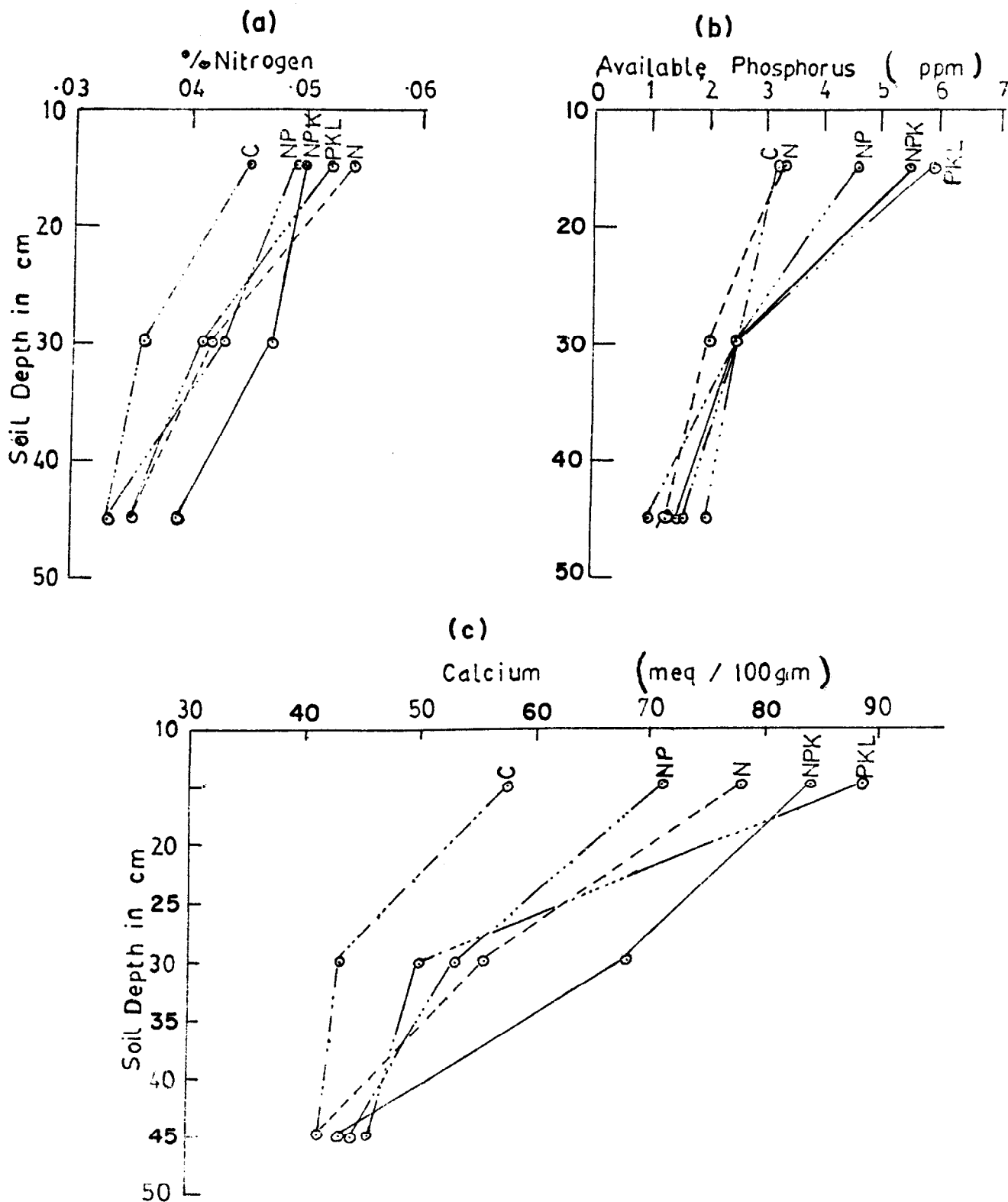


Fig. 1. Effects of different improvement methods on site's (a) nitrogen, (b) available phosphorus, and (c) calcium content of the soil at the end of the 3rd year.

this species increased from 47% at the beginning of the experimental period to 62% at the end of the first year. In the third year it was reduced to an average of 41% for all plots receiving fertilizers only (Table 5) and to 15% for plots oversown with the legume (Table 6). The proportion of *Anihephora ampulacea* decreased the first year but returned to its pre-improvement value in the third year. Despite these changes the 2 species combined still constituted about

60% of the total herbage in the third year, compared to 67% at the beginning of the experiment. Addition of either NP or NPK fertilizers reduced the proportion of *P maximum* in the sward due to concurrent increases in proportions of both *A. ampulacea* and the other species. These changes in proportion of the main species may also help account for the decrease in quality of the herbage from swards under either NP or NPK compared to those under N only.

Harvesting interval also influenced the herbage composition, especially in the third year. There were significant species \times harvesting interval interactions. Harvesting the improved sward either every 4 or 6 weeks for the 3 years maintained the proportion of *P. maximum* while the 8-week interval greatly reduced its proportion. The reverse held for *A. ampulacea* in both the first and third years and for the other species in the third year mainly.

Table 6. Botanical composition (%) of the sward in the first and third years of improvement as influenced by legume oversowing and harvesting interval.

Sward age	Harvesting interval (weeks)			LSD(0.05)
	4	6	8	
	<i>Panicum maximum</i>			
1 year	63	55	65	12.2
3 years	17	15	13	
	<i>Anthephova ampulecea</i>			
1 year	10	10	12	5.5
3 years	14	22	17	
	<i>Sprobulus hamata cv. Veranao</i>			
1 year	5	9	15	8.4
3 years	38	40	43	
	Other species			
1 year	22	26	7	11.9
3 years	31	23	27	

When the sward was improved by legume oversowing (Table 6), proportion of *P. maximum* and *A. ampulacea* was reduced to about 30% irrespective of the harvesting interval. The legume component of the sward substantially increased over the years and generally with increasing harvesting interval. These increases are of interest as they were expected to at least theoretically improve the quality of the sward. However, this expectation was not observed; rather, both yield and quality were lower than for swards receiving NPK fertilizers. On a large scale the economic advantages of legume oversowing will need to be established before deciding on what treatment or combinations of treatment to adopt. It is also possible that the use of other adapted legume species and cultivars may improve the sward.

Soil Component

Available phosphorus, nitrogen, and calcium content at soil depths of up to 45cm are shown in Figure 1. Only at the top 15 cm did fertilizer treatments show differences in P content. All plots receiving P, had higher P content than those with N or the control. For soil N, differences ($P=0.05$) existed at 0-15, 15-30, and 30-45 cm depths. At the 2 lower depths NPK had significantly higher soil N than any other treatment, while at the top 15 cm it was superior only to the control.

Nitrogen fixation by the legume species left as much N in the soil as those from inorganic N application. However, as indicated earlier, organic N was low and not available to the plants, hence the reduced herbage yield by PKL plots. The slightly higher N observed at the 15-cm layer with either N or PKL compared to NPK may be due to lower plant growth and development which then left more of the N unabsorbed. NPK and PKL at the top 15 cm and NPK and N at 15-30 cm significantly improved the calcium content of the soil.

Summary

The productivity of the derived savanna grassland in terms of the dry matter yield can be at least doubled by the addition of NPK

fertilizers without adversely affecting the biotic or soil components of that ecosystem. The use of inorganic fertilizers to improve rangeland productivity is expected to add an extra financial burden to pastoralists. Therefore, much more may be achieved, on a long-term basis, by compromising some yield for lower cost by use of legumes. The development of a more productive legume which could improve the yield and quality of the rangeland would be feasible. However, whatever improvements that may be achieved will need to be sustained by the application of a judicious harvesting interval.

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Ozone-treated Mesquite for Supplementing Steers in West Texas

FRED C. BRYANT, THOMAS MILLS, JOHN S. PITTS, MIKE CARRIGAN, AND ERNIE P. WIGGERS

Abstract

Ozonated-mesquite was compared with cottonseed hulls as the fiber base in supplemental rations fed to growing steers under range conditions. Average daily gains of steers fed the 2 rations for the 2 winter feeding periods were similar. Similarities in concentrations of acetic, propionic, and butyric acids, and acetic:propionic acid ratios between rations indicated no alterations in production of these acids as affected by composition or physical form of the ozonated-mesquite. Therefore, ozonated-mesquite appears to be equal in value to cottonseed hulls as a roughage base in supplemental rations fed to range steers.

Mesquite (*Prosopis glandulosa*) is a rangeland pest that infests millions of acres in the arid Southwest. Attempts to control this woody perennial have included mechanical, pyric, biological, and chemical means. While these methods are effective in managing mesquite, they exclude the use of the tremendous quantity of fiber available in this plant. It has been recently realized that this plant is an untapped reservoir for industrial use or livestock feed. If harvesting and processing becomes economical, all avenues for disposal of the lignocellulose from mesquite should be investigated.

Lignocellulose residues, including wood pulp, have been the focus of livestock feeding experiments for many years. Research has dealt with corn and milo residues (Bolsen et al. 1977, Ward 1978); cereal and grass straws (Durham and Hinman 1979, Church and Champe 1980); soybean residues (Miller et al. 1979); cotton by-products (Arndt et al. 1980); and wood and wood by-products (Dinius and Bond 1975, Lemieux and Wilson 1979).

Many chemical treatments have been applied to increase cellulose digestibility. Some of these included sodium hydroxide (Hendrix and Karn 1976); ammonia (Paterson et al. 1979a); and calcium hydroxide (Paterson et al. 1979b) on crop residues, and sodium hydroxide (Millett et al. 1970); sulfur dioxide (Sherrrod et al. 1978); sulphuric acid (Keith and Daniels 1976); irradiation (Kitts et al. 1969); and ozonization (Schuerch 1963) on wood and wood by-products. Ozonization of mesquite appears to increase cellulose digestion (R.W. Tock, unpublished data; Weakley and Owens 1975).

While most research has been limited to trials *in vitro* or *in vivo* with confined animals in drylot, few studies have attempted to evaluate crop or wood residues in supplemental rations for livestock on dry perennial rangeland. The objective of this study was to compare ozonated mesquite with cottonseed hulls as the fiber base in winter supplemental rations for growing range steers. The supplemental rations tested were similar to the range cubes commonly fed to range cattle.

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Study Area

The study area was on 75 ha of native range on the Texas Tech University campus. The soils are deep sandy and clay loams, well drained, and have deep root zones. Slopes range from 0-3% (USDA 1979). The pasture was in poor-fair range condition and had dense infestations of mesquite, *Mimosa* sp. and broom snake-weed (*Xanthocephalum sarothrae*). Major grasses were blue grama (*Bouteloua gracilis*) and buffalograss (*Buchloe dactyloides*).

Methods

Whole mesquite trees (>2.5 m tall) were mechanically harvested with the Texas Tech University Brush Combine No. IV (Ulich 1983) from rangeland on the campus during the summer of 1980. The combine reduced the entire above-ground plant to 1.2-1.5-cm chips. Chips, after air-drying 7-9 days to a moisture content of 5-10%, were hammermilled through a 6-mm screen. The mesquite meal was ozoned in a continuously stirred tank reactor for 2 hours. Ozonization was accomplished by adding 60% water, by volume, to approximately 20.4 kg of mesquite meal in the reactor and passing O₃ through the mixture. Evidently, water swells the wood lumen allowing O₃ access to the lignin before attacking the holocelluloses. After ozonization, the meal was dried in a forced-air oven at 60°C for 12 hours.

Rations were formulated to provide 25%, by weight, of a fiber base either of cottonseed hulls (control ration) or ozonated mesquite (mesquite ration) (Table 1). Nutrient balancing, particularly

Table 1. Ingredients (%) used in rations fed to steers as a supplement to range forage.

Ingredient	Control	Mesquite
Sorghum	47.2	43.2
Fiber	25.0 ¹	25.0 ²
Cottonseed meal	16.0	20.0
Nutri-binder ³	10.0	10.0
Calcium carbonate	0.8	0.8
Sodium sulphate	0.5	0.5
Trace mineral	0.5	0.5
Vitamins ⁴	+	+

¹Cottonseed hulls

²Processed mesquite pulp

³Protein (8%), fat (2%), crude fiber (3%), ash (3%)

⁴Vitamin A (50 g/ton @ 60,000 Iu/g), vitamin D (1.75 lb/ton @ 200,000 Iu/lb), vitamin E (30 g/ton @ 125,000 Iu/lb)

crude protein, was accomplished by adding cottonseed meal or sorghum grain. Crude protein contents were 16.2 and 14.8% for the control and mesquite rations, respectively, in 1980-81 and 15.0 and 14.3% in 1981-82. A complete nutrient and mineral analysis of the rations was reported by Bryant et al. (1982).

Rations were fed to steers from January through March in 1981 and from November through March in 1981-82. Individual steers were limited to a mesquite or control ration by a Calan Broadbent feeding system (American Calan Inc., Route 4, Northwood, N. H. 03261). This system consisted of an electronic key worn around the

Table 2. Average daily gain (kg/day) of steers supplemented under range conditions with mesquite and control rations.

Ration	1981				1981-82						
	N	Feb.	Mar.	Mean	N	Nov.	Dec.	Jan.	Feb.	Mar.	Mean
Mesquite	6	0.20a	0.12a	0.16a	7	0.41a	0.34a	0.58a	-0.31a	0.13a	0.23a
Control	6	0.22a	0.13a	0.17a	6	0.30a	0.36a	0.28b	-0.70b	0.37b	0.23a

*Means in the same column with the same superscript are not different ($P>0.05$).

neck of a steer which allowed it access to only one feeding bin. The average weight of steers was 250 kg during both winter feeding periods.

The supplement feeding rate in 1981 was 1.8 kg/day. The initial rate in 1981-82 was 0.9 kg/day. This rate was increased to 1.8 kg/day on 23 December 1981, and then to 3.6 kg/day on 5 February 1982. The adjustments were necessary because of a depletion in native forage. During both feeding trials, steers were supplemented at 3-day intervals. Steers were weighed approximately every 30 days and average daily weight gain (ADG) was determined.

Four steers receiving the mesquite and 4 receiving the control ration were fistulated for the collection of reticulo-rumen fluids during the 1981-82 feeding period. Approximately 50 ml of rumen fluids were collected from each steer at the end of November and every 2 weeks thereafter through March. Steers were fasted for 2 hours prior to collection of fluids. Immediately after collection, fluids were placed in a freezer at -10°C and stored there until subsequent analysis. The Vane Dome chromatographic method (AACC Standard Method 04-23) was used to quantify percentage concentrations of acetic, propionic, and butyric volatile fatty acids (VFA) in the reticulo-rumen fluids. Percentage concentrations of these VFA's were the average of two sub-samples of each collection of reticulo-rumen fluids. Fluids were analyzed only for acetic, butyric, and propionic because they are the most important VFA by-products of rumen fermentation, contributing 90 to 96% of the digestible energy supplied by VFA's (Wilson 1971).

Because of unequal sample sizes, significant differences in ADG were established with the Duncan's multiple range test. VFA concentration means were compared with the *t* test to determine if significant differences occurred between steers fed the mesquite and control rations.

Results and Discussion

There was no difference ($P>0.05$) in the ADG of steers fed the mesquite or control rations, 0.16 vs. 0.17 kg, respectively, in 1980-81 and 0.23 vs. 0.23 kg in 1981-82, when averaged for 2 winter feeding trials (Table 2). The ADG of control steers was slightly higher during each weighing interval in the 1981 feeding

trial. Significant differences ($P<0.05$) were determined in the ADG between ration treatment in the January, February, and March weighing intervals in 1982, but one ration did not consistently produce the higher ADG. The monthly differences in ADG are believed to be associated with the depletion of available native forage that occurred during this period. To compensate for the shortage in available forage, the supplemental feeding rate was eventually increased by a factor of 4 by the end of the second winter trial. In March, the increased feeding rate allowed steers on both rations to again gain weight, although the steers on the control ration gained at a significantly ($P<0.05$) higher rate. The lower performance of steers on both rations because of limited available forage indicated more of the rations should have been fed under these stress conditions. If forage supply is adequate and a higher level of performance is desired, rations could be mixed to supply more crude protein and energy.

Rumen concentrations of acetic, propionic, and butyric acids and acetic:propionic (A:P) ratio were not different ($P>0.05$) between ration treatments (Table 3). The VFA concentrations are similar to those reported by Olten et al. (1966), for steers receiving a pelleted corn-soy, molasses ration. Topps et al. (1965) reported higher acetic and lower propionic and butyric acid concentrations than those in our study for steers on winter grassland with a carbohydrate plus protein supplement.

The VFA concentrations in the reticulo-rumen fluid are strongly influenced by diet composition and physical form (Newland et al. 1962, Wood and Rhodes 1962, Weiss et al. 1967). The similar levels of major VFA's between ration treatment suggest that ozone-treated mesquite fiber is comparable to cottonseed hulls as a fiber base in supplemental diets. Further, the relatively low A:P ratio and high concentration of butyric acid indicated the mesquite ration was as efficiently converted to energy as the ration with cottonseed hulls; both rations were apparently converted to energy based on data from Blaxter (1962), Armstrong and Blaxter (1957), and Tonroy and Perry (1974).

Our data suggest ozone-treated mesquite is comparable in value to cottonseed hulls as a fiber base in supplemental rations fed to growing range steers. These results should not be extrapolated to

Table 3. Concentrations (molar %) of major volatile fatty acids from fistulated steers supplemented under range conditions with mesquite and control rations during the 1981-82 winter feeding period.

Ration	N	Volatile fatty acid	Date						Mean
			11-27-81	1-4-82	1-19-82	2-10-82	3-2-82	3-15-83	
Mesquite	4	Acetic acid	50.2 ¹	47.0	43.4	41.4	44.3	38.0	44.1
Control	4	Acetic acid	47.7	45.1	48.3	42.3	40.0	44.0	44.6
Mesquite	4	Propionic acid	26.0	26.6	35.5	34.0	30.2	27.0	29.9
Control	4	Propionic acid	26.6	31.2	27.6	35.6	29.1	28.5	29.8
Mesquite	4	Butyric acid	18.1	23.3	16.8	21.4	20.3	25.0	20.8
Control	4	Butyric acid	20.3	20.8	19.7	19.9	22.5	18.1	20.2
Mesquite	4	A:P ²	1.9	1.8	1.5	1.3	1.5	1.4	1.6
Control	4	A:P	1.8	1.5	1.8	1.2	1.4	1.8	1.6

¹There were no significant differences ($P>0.05$) between rations for similar volatile fatty acids concentrations or A:P ratios within dates.

²A:P = ratio of acetic to propionic acids.

range cows in a reproductive physiological status (gestation/lactation). Suitability of ozonated mesquite as a supplement to producing cows needs further investigation. The use of mesquite as a ration base could provide an economical use of its fiber by helping offset the costs associated with its removal from infested grasslands.

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Circumstances Associated with Predation Rates on Sheep and Goats

ROGER D. NASS, GREG LYNCH, AND JOHN THEADE

Abstract

Factors possibly associated with high (over 5%) and low (0-5%) predation intensities were compared among 95 sheep or goat producers in 5 states to determine if important differences were evident between the 2 groups. Data were compared for the following variables: losses to predation, flock size, type of ranch operation, management practices, predator indices, prey indices, use of U.S. Animal Damage Control program, private control efforts, predation history, timing of predation, and presence of other sheep or goats nearby. Overall, 45% of the producers reported over 5% predation losses of their lambs or kids and predation percentages tended to increase with decreased flock sizes. Feeder lamb and range sheep operations had predominantly low predation loss percentages, but most operations that included goats reported over 5% predation losses due to goat predation. A variety of management practices were used by both groups; however, low loss producers indicated low natural prey and predator populations. Most of the producers used the federal ADC program and some type of private control effort, although more high loss producers used both types. Rough, bottom, and brush grazing lands, historic predation problems, and high predator indices characterized many of the high loss producers.

Predation intensity on livestock among producers is variable (Gee et al. 1977, Nass 1980). Various studies (deCalesta 1978, Schaefer et al. 1981, and others) have shown that livestock losses to predators vary significantly among samples of producers; however, data on reasons for this variability are lacking (Gee et al. 1977). Frequently, experienced animal damage control personnel know or suspect why specific levels of predation are occurring at specific times, but there have been no standardized mechanisms for recording, tabulating, and comparing the information on a ranch-by-ranch basis. Boggess et al. 1980, Meduna 1977, and Schaefer et al. 1981 have explored the effects of some husbandry practices on livestock predation levels.

The objective of our study was to identify factors common to ranches with high sheep or goat predation and compare them with low predation loss ranches.

Methods

Sheep producers in 5 states: California, Idaho, North Dakota, Oregon, and Texas were interviewed to obtain data on their 1979-1980 sheep or goat operations. Producer names were provided by state sheep associations, county agents, and U.S. Fish and Wildlife Service animal damage control (ADC) district supervisors. Information was collected from 95 sheep or goat producers selected from a total listing of about 300 producers. The list did not include all producers in each state. The sample was selected to include a variety of sheep operations through consultations with people knowledgeable about the sheep and goat industries in each state.

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Data were collected on the following features:

Losses to predation	U.S. Animal Damage Control participation
Flock size	Private animal damage control
Type ranch operation	Habitat
Husbandry practices	Predation history
Predator index	Timing of predation
Natural prey index	Other flocks nearby

General habitat types were determined by observation. Predator and natural prey indices were rated on a 1 to 3 scale indicating low, moderate, and high densities by the producers, sheep foremen, or in some instances, the district field assistants, depending upon familiarity with the specific areas involved.

Because of the large Texas goat industry, 7 of 12 producers from that sample raised goats, either alone or in conjunction with sheep, cattle, or both. The producers were assigned to a low predation loss category (0-5%) or a high predation loss category (over 5%). This division was used for convenience in making comparisons; from the producers' viewpoint, losses of less than 5% may be considered excessive and have an adverse economic impact upon their operations.

Results

Overall, 43 (45%) of the producers incurred over 5% loss of lambs or kids to predators; 38 (40%) reported over 5% predation losses when adults were included (Table 1). The percentages of lamb/kid predation were loosely correlated with flock size ($r = -0.22$, $P0.05 = 0.205$). Although there was extreme variation with the sample, percentages of lambs/kids lost to predation tended to

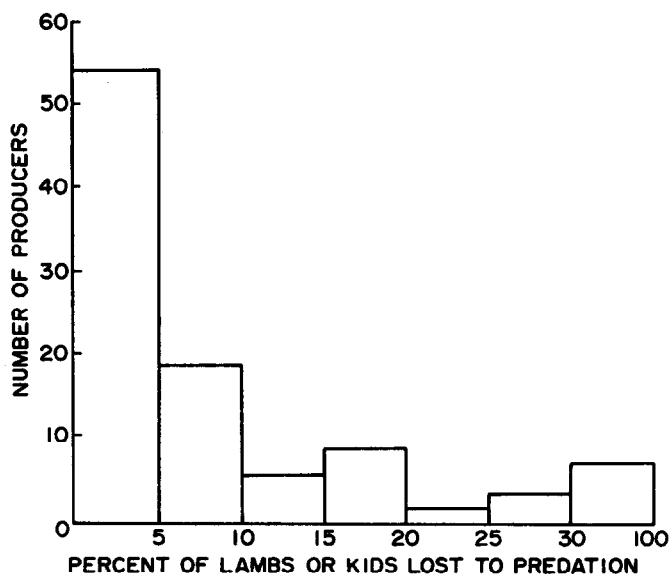


Fig. 1. Intensity of predation on lambs or kids by numbers of producers

Table 1. Percent of ranchers, by state, with high (over 5%) or low (0-5%) reported predation losses.

State	Number of ranches (n)	Percent of ranches at each predation rate			
		Predation on lamb/kids		Total sheep/goat predation	
		Low	High	Low	High
OR	35	57	43	54	46
ID	20	50	50	65	35
ND	13	23	77	38	62
TX	12	33	67	42	58
CA	15	100	0	100	0
Overall	95	55	45	60	40

Table 2. Mean flock or herd size at five levels of predation intensity (no. of producers in parens).

State	None	Levels of reported predation on lambs and kids			
		0>5%	5>10%	10>15%	15>100%
OR	389 (10)	3146 (10)	412 (4)	265 (1)	330 (10)
TX	—	912 (4)	553 (3)	—	494 (5)
ND	435 (2)	1530 (1)	670 (5)	813 (2)	378 (3)
ID	585 (2) ^a	698 (7)	761 (6)	679 (2)	404 (2)
CA	5591 (6)	4561 (9)	—	—	—
Overall \bar{X}	1750 (20)	2169 (31)	599 (18)	586 (5)	401 (20)

^aOne flock with no lambs excluded.

increase as flock size decreased. Twenty producers did not suffer predation losses whereas 20 lost over 15% of their lambs/kids to predation (Table 2). The predation loss distribution by numbers of producers is shown in Figure 1.

The feeder type operations in Oregon and some California producers had large flocks of sheep, thereby increasing mean flock sizes for those states. The mean number of sheep or goats per low-loss producer was 1,875, but this dropped to 703 when the California sample was excluded. The mean number of animals for high-loss producers remained at 560 with and without the California producers.

The types of farm or ranch operations fit seven general categories (Table 3). Forty-four percent of the sheep producers had farm

Table 3. Percentages of 95 producers by type of operation and predation intensity.

Type operation	Percent of producers with lamb or kid predation rates		Percent of producers
	0-5%	over 5%	
Farm flock	45	55	44
Sheep-cattle	61	39	19
Sheep	65	35	18
Sheep-cattle-goat	29	71	7
Range flock	83	17	6
Feeder lamb	100	0	3
Goat-cattle	50	50	2

flocks that usually contained less than 300 sheep. Most combined raising sheep with other types of farming or ranching, such as growing of row or forage crops. A majority, 55% of these producers lost over 5% of their lambs or kids to predation. Although the sample is small, most producers (71%) with sheep, cattle, and goats lost over 5% of their lambs or kids to predation. No feeder lamb

operations lost over 5% of the lambs to predation. Sheep, sheep-cattle, and range flock operations, constituting 43% of the sample, generally had less than 5% loss to predators.

Sheep management (husbandry practices) techniques were arbitrarily separated from use of control methods, although some could appear in either or both lists. For example, the use of electric fencing to exclude coyotes might be considered either a control method or a management practice, as could the use of guard dogs, woven wire fences, and others. The husbandry practices list includes items for which information was available, but does not necessarily include every possible management practice used by every producer (Table 4). Rotation of pastures, use of two herders, and night lighting are examples of practices for which information was not obtained.

Among the 95 producers, use of woven wire fencing (100%), shed lambing (79%), and daily sheep checking (66%) were the most frequently used management practices. Range flock producers used woven wire fences on home ranches, but of course did not use woven wire on open ranges. Producers using these three husbandry techniques were about equally divided between high and low predation on lambs or kids with over 5% losses incurred by 45% of those with woven wire fences, by 47% that shed lambed, and by 46% who checked their sheep daily. Keeping sheep close to buildings at night, penning at night, and using herders were the next most prevalent management techniques noted. Most producers who penned sheep at night and used herders had low losses to predators. Thirty-nine producers (41%) were using one or more of these techniques in their sheep or goat management. Keeping sheep close to buildings at night and penning at night were used for smaller farm flocks, whereas herders were used with larger flocks in fenced pastures or on open range. Other practices, such as confinement of lambs, bells on sheep, and predator proof electric fencing were reported infrequently.

Producers' impressions of predator and natural prey abundance showed lower indices for both prey (2.1) and predators (2.2) from those ranches with low predation rates. Reports of higher natural prey (2.3) and predator (2.6) indices came from high-predation-

Table 4. Use of some management techniques among 95 producers in relation to predation rates.

Management technique	Lamb/kid predation class				Total producer use (%)
	0-5%		>5%		
	No. producers	%	No. producers	%	
Use of woven wire fences	52	55	43	45	100
Use shed lambing	40	53	35	47	79
Check sheep daily	34	54	29	46	66
Keep sheep close to barn at night	9	47	10	53	20
Pen at night	8	73	3	27	12
Use herders	8	89	1	11	9
Confine lambs	2	67	1	33	3
Use bells on sheep	3	100	0	0	3
Use goats with sheep	1	50	1	50	2
Move sheep after predation	1	100	0	0	1
Use predator electric fence	0	0	1	100	1
Reduce sheep numbers	1	100	0	0	1

loss ranches. Mean indices for all ranches were 2.2 for prey species and 2.4 for predators.

Most producers used some type of animal damage control (Table 5), either private (self or contract) or through the U.S. Fish and Wildlife Service Animal Damage Control program. Only three producers did not use any program or methods for depredation reduction. Among low loss producers, 88% used the federal program and 67% carried out private control of some type. The federal program was used by 98% of the higher loss producers and 93% of these added private control efforts of some type.

Shooting coyotes was the most common form of private control work done by all producers (60%). This included attempts to shoot coyotes, calling or actively looking for coyotes, and incidental shooting when coyotes or dogs were observed during routine ranching activities. Personal trapping (11%), hiring trappers (5%), and hiring helicopters for aerial gunning (5%) were the next three popular forms of private control (Table 5). Use of guard dogs, hunting with snowmobiles, and shooting dogs were each reported by 3% of the producers. Producers with high predation losses used more methods and were more active in using private control efforts than were the producers with low losses.

Areas that are unsuitable for other purposes are frequently used for grazing sheep and goats. This is reflected in our sample where 46 (48%) of the producers used a combination of rough, bottom, and brush lands for their sheep or goats. Another 13 (14%) had similar areas adjacent to or near their ranches. Nine (21%) high-loss producers, but only 4 (8%) low-loss producers, had rough terrain and bottom areas adjacent to or near their grazing areas. Combinations of brush, timber, and grass or brush, and pasture

made up grazing areas for 21 (22%) of the producers and included 12 (23%) of the low loss producers and 9 (19%) of the high loss producers. Open type (mainly grass) pastures were utilized by 12 (23%) and 3 (7%) of the low- and high-loss producers, respectively. When only considering those 19 producers with no predation of lambs, 7 (37%) used open type, mainly grass, pastures, 9 (47%) used pastures with predominant brush or timber, and 3 (16%) used rough, bottom, and brush land. Two of these last three producers raised their lambs in confinement because of historic heavy predation, but they did allow ewes to graze the rugged pastures.

Predation history assessment by producers tended to follow current predation loss problems. Some low-loss producers assessed historical predation as high (56%), and others as low (24%). Eighty-four percent with high losses indicated predation was high historically, and only 2% had minor predation losses previously. Other producers cited yearly fluctuations in predation, extenuating circumstances related to predation, or varying predation rates related to yearly control efforts.

Most predation for low loss producers (45%) occurred during March, April, and May; however, 31% indicated predation could occur any time while the sheep or goats were grazing. Higher-loss producers also said losses could occur any time while animals were grazing (28%), but their high-loss months were April, May, and June (37%). Overall, 46% of the sample indicated that March through June were the months when predation could be severe.

Only 5 of 95 producers raised sheep or goats in isolation from other flocks or herds; therefore, the sample size was too small for speculation on the importance of this factor.

Table 5. Use of private predation control methods by 95 sheep/goat producers in relation to predation rates.

Control method	Lamb/kid predation class				Total producer use (%)
	0-5%		>5%		
	No. producers	%	No. producers	%	
Shoot coyotes	24	25	33	35	60
Trap coyotes	4	4	6	6	11
Hire trapper	3	3	2	2	5
Hire helicopter	3	3	2	2	5
Use guard dogs	1	1	2	2	3
Hunt with snowmobile	1	1	2	2	3
Shoot dogs	3	3	0	0	3
Use hounds	0	0	2	2	2
Pay bounty	0	0	1	1	1
Use poison	0	0	1	1	1
Use no private control	17	18	3	3	21

Discussion

The distribution of losses to predation in our sample is similar to those shown by Boggess et al. 1978, Dorrance and Roy 1976, Schaefer et al. 1981, and others. The tendency of producers with fewer animals to lose greater percentages of their sheep or goats than those with larger flocks might indicate that substantial differences occur in predator control policies between small and large operations. This does not appear to be true for the various features possibly affecting predation that were examined in our study, even though modes of operation generally differed with flock size. Overall, private control efforts, federal control efforts, general managerial practices, and other factors were similar between the large and small operations.

Range flock and feeder lamb operations had low predation loss percentages; however, some still reported large losses to predators. Feeder lamb producers usually restrain their flocks in confinement or semiconfinement and have close control over their flocks; both types of production are suited to large flocks. Ranches that included goats and farm flocks had higher predation loss percentages than did other types of operations. Goats are frequently raised in isolated pastures and are subject to severe predation in the brush areas of Texas (Wade 1982). Because farm flocks have modest numbers of animals, one or a few incidences of severe predation may result in substantial impact upon these producers. Even though loss percentages were low, most producers with predation problems and large flocks lost more animals to predation than did those with smaller flocks.

The four most widely used husbandry techniques were practiced about equally by producers with high and low predation losses. Penning at night and using herders were associated with low loss percentages; however, only 12% and 9%, respectively, of the total sample utilized these techniques. Davenport et al. (1973) found that Utah sheep producers using herders might have significant predation losses, but those losses were lower than for producers who did not use herders. Predation, in our sample, did not seem to be directly related to specific husbandry techniques. Husbandry practices are most efficient when used in conjunction with lethal control methods and their usefulness may be related to effort expended on such methods.

Most high-loss producers used the federal animal damage control program, utilized some form of private control, and indicated that predator and natural prey populations were relatively dense.

Persistent predation problems tend to generate increased efforts for predation reduction; therefore, it is not surprising that high-loss producers made extensive use of the federal animal damage control program. A similar situation existed for private control method efforts; increased predation resulted in the use of more methods in attempts to stop or reduce predation losses. Private control efforts were not used by 17 of the low loss producers, presumably because their predation problems or lack of them did not warrant the expense. Predator and prey index assessments indicated more coyotes or coyote signs and natural prey species or signs were seen on ranches with higher predation levels. This index was not precise, reflecting only general observations; thus, ranchers

with high losses may have only assumed that coyotes were abundant. A pair or two of coyotes can kill many lambs or kids, especially when litter energy demands are high (Till and Knowlton 1982), thus giving an impression of numerous coyotes present.

High-loss producers grazed animals in rough, bottom, or brush areas, or had these types close by (72%) in more instances than did low loss producers (53%). Generally, predation losses tended to be low for open, grassy, grazing areas. Frequently, habitats with dense vegetation and broken landscape contain large numbers of prey species, thus hold greater numbers of predators than do open areas. Control efforts may also be hampered by dense vegetation and rough terrain by restricting foot, horse or vehicular access and limiting the efficiency of aerial shooting. Historically, predation on many ranches varied from year to year, but higher predation losses were reported on ranches with a high-predation-loss history.

Most predation occurred in spring when lambs or kids were available in large numbers and when predators are typically provisioning young. Younger animals are most susceptible to predation; frequently the remains of small carcasses are not easily detected, therefore the predation of young animals may be difficult to detect and remedy.

Suitable terrain for predators, historic loss patterns, and higher predator indices tended to be associated with increased percentages of lambs or kids lost to predation. Surely, a combination of other factors is also involved: for example, the management practices and control efforts on adjacent ranches, the quality of husbandry and depredation control, and the relative abundance of resident coyotes.

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Climax Theories and a Recommendation for Vegetation Classification—A Viewpoint

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Introduction

Tansley (1920) reported, "The opinions and practices of synecologists in regard to the classification of vegetation appear superficially to be in as great a confusion today as they did 20 years ago..." One needs to spend little time discussing the subject to discover that Tansley's statement made 60 years ago still holds true today. This is indicated by Shimwell (1972), who reported that the classification of vegetation suffers greatly from overstatement, ambiguity, and inevitably some misinterpretation. After careful consideration of these statements, one may ask why we need classification? Fosberg (1967) pointed out that vegetation classification serves to facilitate the recording of information, to provide for intelligent discussion of vegetation, to aid in understanding the phenomenon itself, and to enable people to communicate vegetation information easily and unambiguously.

The purpose of this paper is to discuss one aspect of classification. This is the complexing viewpoint of climax theory.

Why Climax?

Why use any climax theory as the major criterion for a vegetation classification? The answer is not readily apparent.

Odum (1971) indicated that the degree of deviation from a theoretical climax can be measured and the factors responsible for the deviation can therefore be determined when there is a basic yardstick available for comparison. A vegetation classification based on climax establishes a basis for decision making and evaluating the effects of resource management. Clements (1936) viewed the relation between climax and classification this way: "Climax constitutes the major unit of vegetation and as such forms the basis for the natural classification of plant communities." Hall (1970) reported that the separation of climax and seral continuum gradients is essential for management, silvicultural guides, and field application of research results.

The climax concept is an accepted basis for many land management agencies and worldwide vegetation classification systems. For example, climax is used, in most cases, as the basis for the United Nations Educational, Scientific, and Cultural Organization (UNESCO 1973) vegetation classification. UNESCO serves as the pattern for the vegetation element of the Ecological Land Classification Framework for the United States (Driscoll et al. 1984). Climax is also used for USDA Soil Conservation Service range site descriptions (USDA SCS [Range Handbook] 1976), the USDI Bureau of Land Management soil-vegetation inventory (USDI BLM [SVIM]), the USDI Bureau of Indian Affairs range site descriptions (USDI BIA 1958), and the USDA Forest Service range allotment analysis procedures (USDA FS [Manual 2200] 1979).

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Climax Concepts and Theory

While there are numerous theories and versions of each, this manuscript explores 5 major climax theories: monocl意思, polyclimax, polyclimatic climax, climax pattern, and site climax. The 5 were chosen because of their ability to be of value to management. As a consequence, theories such as the dynamic functional concept (Odum 1969, Bazzaz 1979, and MacMahon 1980) were not considered, even though they are as worthy of consideration on the grounds of soundness of theory. It is the intent here to analyze these 5 theories and identify their basic differences. Once this has been done, the version that presents the best basis for a classification system can be recommended.

The Monocl意思 Theory

The monocl意思 theory, as developed by Clements (1916, 1936), is often described as the origin of dynamic ecology. The major concepts are succession and climax. Although the monocl意思 theory has come under considerable attack and rejection by many, Cain (1939) stated that Clements has evolved a philosophy, a set of principles, and terminology to meet nearly every situation.

The major assumptions of the monocl意思 theory are:

1. All successions of a region lead through time to the same adult organism (the climax) regardless of earlier site differences (Clements 1936).
2. Climatic factors determine the dominant species that can be present in a region, and completion results in selection of one or more species as the final dominants (Clements 1916).
3. Although climax is permanent because of its harmony with a stable habitat, the equilibrium is dynamic and not static. Superficial modifications may occur with the season, year, or cycle. However, these modifications, which are constantly at work, do not destroy the climax because they are within the fabric and limits of the climax.

The monocl意思 theory proposes that every region has only 1 climax plant community toward which all are developing (Krebs 1972). In other words, Clements viewed the successional development of a xerosere and hydrosere that occurred under the same macroclimate as eventually ending in a similar mesophytic community. He also presents climate as the major factor to determine the climax community. The monocl意思 theory views climax as a permanent dynamic community, not as a static condition. This theory accounted for the climax and seral unit hierarchy that Clements (1936) developed.

Although Clements believed that the climatic formation is the only climax of successional development (Clements 1916), he recognized succession may stop in practically any stage for a period of time for one reason or another. To deal with plant communities that did not conform to the climax type, he employed the terms disclimax, preclimax, postclimax, subclimax, and sereclimax (Weaver and Clements 1938).

Some criticisms of the monocl意思 theory deal with the very basis of the hypothesis: that plant communities formed in an open water body and those developed on bare rock will eventually form

a single climax community within a macroclimatically uniform region. One of the major reasons the hypothesis has lost acceptance is pointed out by DuRietz (1930). He described the contrast in vegetation on 2 soils that had developed from 2 different parent materials on level topography and under the same macroclimate. Although the successional development of the vegetation had been undisturbed since Tertiary, the contrast in vegetation between the 2 soils was evident. This points out that differences between certain soils, due to parent material, may not be eliminated even in areas with level landscapes and adequate moisture relations.

While many reject the monoclimate theory, one must not overlook the service Clements provided the plant ecology field. Whittaker (1953) pointed out: "The Clementsian system had a fine design if its premises were granted; and for its erection Clements may rank as one of the truly creative minds of the field."

The Polyclimax Theory

Tansley (1939) is credited with developing the polyclimax theory to its full perspective. However, it was Moss (1913) who set the stage for its development after Cowles (1899, 1901) laid the basic foundation. The polyclimax theory states that there may be a number of different climax communities within a climatic region. Each climax unit can be in dynamic equilibrium with the local habitats and their controlling environmental factors. Thus, Mueller-Dombois and Ellenburg (1974) reported that a climax landscape consists of a mosaic of edaphic, topographic, or ecoclimatically different communities with one usually geographically dominant, the climatic climax.

Support for the polyclimax hypothesis (DuRietz 1930, Domin 1923, Daubenmire 1968, Gleason 1939, Tansley 1929) is due largely to the recognition of edaphic climaxes (Cain 1939). The polyclimax theory accepts a fire climax where naturally occurring fires periodically arrest the development of vegetation, permitting fire-adapted species to dominate. The resulting plant community is termed disclimax (Daubenmire 1968).

Recognition of fire by the polyclimax theory differs little from the monoclimate theory. Clements recognized a plant community that was periodically arrested by fire as subclimax. Thus, on this point and others, the major difference between the monoclimate and polyclimax hypotheses is terminology (i.e., disclimax and subclimax, both being deviates).

Muller-Dombois and Ellenburg (1974) showed the correlation between the 2 theories more clearly by indicating that, "The more widely known polyclimax concept is still an offspring of the monoclimate concept insofar as it recognizes only one climatic climax in a macroclimatic region (namely the natural or near-natural community on well-drained substrates) plus a number of other climax communities that are controlled primarily by topographic, edaphic, or other factor complexes."

Since the major difference between the 2 theories, poly and monoclimate, is semantics, it seems illogical to accept one and reject the other. However, Shimwell (1972) indicated that the polyclimate theory has some advantages when he said, "It is infinitely simpler than the monoclimate theory which involves suppositions, climatic regulatory processes, and vegetation convergence in spite of environmental differences."

The Polyclimate Climax Theory

Since the monoclimate theories recognize only 1 climatic climax, a new concept was developed, the polyclimate climax. The polyclimate climax theory was developed primarily by Tuxen (1933), Tuxen and Diemont (1937), and Ellenburg (1959). Although it is a modified version of the polyclimax theory, it has 1 major distinction. The polyclimate climax recognizes that more than 1 climatic climax community can exist in a macroclimatic region.

Two major propositions of the polyclimate climax theory are:

1. Any macroclimatic region may contain more than 1 climatic climax due to the different mature soil types that may occur in the region (Tuxen 1933).

2. The different mature soils, which may result from different parent material, show no indication of ever merging into 1 soil type. Thus, the climax plant communities that occupy these different mature soils also show no indication of ever merging into 1 climatic climax community (Mueller-Dombois and Ellenburg 1974).

One disadvantage of the polyclimate climax theory, is that it is impossible for a plant community to be considered climax unless it occurs on a well-developed or mature soil. Thus, before a plant community can be considered climax, it must occur within a stable ecosystem. According to Mueller-Dombois and Ellenburg (1974), community stability must be seen as equal to stability in soil development and geomorphological development.

The Climax Pattern Theory

The climax pattern theory was developed by Whittaker (1951, 1953). According to Shimwell (1972) the climax pattern theory evolves around 3 major propositions on the nature and structure of climaxes and their relativity:

1. "The climax is a steady-state of community productivity, structure, and population, with the dynamic balance of its populations determined in relation to its site."
2. "The balance among populations shifts with change in environment, so that climax vegetation is a pattern of populations corresponding to the pattern of environmental gradients, and more or less diverse according to diversity of environments and kinds of populations in the pattern."
3. "Since whatever affects populations may affect climax composition, this is determined by, or in relation to, all factors of the mature ecosystem-properties of each of the species involved, climate, soil and other aspects of site, biotic interrelation, floristic and faunistic availability, chances of dispersal and interaction, etc. There is no absolute climax for any area, and climax composition has meaning only relative to position along environmental gradients and to other factors."

It is clear from these 3 propositions, that Whittaker rejected the basic units of vegetation which were an integral part of the monoclimate, polyclimate, and polyclimate climax theories. This reflected Whittaker's view that no 2 stands of undisturbed vegetation are alike. He, therefore, supported the individualist hypothesis of Gleason (1939) that vegetation occurs as a continuum rather than as discontinuous stands. Although the continuum theory (Curtis and McIntosh 1951) rejects vegetation classification into discrete communities, it does allow it to be arranged along a continuum according to the degree of similarity among the vegetation stands.

One method of determining the continuum is by gradient analysis which was developed extensively by Whittaker (1951, 1956, 1967). It is, therefore, fitting that Whittaker's main approach to the definition of climax was via gradient analysis.

Another major distinction between the climax pattern theory and the monoclimate, polyclimate, polyclimate climax theories is that it does not require geomorphological equilibrium. However, to accept the climax pattern theory, one has to reject the association concept, as used by Braun-Blanquet (1932) or Clements (1936), and consider vegetation as a continuum through gradient analysis.

The (Site) Climax Theory

Dyksterhuis (1949, 1958a) discussed a climax theory in relation to range site classification. The term "site climax" will be used to refer to this theory."

Dyksterhuis (1949) reported: "We accept products of man-caused erosion along with intrazonal and azonal soils as potentially stable soils or sites and consider the relatively stable plant community in equilibrium with such soils as climax. Summarily, the term climax as used here refers to climatic, edaphic, or physiographic climaxes and is usually synonymous with original vegetation." Therefore, Dyksterhuis, like Whittaker, views climax in a

very fundamental aspect. The major difference between the site climax theory and the monocl意思, polyclimax, polyclimatic climax theories is that it does not require geomorphological equilibrium and soil maturity. In this respect, it resembles the climax pattern theory.

Even though the site climax and climax pattern theories are similar in basic philosophical concepts, they differ in their approach to fulfilling these concepts. The climax pattern theory follows the continuum approach while the site climax theory follows the discontinuous approach.

The meaning of original vegetation and man-caused eroded soils is important. Original vegetation, as used by Dyksterhuis, refers to the native plant population and excludes introduced species, whether they are naturalized or not.

In cases where a particular soil series has eroded or has had another major disturbance occur, such as the water table being lowered on a soil characterized by a high water table, the changed habitat affects the site climax plant association. It also affects that particular soil series, or phase, because it no longer has the same distinguishing characteristics. Thus, a phase of that soil series or a new soil series may need to be developed in order to reflect these changes. This will also reflect a change in the climax plant association; namely, the same site climax which occurred before disturbance is no longer capable of inhabiting the site. Therefore, the highest plant succession that is now capable of inhabiting this eroded soil is considered to be the climax for that site. Dyksterhuis (1958b) pointed out that climax vegetation for a site can be measured (quantitatively) to show the differences between sites resulting from different soils and climate.

Climax and Classification Summary

Of the 5 climax theories, only 2 appear to be compatible with today's need of delineating current vegetation in relation to its potential with consideration of trend. These are the climax pattern and site climax theories. These 2 are considered the best choices because neither requires maturity in soil development or geomorphological development for a plant community to be considered "climax". In contrast, the mono, poly, and polyclimatic theories require soil maturity. One of the major objectives of a classification is to provide management with a useful tool to know what and how much it is managing. For a classification to be most useful to management (i.e., resource managers), the most logical choice is the site climax approach. Site climax is already used widely with the USDA Soil Conservation Service and the USDI Bureau of Land Management and Bureau of Indian Affairs.

Determining the site climax vegetation may be difficult for some areas of the United States. Shiflet (1973) gave 5 methods to use to determine climax vegetation where it is absent:

1. Evaluate climax vegetation on associated soils subjected to minimal disturbance.
2. Compare areas receiving varying degrees of use with similar areas receiving no use.
3. Evaluate and interpret research dealing with natural plant communities and soils.
4. Review early historical and botanical literature.
5. Extrapolate existing vegetation information to areas of similar soils, climate, and microenvironment.

It is necessary to know the soil series (and phases when applicable) to place a plant community that has departed from climax in the correct site climax. If a plant community is in a low ecological stage, the only characteristic it may have in common with the site climax plant community is the soil series (and phase).

Although a classification should be based on climax vegetation, there is a need to know the current vegetation of an area. Information about the existing vegetation is necessary to establish ecological status and vegetation trend needed to make management decisions. Therefore, it is necessary to use the current vegetation in conjunction with climax vegetation classification. While no climax

theory can be all things to all people, site climax as proposed appears to be a very logical choice as the basis for a classification system for management purposes.

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Livestock Impacts on Riparian Ecosystems and Streamside Management Implications... A Review

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Historically, riparian vegetation has been defined as vegetation rooted at the water's edge (Campbell and Franklin 1979). Quite often, however, the stream influences vegetation in many ways and well beyond the water line. In lotic systems, the stream is not only responsible for increased water availability, but also for the soil deposition, unique microclimate, increased productivity, and the many consequential, self-perpetuating biotic factors associated with riparian zones. These factors all contribute in the formation of a unique assemblage of plant communities quite distinct from upland communities surrounding the riparian zone. Therefore, along streambanks, other lotic systems, and even ephemeral drainages, riparian ecosystems could best be defined as those assemblages of plant, animal, and aquatic communities whose presence can be either directly or indirectly attributed to factors that are stream-induced or related (Kauffman 1982).

Riparian zones can vary considerably in size and vegetation complexity because of the many combinations that can be created between water sources and physical characteristics of a site (Odum 1971, Platts 1979, Swanson et al. 1982). Such characteristics, include gradient, aspect, topography, soil type of streambottom, water quality, elevation, and plant community (Odum 1971). However, riparian zones, particularly those bordering streams or rivers, have several characteristics in common. They are ecotonal, with high edge to area ratios (Odum 1978). As functional ecosystems they are very open with large energy, nutrient, and biotic interchanges with aquatic systems on the inner margin (Cummins 1974, Odum 1978, Sedel et al. 1974) and upland terrestrial ecosystems on the other margin (Odum 1978).

Thomas et al. (1979) stated that all riparian zones within managed rangelands of the western United States have the following in common: (1) they create well-defined habitat zones within the much drier surrounding areas; (2) they make up a minor proportion of the overall area; (3) they are generally more productive in terms of biomass—plant and animal—than the remainder of the area; and (4) they are a critical source of diversity within rangelands. Both density and diversity of species tends to be higher at the

land/water ecotones than in adjacent upland, especially where regional climates are characterized by dry periods (Odum 1978). Ganskopp (1978) described 44 vegetation communities in a 49-hectare riparian zone in the Blue Mountains of northeastern Oregon. Kauffman et al. (1984) stated that the several biotic, environmental and other abiotic factors interacting in a riparian zone in Oregon created a disproportionately greater number of niches compared to surrounding upland ecosystems. Two-hundred and fifty-eight stands of vegetation representing 60 discrete plant communities were identified within this study area. The higher diversity, productivity, and other unique factors associated with the riparian zone when compared to the surrounding uplands are the primary factors that create the importance of these areas as focal points for the management of the livestock, fishery, and wildlife resources.

Importance of Riparian/Stream Ecosystems

Importance to Instream Ecosystems

Vegetation along small streams is an important component of the riparian/stream ecosystem (Campbell and Franklin 1979, Jahn 1978). Riparian vegetation produces the bulk of the detritus that provides up to 90% of the organic matter necessary to support headwater stream communities (Cummins and Spengler 1978). In these tributaries of forest ecosystems 99% of the stream energy input may be imported from bordering riparian vegetation (i.e., it is heterotrophic) and only 1% derived from stream photosynthesis by attached algae (periphyten) and mosses (Cummins 1974). Berner (in Kennedy 1977) found that even in large streams such as the Missouri River, 54% of the organic matter ingested by fish is of terrestrial origin. The riparian zone vegetation functions both in light attenuation and as the source of allochthonous inputs, including long-term structural and annual energy supplies (Cummins 1974).

Vegetation along streams exercises important controls over physical conditions in the stream environment. It acts as a roughness element that reduces the velocity and erosive energy of over-bank flow during floods (Li and Shen 1973). The result is a higher flood peak than a channel without riparian vegetation but lower erosional factors acting on the floodplain and bank (Schumm and Meyer 1979). Healthy riparian vegetation tends to stabilize

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streambanks, determines bank morphology and may help reduce streambank damage from ice, log debris, and animal trampling (Platts 1979, Swanson et al. 1982).

Channel and floodplain obstructions such as branches, logs, and rocks enhance detention and concentration of organic matter, thereby facilitating its use locally rather than washing downstream (Everest and Meehan 1981, Jahn 1978, Swanson et al. 1982). In addition, wood debris in channel bottoms appears to play an important role in the dynamics of stream morphology. Large pieces of woody debris in streams dissipate stream energy, control routing of sediment and water through channel systems, and serve as substrates for biological activity by microbial and invertebrate organisms (DeBano 1977, Swanson et al. 1982).

Streamside vegetation strongly influences the quality of habitat for anadromous and resident coldwater fishes (Duff 1979, Everest and Meehan 1981, Marcuson 1977, Meehan et al. 1977). Riparian vegetation provides shade, preventing adverse water temperature fluctuations (Meehan et al. 1977). The roots of trees, shrubs, and herbaceous vegetation stabilize streambanks, providing cover in the form of overhanging banks (Marcuson 1977, Meehan et al. 1977). Streamside vegetation acts as a "filter" to prevent sediment and debris from man's activities from entering the stream (Meehan et al. 1977). Riparian vegetation also directly controls the food chain of the ecosystem by shading the stream and providing organic detritus and insects for the stream organisms (Cummins 1974, Meehan et al. 1977).

Importance to Wildlife

It is believed that, on land, the riparian/stream ecosystem is the single most productive type of wildlife habitat, benefiting the greatest number of species (Ames 1977, Hubbard 1977, Miller 1951, Patton 1977). The riparian zone provides an almost classic example of the ecological principles of edge effect (Odum 1978). Riparian habitat provides living conditions for a greater variety of wildlife than any other types of habitat found in California (Sands and Howe 1977), the Great Basin of southeast Oregon (Thomas et al. 1979), the Southwest (Hubbard 1977), the Great Plains (Tubbs 1980), and perhaps the entire North American continent (Johnson et al. 1977).

Examples of the wildlife values of riparian habitat are numerous (Carothers et al. 1974, Carothers and Johnson 1975, Henke and Stone 1978, Hubbard 1977, Thomas et al. 1979). Hubbard (1977) reported that 16-17% of the entire breeding avifauna of temperate North America occurs in 2 New Mexico river valleys over the course of a "few score" miles. Johnson et al. (1977) reported that 77% of the 166 nesting species of birds in the Southwest are in some manner dependent on water related (riparian) habitat and 50% are completely dependent on riparian habitats. In western Montana, 59% of the land bird species use riparian habitats for breeding purposes and 36% of those breed only in riparian areas (Mosconi and Hutto 1982). Thomas et al. (1979) stated that of the 363 terrestrial species known to occur in the Great Basin of southeastern Oregon, 299 are either directly dependent on riparian zones or utilize them more than any other habitats.

When riparian vegetation is eliminated, several wildlife species dependent on riparian ecosystems may be either severely reduced or may disappear altogether. Henke and Stone (1978) found 93% fewer bird numbers and 72% fewer avian species on 2 riprapped plots from which riparian vegetation had been removed, and 95% fewer birds and 32% fewer species on cultivated lands previously occupied by riparian forests.

The influence of riparian ecosystems on wildlife is not limited to those animal species that are restricted in distribution to the streamside vegetation. Population densities of birds in habitats adjacent to the riparian type are influenced by the presence of a riparian area (Carothers 1977). When a riparian habitat is removed or extensively manipulated, not only are the riparian species of the area adversely influenced, but wildlife productivity in the adjacent habitat is also depressed (Carothers 1977).

Riparian ecosystems are valuable to wildlife as a source of water, food, and cover (Stevens et al. 1977, Thomas et al. 1979). They also provide nesting and brooding habitat for avian species (Carothers et al. 1974, Johnson et al. 1977, Tubbs 1980). By furnishing abundant thermal cover and favorable micro-climates, especially when surrounded by nonforested ecosystems, they facilitate the maintenance of homeostasis, particularly for big game (Thomas et al. 1979). Riparian ecosystems also serve as big game migration routes between summer and winter range (Thomas et al. 1979), and provide routes and nesting cover for migrating avian species (Stevens et al. 1977, Wauer 1977).

Importance to Livestock

Livestock grazing on rangelands is the most extensive form of land use in the interior Pacific Northwest (Skovlin et al. 1977). Cattle tend to congregate on meadows and utilize the vegetation much more intensively than the vegetation of adjacent ranges (Reid and Pickford 1946).

In northeast Oregon, Reid and Pickford (1946) stated that moist meadow soils in riparian ecosystems are generally so highly productive than an acre of mountain meadow has a potential grazing capacity equal to 10-15 acres of forested range. Although riparian meadows cover only about 1-2% of the summer range area of the Pacific Northwest, potentially they can produce 20% of the summer range forage (Reid and Pickford 1946, Roath and Krueger 1982). However, Roath and Krueger (1982) found that because of livestock concentrations, limits on livestock movements imposed by steep slopes, and erratic distribution of watering areas away from the creek, the riparian zone (covering about 2% of a Blue Mountain grazing allotment) accounted for 81% of the total herbaceous vegetation removed by cattle.

Cattle exhibit a strong preference for riparian zones for a number of the same reasons other animals prefer and use these areas. The main attributes believed to attract and hold cattle to riparian areas are the availability of water, shade, and thermal cover, and the quality and variety of forage (Ames 1977, Severson and Boldt 1978). In addition, sedges (*Carex* spp.) tend to retain relatively constant crude protein levels until the first killing frost. Several sedges common to riparian zones of the Pacific Northwest outrank key upland forage species in sustained protein and energy content (McLean et al. 1963, Paulsen 1969, Skovlin 1967).

Livestock Riparian Relationships

The impact of livestock on riparian zones in public grazing lands of the western states has received much attention recently. Several studies are presently underway examining the impact of livestock grazing on stream ecology, water quality, channel stabilization, salmonid fish habitat and physiology, terrestrial riparian wildlife populations, and riparian vegetation.

It is often difficult for one to interpret science from opinion in the literature. Many of the studies reported in this paper have not necessarily followed the generally accepted "scientific method" for research today. However, it is not the purpose of this paper to determine, even if possible, which published reports represent quality scientific results and which are little more than a forum to express one's opinion. Rather the purpose of this paper is to familiarize the reader with the accepted facts and management theories available today concerning livestock interactions in riparian zones with the other valid resources also dependent or utilizing this resource. Where possible, in this paper, results of properly conducted research are reported using terms such as "significant", referring to a statistically significant result and those of reports relying on observational data or "hearsay" will be reported as suggestions or observations.

General Considerations for Livestock-Riparian Management

The quality of the riparian habitat and its associated aquatic environment, both formed over geologic time, are fragile ecosystems which currently serve as focal points for management of

livestock, recreation, and fisheries and timber resources. It has been reported that inappropriate livestock management results in overuse and subsequent degradation of the riparian/stream ecosystem (Behnke and Raleigh 1978, Oregon-Washington Interagency Wildlife Council 1978, Platts 1979). Davis (1982) suggested that one of the most destructive forces in riparian ecosystems is the long-term impact of overgrazing by cattle. Livestock grazing can affect 4 general components of an aquatic system-streamside vegetation, stream channel morphology, shape and quality of the water column and the structure of the soil portion of the streambank (Behnke and Raleigh 1978, Marcuson 1977, Platts 1979, Platts 1981). Improper livestock use of riparian ecosystems can affect the streamside environment by changing, reducing, or eliminating vegetation bordering the stream (Ames 1977, Behnke and Raleigh 1978, Platts 1979). The channel morphology can be changed by widening and shallowing of the streambed, gradual stream channel trenching, or braiding, depending on soils and substrate composition (Behnke and Raleigh 1978, Gunderson 1968, Marcuson 1977, Platts 1979). The water column can be altered by increasing water temperatures, nutrients, suspended sediments, bacterial counts and by altering the timing and volume of water flow (Behnke and Raleigh 1978, Johnsen et al. 1978, Rauzi and Hanson 1966, Platts 1979). Overgrazing can cause bank sloughoff creating false setback banks, accelerated sedimentation, and subsequent silt degradation of spawning and food producing areas (Behnke and Raleigh 1978, Everest and Meehan 1981, Platts 1979, Platts 1981). These impacts on the water column due to abusive livestock practices result in decreased fish biomass and in percent of salmonid fishes in the total fish composition (Behnke and Raleigh 1978, Bowers et al. 1979, Duff 1979, Gunderson 1968, Marcuson 1977).

Livestock abuse of riparian areas can severely impact terrestrial wildlife habitat causing a subsequent decrease in wildlife species and numbers (Ames 1977, Townsend and Smith 1977, Tubbs 1980, Wiens and Dyer 1975).

Improper grazing can have a considerable effect on vegetation, resulting in decreased vigor, biomass and an alteration of species composition and diversity (Ames 1977, Bryant et al. 1972, Evans and Krebs 1977, Knoph and Cannon 1982, Pond 1961).

While various other land management activities have caused serious losses or reductions in wildlife habitat productivity, livestock grazing has been suggested as the major factor identified in numerous studies throughout the 11 western states (Oregon-Washington Interagency Wildlife Council 1978). Conversely, Busby (1979) suggested that it was not reasonable to conclude that livestock grazing is the only, nor necessarily the major cause of impacts to riparian ecosystems.

Impacts of Livestock on the Instream Ecology

A healthy instream environment is vital for the aquatic life forms inhabiting the stream, as well as for various human needs that directly depend on water quality. High concentrations of suspended solids or other sediment loads, and fecal coliforms or fecal streptococci are usually associated with the degree of impact of man's activities, and can have a major impact in altering an existing stream ecosystem or even creating an entirely new ecosystem (Johnson et al. 1977, Johnson et al. 1978, McKee and Wolf 1963).

During the grazing season, Johnson et al. (1978) could not find any significant differences in physical and chemical properties of streamwater (suspended solids, total dissolved solids, and orthophosphates) between an area grazed at 1.2 ha/AUM and an ungrazed area. After the grazing season, however, there was a significant increase in total dissolved solids which indicated that some livestock waste products may have eventually reached and enriched the stream, probably from the action of rain showers. The presence of cattle significantly elevated the fecal coliform and fecal streptococci for about 9 days after cattle were removed.

Winegar (1977) found sediment loads were reduced 48-79% while flowing through 3.5 miles of a stream protected from grazing.

Rauzi and Hanson (1966) found a nearly linear relation between

runoff and infiltration to the degree of grazing intensity. They found that runoff from a heavily grazed watershed (1.35 acre/AUM) was 1.4 times greater than from a moderately grazed watershed (2.42 acre/AUM) and 9 times greater than from a lightly grazed watershed (3.25 acre/AUM).

Changes in water temperature have been shown to have drastic effects on fisheries and aquatic insect populations (Johnson et al. 1977). Changes in average temperature or daily fluctuations can in effect create an entirely new aquatic ecosystem (Johnson et al. 1977).

Van Velson (1979) found average water temperatures dropped from 24°C to 22°C after 1 year of livestock exclusion on a creek in Nebraska. Claire and Storch (unpublished) compared stream temperatures between an area that had been grazed season long (June 1-October 15) and an area that had been rested for 4 years and, thereafter, grazed only after August 1. The maximum water temperatures outside and downstream from the enclosure averaged 7°C higher than those sampled within the enclosure. Daily fluctuations of water temperatures averaged 15°C outside the enclosure as compared to 7°C inside the enclosures. Winegar (pers. comm. 1982) observed similar results in an enclosure along Beaver Creek in central Oregon.

The effects of livestock grazing have been shown to vary greatly depending upon several factors, in particular, the nature of the stream studied. Duff (1979) stated that introduction of livestock for 6 weeks into a riparian area rested for 4 years resulted in elimination of overhanging banks and a fracturing of the streambank, causing it to erode into the stream. In contrast, after 6 weeks of mid-summer grazing by cattle, Roath (1980) gave a visual estimate of 90% bank stability with little indication that trampling was contributing to or causing erosion. He attributed nearly all erosion present to geologic erosion caused by the actions of streamflow.

Buckhouse et al. (1981) could find no particular relationship between streambank erosion and various grazing treatments (including nonuse) in northeastern Oregon. There appeared to be no significant patterns of accelerated streambank deterioration due to moderate livestock grazing (3.2 ha/AUM and 60-65% utilization of the riparian vegetation). Most bankcutting losses in this system were associated with over-winter periods where ice floes, high water, and channel physiognomy were critical factors involved in the erosional process.

Hayes (1978) found that stream channel movement did not occur more frequently in grazed riparian meadows under a restoration grazing scheme compared to ungrazed meadows after 1 year of study. Rather, streambank degradation appeared to occur more often and to a greater magnitude along ungrazed streams. However, Hayes stated that sloughoff increased as forage removal was above 60%. High forage removal, high amount of foraging time along banks, and high percentages of palatable sedges along the bank were shown to significantly increase the probability of sloughoff occurring during the grazing season.

Kauffman et al. (1983b) measured significantly greater streambank losses in grazed areas (1.3-1.7 ha/AUM) compared to ungrazed areas in northeastern Oregon. The grazed pastures had utilization levels greater than 35% and less than 85% on the different vegetation stands while utilization by native animals was less than 20% on every stand. During 2 late season grazing periods (late August-mid-September), a mean of 13.5 cm of streambank was lost in grazed areas and 3.0 cm was lost in ungrazed areas. Total annual streambank losses were 30 cm in grazed areas and 9 cm in ungrazed areas.

Marcuson (1977) found the average channel width to be 53 meters in an area grazed season long at 0.11 ha/AUM and an average channel width of only 18.6 meters in areas that were ungrazed. Marcuson (1977) also recorded 224 meters of undercut bank/km in the grazed area and 686 meters of undercut bank/km in the ungrazed area. Heavy grazing and trampling by cattle were suggested to cause the excessive erosion.

Duff (1979) found the stream channel width in a grazed area was 173% greater than the stream channel not grazed for 8 years inside an enclosure. Similar results have been reported (Behnke and Zarn 1976, Dahlem 1979, Gunderson 1968, Heede 1977) where overgrazing and excessive trampling caused a decrease in bank undercuts, increases in channel widths, and a general degradation of fish habitat.

Claire and Storch (unpublished) stated that the production of game fish in headwater streams can be used as a biological indicator of the quality of land management that is occurring within the watershed and/or streamside. Overgrazing, causing a reduction in vegetative cover and the caving in of overhanging banks, has been suggested as one of the principal factors contributing to the decline of native trout in the West (Behnke and Zarn 1976).

Bowers et al. (1979) reported an average increase in fish production of 184% for 5 independent studies where livestock use was light or eliminated by fencing. They concluded with a prediction that trout production in streams currently being heavily grazed could be increased about 200% if management decisions were made to optimize habitat conditions for trout.

Van Velson (1979) found rough fish made up 88% of a fish population before relief from grazing and only 1% of the population after 8 years' rest. Rainbow trout (*Salmo gairdneri*) made up 1% of the fish population before cessation of grazing and 97% of the population after relief from grazing. Marcuson (1977) found that an overgrazed section (.11 ha/AUM) of Rock Creek, Montana, supported only 71 kg of brown trout (*Salmo trutta*) per hectare; whereas an ungrazed section produced 238.8 kg of brown trout per hectare. Claire and Storch (unpublished) found in the Blue Mountains of Oregon that game fish were 24% of the total population in area grazed season long, contrasted to a 77% game fish composition within a livestock enclosure.

Chapman and Knudsen (1980) found 8 sections of streamside vegetation in western Washington, judged to be moderately to heavily affected by livestock, had significant reductions in total biomass for Coho salmon (*Oncorhynchus kisutch*), Cutthroat trout (*Salmo clarki*), and all salmonids compared to those areas that had not been grazed. Similar relationships between livestock grazing and salmonid fish populations have been reported by Dahlem (1979), Duff (unpublished), Gunderson (1968), Keller et al. (1979), and Lorz (1974).

Impacts of Livestock on Terrestrial Wildlife

Riparian zones are the most critical wildlife habitats for many species in managed rangelands (Thomas et al. 1979). It is readily apparent that riparian ecosystems are of paramount importance in producing and maintaining a large degree of biotic diversity in North America (Hubbard 1977, Johnson et al. 1977).

Changes in plant vigor, growth form and species composition due to grazing have frequently been related to the increase or decline of various species of birds (Townsend and Smith 1977). Several studies have shown a negative impact on certain avian populations due to grazing (Dambach and Good 1940, Overmire 1963, Owens and Meyers 1973, Reynolds and Trost 1980, Smith 1940). The tendency for livestock to congregate and linger around ponds and streambanks may result in the elimination of food and cover plants and reduces nest sites and habitat diversity (Buttery and Shields 1975, Behnke and Raleigh 1978, Crouch 1978, Evans and Krebs 1977). However, grazing may improve habitat for some avian species (Burgess et al. 1965, Crouch 1982, Kirch and Higgins 1976). In areas of higher precipitation (or productivity), grazing may be highly desirable to open up "roughs" and provide more diversity and patchiness (Ryder 1980). Grazing effects on breeding avifaunas are not uniform nor easily defined, primarily because grazing varies so much in its local intensity and because of the general difficulties in unraveling cause-effect relationships in rangeland faunas (Wiens and Dyer 1975).

Several studies have shown wildlife numbers increased when a riparian area that was abused by improper grazing practices was

fenced and allowed to recover (Crouch 1978, 1982, Duff 1979, Van Velson 1979, Winegar 1977). Duff (1979) reported a 350% increase in small mammal songbird and raptor use after 8 years' rest from grazing. Van Velson (1979) reported increased pheasant (*Phasianus colchicus*) production, increased deer populations, and that waterfowl production occurred for the first time in the rested area. Crouch (1982) found more ducks (primarily mallards) (*Anas platyrhynchos*), more upland game animals, and twice as many terrestrial birds in an ungrazed bottomland rested for 7 years compared to adjacent grazed bottomlands on the South Platte River in northeastern Colorado. The grazed areas, utilized at "varying intensities, provided habitat for significantly more aquatic species of birds.

Mosconi and Hutto (1982) found no significant differences in total bird densities between heavily grazed riparian communities (2.5 cow-calf units/ha) and lightly grazed riparian communities (0.3 cow-calf units/ha). However, significant differences were recorded in bird species composition and foraging guilds. The majority of the bird species significantly affected were of the flycatcher, ground-foraging thrush, or foliage-gleaning insectivore guilds.

Similar results were reported by Kauffman (1982) and Kauffman et al. (1982). No significant differences in total avian densities were noted between riparian communities grazed under a late-season grazing scheme (2.0–2.5 ha/AUM) and those totally excluded from grazing. However, forage removal causing a change in habitat physiognomy did appear to cause some differential use in species and foraging guilds. These differences were particularly evident immediately after forage removal and negligible during seasons when cover and plant growth were similar between treatments. The grazed riparian communities were preferred by birds of insect foraging guilds; ungrazed riparian communities were preferred by birds of herbivorous/granivorous foraging guilds.

Livestock grazing and the subsequent removal of forage in the riparian zone has been shown to cause significant short-term decreases in small mammal composition and densities (Kauffman et al. 1982). When mammal densities before and after the grazing season in 1979 (stocking rate of 2.0–2.5 ha/AUM) were compared, small mammal communities decreased from 800 to 83 mammals/ha in Douglas hawthorn (*Crataegus douglasii*)-dominated communities; from 450 to 60 mammals/ha in riparian meadow communities; and from 129 to 42 mammals/ha in black cottonwood (*Populus trichocarpa*)-mixed conifer communities. By late summer the following year (10 months after grazing) and just prior to the grazing season, small mammal densities were not significantly different between grazed and ungrazed areas.

When properly managed, the grazing of domestic livestock is generally compatible with wildlife, and may even increase the numbers of some species (Tubbs 1980). Nongame wildlife which depend on riparian ecosystems have intangible values which are very hard to evaluate (Peterson 1980). It has been demonstrated that livestock can graze streambanks without causing serious damage, and the capability to achieve positive on-site livestock control appears to be the limiting factor (Claire and Storch unpublished).

Impacts of Livestock on Riparian Vegetation

Recently there has been much published research and opinion on the effects of livestock in riparian ecosystems. Specifically, these reports have dealt with soil compaction and its relationship to root growth; plant succession and productivity; and species diversity and vegetation structural diversity. Opinions on the subject have varied from there being no evidence of heavy, season-long cattle grazing affecting the productivity of a riparian zone, or causing bank deteriorations by trampling (Roath 1980) to grazing only a few days seriously impairing a riparian zone's reproductive capability.

Impacts to riparian vegetation induced by livestock can basically be separated into: (a) compaction of soil, which increases runoff and decreased water availability to plants; (b) herbage removal,

which allows soil temperatures to rise and increases evaporation to the soil surface; and (c) physical damage to vegetation by rubbing, trampling, and browsing (Severson and Boldt 1978).

Impacts of Trampling

The impact of livestock trampling on soil compaction bulk density and subsequent effects on forage growth have been documented. Alderfer and Robinson (1949), Bryant et al. (1972), Orr (1960), and Rauzi and Hanson (1966) all found soil compaction increased linearly with increases in grazing intensity.

Alderfer and Robinson (1949) found grazing and trampling Kentucky bluegrass (*Poa pratensis*) upland pastures to a 1-inch (2.5 cm) stubble height reduced vegetation cover, lowered yields, decreased noncapillary porosity, and increased the volume weight of the 0-1 inch (0-2.5 cm) layer of soil.

Rauzi and Hanson (1966) found water intake rates on silty clay and silty clay loam soils to be 2.5 times greater in an area grazed at 1.35 acres/AUM compared to an area grazed at 3.25 acres/AUM. After 22 years of grazing at this intensity, not only had species composition been altered but soil properties had been changed as well.

In a riparian zone continuously grazed season long, Orr (1960) found bulk density and macropore space to be significantly greater in grazed areas over exclosures. Differences in total pore space (both macro- and micro-pores) between grazed and exclosed areas were small because of a transformation of macropore spaces to micropore spaces by trampling. Macropore space is a more sensitive indicator of compaction or recovery from compaction than either micro or total pore space (Orr 1960).

Bryant et al. (1972) found increasing trampling pressure had an adverse effect on Kentucky bluegrass swards, particularly during the months of June and September. After one overwinter period, there was a significant difference in soil compaction between an area trampled by 120 cow trips over bluegrass plots and an area that was untrampled.

Impacts of Herbage Removal

Impacts of herbage removal can be divided into 2 categories according to vegetation structure: (1) utilization of herbaceous vegetation and subsequent impacts on species composition, species diversity, and biomass produced and (2) utilization of woody vegetation and subsequent impacts on foliage cover, structural height diversity and stand reproduction.

A major vegetation change that has taken place in mountain riparian systems of the Pacific Northwest is replacement of native bunchgrass with Kentucky bluegrass. It has successfully established itself as a dominant species in native bunchgrass meadows as a result of overgrazing by herbivores and subsequent site deterioration (Volland 1978).

Pond (1961), in Wyoming, found clipping native bunchgrass meadows every 2 weeks for 4 years caused a marked reduction in native sedges (*Carex* spp.), tufted hairgrass (*Deschampsia caespitosa*) and fostered the appearance of Kentucky bluegrass where it was not present before. Kauffman et al. (1983a) found that when grazing was halted in moist meadows, succession towards a more mesic/hydric plant community occurred. Exotic grasses such as meadow timothy (*Phleum pratense*) and forbs more attuned to drier environments were decreasing and were being replaced by native sedges and mesic forbs.

In central Oregon, Evenden and Kauffman (unpublished) compared plant communities on each side of a fence that was heavily grazed on one side and protected from grazing on the other. The grazed site was dominated by Kentucky bluegrass and Baltic rush (*Juncus balticus*), while the ungrazed site was dominated by panicled bullrush (*Scirpus microcarpus*). Twenty herbaceous species were recorded in the grazed area with 12 herbaceous species recorded in the ungrazed area. Dobson (1973) also found an increase in species numbers due to grazing in a riparian zone in New Zealand. He concluded the effect of grazing had been to open

up the vegetation, creating more niches in which weeds could establish themselves. Hayes (1978) in central Idaho also observed that the abundance of forb species appeared to be higher in grazed areas than in pristine areas.

The impact of cattle on herbaceous productivity in riparian zones has been examined along several streambanks in the western United States. Duff (1979), Gunderson (1968), Kauffman et al. (1983a), Marcuson (1977), McLean et al. (1963), and Pond (1961) found either decreases in biomass due to herbage removal or increases in biomass due to cessation of grazing in riparian ecosystems.

Kauffman et al. (1983a) compared grazed and ungrazed responses on 10 riparian plant communities in northeastern Oregon from 1978 to 1980. Three of 10 communities displayed significant standing biomass differences. Production in ungrazed moist meadows dominated by Kentucky biomass, meadow timothy, and sedges was significantly less after 2 years of rest compared to grazed meadows but was not significantly different after 3 years of rest. Standing biomass in a Douglas hawthorn-dominated community and in a Kentucky bluegrass-dominated community was significantly greater in ungrazed stands compared to grazed stands after 3 years. Conversely, Volland (1978) could find no significant differences in biomass between a Kentucky bluegrass meadow grazed annually and one that had been rested for 11 years.

Effect of herbivory on shrub and tree production is a critical impact in riparian ecosystems, because of the importance of the woody vegetation to wildlife habitat and its dominant influence in altering the riparian microclimate. While mature vegetation approaches senescence, excessive grazing pressures have prevented the establishment of seedlings, thus producing an even-aged non-reproducing vegetative community (Carothers 1977, Glinski 1977).

The effects of excessive herbivore use on woody vegetation bordering streambanks can generally be termed as negative. Knopf and Cannon (1982) found that cattle significantly altered the size, shape, volume, and quantities of live and dead stems of willows. Cattle grazing was also found to influence the spacing of plants and the width of the riparian zone. Marcuson (1977) found shrub production to be 13 times greater in an ungrazed area than in a severely overgrazed area. Cover was 82% greater in the natural area. On a stream rested from continuous grazing for 10 years, Claire and Storch (unpublished) found alders (*Alnus* sp.) and willows (*Salix* spp.) provided 75% shade cover over areas that had been devoid of shrub canopy cover before exclosure. Similar herbivore-woody vegetation relations have been reported by Crouch (1978), Davis (1982), Duff (1979), Evenden and Kauffman (1980), Gunderson (1968), and Kauffman (1982).

Management of Riparian Ecosystems

Recognizing and understanding the impacts on the streambanks which resulted from all previous land use practices is a prerequisite to streamside planning (Claire and Storch unpublished). Because of their small extent, riparian zones in the past were considered "sacrifice areas" (Oregon-Washington Interagency Wildlife Council 1978, Skovlin et al. 1977). Riparian vegetation has been intensively used by livestock over several decades causing a reduction in the productivity of fish and wildlife habitats and degrading water quality as well as promoting increases in flow fluctuations (Oregon-Washington Interagency Council 1978).

Platts (1979) indicated that riparian ecosystems are the most critical zones for multiple-use planning and offer the most challenge for proper management; therefore, stream habitats should be identified as separate management units from the surrounding upland ecosystems. Even among riparian zones the need to identify and classify them adequately is important for proper stewardship of these systems (Claire and Storch unpublished, Platts 1978, 1979).

However, there have been few attempts to come up with a viable classification scheme of riparian vegetation that is feasible for land

management activities (Cowarden 1978, Norton et al. 1981, Padgett 1982, Pase and Layser 1977, Tuhy and Jenson 1982). The major problem has been the lack of successional knowledge to formulate classification schemes based upon potential climax communities. Other problems have been the lack of continuity of terminology. For example, terms such as riparian dominance type (Padgett 1982), community type (Tuhy and Jenson 1982), and riparian type (USFS-R-4 file data) have all been used to define the basic unit of land which supports a riparian community.

Land management agencies responsible for managing livestock grazing have not adequately considered the influence of grazing on the other uses and users of riparian ecosystems (Platts 1979). Often what is good range or timber management (in short-term economic terms) is not good riparian or stream management (Platts 1979). On the other hand, it has been suggested that proper stream management practices that protect stream banks from damage also improve the potential for riparian zones to enhance fisheries, wildlife, and livestock uses (Gunderson 1968, Marcuson 1977).

Methods discussed for riparian zone rehabilitation include exclusion of livestock grazing, alternative grazing schemes, changes in the kind or class of animals, managing riparian zones as "special use pastures," in-stream structures and several basic range management practices (eg. salting, alternative water sources, fencing, range riders, etc.).

The use of instream structures as a method of riparian rehabilitation has met with some success where instream structures are combined with rest from livestock grazing (Duff unpublished, Heede 1977). Bowers et al. (1979) indicated that some instream structures (e.g., trash catchers, gabions, small rock dams, individual boulder placement, rock jetties, and silt log drops) could serve the dual purpose of increasing the water table in areas of former wet meadows as well as improving salmonid habitat.

Heede (1977), combining rest from grazing with construction of check dams, obtained vegetation cover improvements, a change from an ephemeral stream flow to a perennial flow and a stabilization of gully erosion.

After losing 23 out of 26 instream structures in a grazed area in Utah, Duff (unpublished) suggested that stream improvement structures cannot work effectively to restore pool quality and streambank stability as long as livestock grazing continued. Keller et al. (1979) in Idaho found that rest from grazing negated the need for artificial instream structures intended to enhance trout production for stream ecosystems. Kimball and Savage (in Swan 1979) found aquatic ecosystems can be restored through intensive livestock management at a lower cost than through installation of instream improvement structures.

Grazing systems have achieved some success in riparian rehabilitation and much success in riparian ecosystem maintenance. The damage caused by heavy season or yearlong grazing is well documented (Evans and Krebs 1977, Gunderson 1968, Marcuson 1977, Severson and Boldt 1978). It appears that rest-rotation grazing schemes and/or specialized grazing schemes in which riparian zones are treated as special use pastures have been the most successful.

Hayes (1978), in Idaho, stated that species composition appeared to be improved under a rest-rotation grazing system and bank sloughoff occurrences were not increased if utilization was under 60%. In other Idaho mountain grazing studies, Platts (1982) stated that when rest-rotation strategies call for livestock to utilize riparian vegetation at a rate of 65% or more, some riparian habitat alteration occurs. He also indicated that riparian alteration may be insignificant when utilization is equal to 25% or less.

Claire and Storch (unpublished) found a rest-rotation system to be favorable for achieving desired streamside management objectives if 1 year's rest out of 3 is included in the scheme.

Davis (1982), in Arizona, found that a four-pasture rest-rotation system was a cost-effective and successful method for rehabilitation of the riparian resource when each pasture received spring-

summer rest for 2 years out of 3. On 2 grazing allotments, cottonwood and willows had a mean increase from 78 plants/ha to 2,616 plants/ha, 2 years after implementation of the system. A rest-rotation system also obtained a very favorable response for vegetation surrounding a livestock pond in South Dakota (Evans and Krebs 1977).

Criticism of rest-rotation systems includes reports that objectives for herbaceous vegetation were not being achieved within desired time limits (Storch 1979), and that rest-rotation systems may increase trailing and trampling damage, causing streambank erosion and instability (Meehan and Platts 1978).

Fencing and managing riparian zones separately from terrestrial upland sites as special use pastures has been shown to be an adequate multiple use system of riparian zone management (Kauffman 1982, Winegar 1977). Simulated grazing of a fenced riparian zone annually after August 1 had no measurable effect on production or species composition in riparian meadows, contrasted to decreased production and composition in a simulated season-long scheme in northcentral Wyoming (Pond 1961).

Kauffman (1982) suggested that positive characteristics of a late season grazing scheme on a riparian zone in Oregon included increased livestock production, good plant vigor and productivity, minimal soil disturbance, and minimal short-term disturbance to wildlife populations dependent on riparian ecosystems.

Another grazing system for fenced riparian zones includes winter grazing, where possible, to minimize damage (Severson and Boldt 1978). For riparian meadows dominated by Kentucky bluegrass, Volland (1978) recommended an initial year's rest, then late spring grazing alternated with late fall grazing to discourage flowering, increase tiller development, maintain plant vigor, and maximize productivity.

Changes in the kind or class of animal as well as selective culling and breeding may be another positive tool for riparian rehabilitation or maintenance. Roath (1980) found that cattle exhibited distinctive home range patterns in which certain groups of cattle preferred upland sites and groups preferred riparian sites. As forage became limiting on stream bottoms, some cattle actually decreased intake rather than move away from the riparian zone. Selective culling of these cattle and replacing them with those that prefer uplands may be beneficial for the livestock operator as well as for the riparian zone.

Platts (1982) stated that because sheep grazing on public lands is usually controlled by the use of herders, it may be possible to graze a watershed without exerting direct significant influence on riparian habitats. May and Davis (1982) suggested that sheep have been shown to exert a lesser influence on certain riparian and aquatic ecosystems and conversions back to a sheep operation may be necessary to improve some riparian areas.

The most successful riparian management alternative on public lands to date has been intensive livestock management by permit holders (Storch 1979). Herding livestock on a somewhat daily basis has been successful in limiting the number of livestock that visit streambottoms and improving utilization of upland areas. Proper stewardship of riparian ecosystems is, in effect, money in the bank for the floodplain rancher (Marcuson 1977). Proper management of riparian zones means decreased streambank erosion and floodplain losses (Duff 1979, Gunderson 1968, Marcuson 1977), increased forage production (Evans and Krebs 1977, Pond 1961, Volland 1978), and an increased wildlife and fisheries resource (Buttery and Shields 1975, Duff 1979, Tubbs 1980, Van Velson 1979).

In conclusion, public grazing lands must be managed on a true multiple use basis that recognizes and evaluates the biological potential of each ecological zone in relation to the present and future needs of our society as a whole (Behnke et al. unpublished). Management strategies that recognize all resource values must be designed to maintain or restore the integrity of riparian communities (Behnke et al. unpublished).

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Impact of Small Mammals on the Vegetation of Reclaimed Land in the Northern Great Plains

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Abstract

This paper analyzes the impact of small-mammal activity on the standing crop of vegetation on areas reclaimed after coal strip-mining in northeastern Wyoming. The small-mammal community included 2 carnivorous, 2 herbivorous, and 4 omnivorous species. Deer mice (*Peromyscus maniculatus*) dominated the population on all areas, constituting 85.4% of small mammals live-trapped. Plant species preferred as food by deer mice included sainfoin (*Onobrychis viciaefolia*), fireweed summercypress, (*Kochia scoparia*), and fourwing saltbush (*Atriplex canescens*). Grasses had lower preference rankings than forbs. The deer mouse population consumed 20 g/ha/day of plant matter. They consumed 0.11% of the aboveground peak standing crop (PSC) during the growing season, and the consumption of the total small-mammal community was less than 1% of PSC. However, the PSC of sainfoin was significantly affected by grazing of small-mammal populations.

Large tracts of land in the shortgrass prairie of the Northern Great Plains have been strip-mined for coal and require reclamation to levels of productivity that existed before the disturbance. Understanding the role of plant-animal interactions in the reestablishment of vegetation after reclamation is essential to designing successful reclamation procedures for strip-mined land. Small mammals can limit the effectiveness of seedings on rangeland (Nelson et al. 1970), burned brushlands (Howard 1950), and disrupted forest habitat (Radvanyi 1980). Grazing by small mammals specifically has been found to decrease primary production in arctic tundra (Batzli 1975) and desert scrub (Soholt 1973) and the

volume and cover of vegetation in temperate grassland (Batzli and Pitelka 1970). In simpler ecosystems, greater proportions of total available food are removed by small mammals, up to 10% in some systems (Petruszewicz and Grodzinski 1975).

The objective of this study was to determine the effect of small-mammal herbivory on the standing crop and species composition of vegetation on land of different ages after reclamation. This paper describes the dietary preferences of deer mice and compares consumption of vegetation during the growing season, estimated from dietary composition, with changes in standing crop of those plant species on plots exclosed from small-mammal populations. Successional changes in small-mammal populations in response to vegetation changes on reclaimed land in the Northern Great Plains are reported elsewhere (Hingtgen 1982).

Methods

Site Description

Research was conducted on the Belle Ayr Mine owned by the AMAX Coal Company, located at an elevation of 1,402 m, 30 km south of Gillette, Wyo. Climate in the eastern region of the Powder River basin is semiarid, with an average temperature of 7.4 C, average annual precipitation of 360 mm, and a frost-free season from approximately May 21 to September 25. Rangeland vegetation in the vicinity is dominated by big sagebrush (*Artemisia tridentata*), needle-and-thread grass (*Stipa comata*), and blue grama (*Bouteloua gracilis*).

Reclamation procedures return the overburden to the horizontal strata from which it was removed. After the topsoil has been replaced, seed and fertilizer are drilled into the soil. The basic seed mix consists of wheatgrasses (*Agropyron* spp.), green needlegrass (*Stipa viridula*), blue grama, alfalfa (*Medicago sativa*), yellow sweetclover (*Melilotus officinalis*), sainfoin, fourwing saltbush, winterfat (*Ceratoides lanata*), sunflower (*Helianthus* spp.), basin wildrye (*Elymus cinereus*), and winter wheat (*Triticum aestivum*).

Two reclaimed areas were studied in 1980, a 2-year-old area and a 4-year-old area. In 1981, 4 reclaimed areas were studied, a pair of 2-year-old areas, a 3-year-old area, and a 5-year-old area. The

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similarity of vegetation and small-mammal populations on the 3- and 5-year-old areas in 1981 (Hingtgen 1982) led us to treat these similarly throughout our analyses. All reclaimed areas studied are located on north-facing slopes except one 2-year-old area, which is level.

Trapping

Small mammals were live-trapped monthly on each of the areas from June to August in 1980 and in May, June, August, and September 1981. Species, age (either adult, or juvenile), sex, and reproductive condition of the animals were recorded before they were marked and released (Hingtgen 1982). Population densities were estimated from models for closed populations developed by Otis et al. (1978). To determine food preferences, small mammals were snap-trapped on similarly aged reclaimed areas adjacent to the live-trapping grids.

Vegetation Sampling

Peak standing crop (PSC) was estimated for each species by harvesting plots exclosed from small mammals by 0.6-cm mesh hardware cloth 1 m tall, buried 12–15 cm in the ground, and lined across the top with aluminum flashing. Baited snap-traps placed inside the exclosures for 1 week in late summer indicated that the barrier was rodent-proof. Quadrats within plots were 0.10 m² in 1980 and 0.25 m² in 1981, and were circumscribed by an unharvested 0.25-m strip within the exclosures. Aboveground vegetation was harvested from randomly selected quadrats in each plot at 2-week intervals in July and August 1980 and at monthly intervals from May to August 1981. In June and August 1981, 2 quadrats were harvested in each paired plot to increase the number of samples during peak seasons of growth. Harvested samples were sorted into green and dead standing material, and green vegetation was sorted by species. The standing crop of vegetation at each clipping was estimated from oven-dry weights of green vegetation.

Reference Ranking

Stomach contents of the animals were reduced to uniform particle size, oven-dried, weighed, and examined under a microscope to determine percentage relative densities of species in the stomach contents. In 1981, oven-dried, stomach samples were sent to the Composition Analysis Laboratory (Department of Range Science, Colorado State University, Fort Collins) for analysis. Values for percentage relative densities of food species were converted to percentage dry weight of the food in the stomach contents (Sparks and Malechek 1968). We treated food items such as seeds and arthropods similarly to plant materials when estimating relative dry weight in the diet and food consumption rates. Analogous structures, such as undigested plant epidermal remnants, seed coats, and chitinous remnants of arthropods, were used to identify food items in the histological analysis. Preferences of deer mice for plant species were determined by comparing mean absolute ranks of dietary occurrence and availability for each food item (Johnson

1980). Standing crop of a species was assumed to reflect availability of that species to the small mammals.

Consumption Rates

The amount of the PSC consumed by deer mice was estimated from the relative proportion of the food items in the diet, density of consumers, and caloric requirements of the consumers. Energetic costs were estimated by summing energy costs of maintenance and growth and dividing by the coefficient of digestibility (proportion of the ingested food that is digested) for deer mice (Schreiber 1979:148). The caloric content of arthropods, seeds, and green vegetative material is 5.67, 5.25, and 4.88 kcal/g, respectively (Cummins and Wuycheck 1971).

Estimates of consumption by thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) were calculated on the basis of minimum energetic costs of existence of 0.233 kcal/g/day reported by Scheck and Fleharty (1979), assuming that the diet included 55% plant material (Flake 1973). Schreiber (1979) estimated consumption of western harvest mice (*Reithrodontomys megalotis*) in shrub-steppe vegetation, and we assumed similar consumption rates and a dietary composition similar to that observed for deer mice.

In the results that follow, all means are reported plus or minus one standard error. Probabilities given are the exact probabilities of obtaining the test statistics, assuming that the null hypothesis is true.

Results

Small Mammal Abundance

The small-mammal community on reclaimed land consisted of 4 omnivorous, 2 herbivorous, and 2 carnivorous species (Hingtgen 1982). Omnivores dominated the population, and deer mice constituted 85.4% of small mammals captured. All species were captured in greater numbers on older, established reclaimed areas (3-, 4-, and 5-years old) except the western harvest mouse in 1980. Densities of deer mice were similar on 2-year-old and established reclaimed areas averaging 13.0±1.5 and 13.9±1.5/ha, respectively. Naive density estimates (Otis et al. 1978) of western harvest mice on 2-year-old and established reclaimed areas averaged 0.6±0.4 and 1.5±0.4/ha, respectively. Density of thirteen-lined ground squirrels averaged 0.6±0.3/ha on 2-year-old areas and 1.4±0.3/ha on established areas. Densities of other species could not be accurately estimated because of the relatively small numbers of captures (Hingtgen 1982).

Food Preferences of Deer Mice

Plant matter composed an average of 83.2% dry weight of the stomach contents in 1980 (n=62) and 45.3% in 1981 (n=68). The preference rankings of plant species in the diets of deer mice are shown in Table 1. In general, forbs ranked higher than grasses as preferred food species. Sainfoin was the most consistently high-

Table 1. Preference ranking of plant species used as food by deer mice on reclaimed land in northeastern Wyoming. Species in the same column with different numbers have significantly different ranks.

1980 Reclamation Age		1981 Reclamation Age	
2 Years	4 Years	2 Years	3-5 Years
Yellow sweetclover1	Yellow sweetclover1	Fourwing saltbush1	Sainfoin1
Fireweed summercypress1	Fourwing saltbush2	Sainfoin1,2	Fireweed summercypress1
Sainfoin1,2	Sainfoin3	Needlegrass-ricegrass1,2,3	Mustards2
Fourwing saltbush2,3,4	Alfalfa3	Mustard2,3,4	Common Russianthistle2
Needle-and-thread grass3	Needle-and-thread grass4	Brome grasses3	Brome grasses3
Alfalfa4	Fireweed summercypress4	Common Russianthistle4,5,6	Fourwing saltbush4
Common Russianthistle5	Common Russianthistle4	Wheatgrasses5	Alfalfa-sweetclover5
Green needlegrass6	Green needlegrass5	Fireweed summercypress6	Needlegrass-ricegrass5
Wheatgrasses7	Wheatgrasses6	Alfalfa-sweetclover7	Wheatgrasses6

Table 2. Estimated average daily food consumption for the deer mouse population during the growing season in 1981 on reclaimed land in northeastern Wyoming (g/ha/day).

Food Type	2 Years			3-5 Years		
	May	June	August	May	June	August
Total	41.8±3.0	42.1±3.0	44.3±3.2	43.2±3.1	42.1±3.0	44.8±3.2
Arthropods	33.4±3.5	26.4±3.8	18.4±4.4	26.5±4.8	26.6±4.4	11.8±3.7
Sainfoin	0.1±0.1	0.3±0.2	14.9±4.7	13.1±5.2	4.4±2.1	13.2±4.0
Seeds	0.9±0.7	13.5±3.8	1.2±1.1	0.4±0.2	9.2±3.3	9.7±3.5
Fireweed summercypress	5.4±2.7	0.8±0.3	4.1±1.6	1.5±0.6	1.0±0.6	6.1±2.9
Common Russianthistle	0.8±0.5	0.4±0.2	2.8±2.6	0.0±	0.2±0.1	0.3±0.1
Mustards	0.0±	trace	1.7±1.1	trace	0.4±0.3	trace
Fourwing saltbush	0.0±	trace	0.8±0.6	0.1±0.1	0.0±	0.2±0.2
Alfalfa-sweetclover	trace	0.6±0.5	0.0±	0.5±0.3	0.4±0.2	0.0±
Wheatgrasses	0.0±	trace	0.2±0.2	0.2±0.1	0.0±	trace

ranking food species, and wheatgrasses were most consistently ranked low. Fourwing saltbush and fireweed summercypress were more preferred than common Russianthistle (*Salsola kali*) and alfalfa, and needlegrasses were most preferred grass species. Mustard species (primarily *Camelina microcarpa*, *Descurainia sophia*, and *Thlaspi arvense*) were not present in harvested plots of vegetation on reclaimed land in 1980.

Sainfoin was particularly abundant in the diet in August on 2-year-old areas (33.6% of the estimated average daily food consumption) and in May and August on 3- and 5-year-old areas (30.0% of daily food consumption, Table 2). It was consumed in significantly greater quantity on 3- and 5-year-old areas than on 2-year-old areas in May ($P=0.022$) and June ($P=0.058$). Fireweed summercypress also was relatively abundant in the diet of deer mice, constituting 8.0% of the estimated total dry weight of food consumed on 2-year-old areas and 7.4% on 3- and 5-year-old areas.

Arthropods made up 66.8±4.4% of the estimated average daily dry weight of food consumed by deer mice during May and June, 1981 (Table 2) and decreased significantly in August on 3- and 5-year-old reclaimed areas ($P=0.019$). The decrease in consumption of arthropods was not associated with a decrease in their relative abundance as measured by pitfall and sweepnet samples. Seeds became more important in the diet in midsummer as they became available. Seed consumption increased from May to June on both 2-year-old ($P=0.005$) and 3- and 5-year-old ($P=0.018$) areas. In August, seed consumption remained relatively high on 3- and 5-year-old areas, compared with significantly less consumption of this food type on 2-year-old areas ($P=0.028$).

Consumption Rates

The estimated daily energy requirement for male deer mice, weighing 18.4 g as adults, was 14.2 kcal/day. Similarly, nonpregnant adult females weighed 19.0 g and required 20.4 kcal/day, assuming 1.32 litters produced during the growing season (Schreiber 1979), with 5.3 young/litter (Brown 1966). A weighed average value of 17.3 kcal/day was used to calculate amount of daily consumption for the deer mouse population. Average daily consumption of food by individual deer mice on reclaimed land during the 128-day growing season was 3.23±0.02 g/day. Plant material composed an average of 66% of this daily consumption over the 2 years. Total daily consumption by the deer mouse population (mean consumption per individual × density) was 43.2±3.1 g/ha/day of which approximately 20 g/ha/day was plant material (Table 2).

The average weight of thirteen-lined ground squirrels captured on reclaimed land was 80 g. Assuming 5.3 kcal/g average energy content of their food and a digestibility ratio of 0.88, similar to that reported by Schreiber (1979) for other rodents, each squirrel would require 4.0 g/day of food. If the diet is 55% plant material, 2.2 g/day of vegetation would be consumed to exactly balance the individual energy requirement. On the basis of our density estimates, the ground squirrel population would consume between 1.3

and 3.1 g/ha/day. On the basis of Schreiber's (1979) estimate, individual harvest mice would consume 1.3 g/day of the plant material. Thus, the harvest mouse population would consume up to 2.0 g/ha/day. The total consumption rate of vegetation by the small-mammal community, including all the species of rodents for which we had reasonable estimates, was 25 g/ha/day.

Plant Communities and Small-mammal Herbivory

Dominant plant species on the 3- and 5-year-old areas in 1981 were wheatgrasses, alfalfa, green needlegrass, and fourwing saltbush. In contrast, the dominant species on 2-year-old areas in 1981 were summercypress, alfalfa, common Russianthistle, and mustard species. Total PSC was similar on 2-year-old and 3- and 5-year-old areas in 1981, (Table 3). However, PSC of grasses was

Table 3. Peak standing crop in 1981 on reclaimed land in northeastern Wyoming (g/sq.m).

Species	Reclamation Age	
	2 Years	3-5 Years
Total	229.1±14.5	238.5±14.5
Grasses	13.5±5.7	94.9±5.7
Forbs and (saltbush)	215.1±13.3	142.8±13.3
Legumes	64.8±9.0	100.6±9.0
Alfalfa	52.2±8.9	97.2±8.9
Yellow sweetclover	11.4±2.2	0.0±
Fourwing saltbush	0.2±0.1	8.1±3.2
Sainfoin	1.2±0.6	1.0±0.2
Fireweed summer-cypress	94.4±12.4	0.8±0.9
Needlegrass	0.4±0.2	23.0±2.1
Common Russianthistle	33.1±5.5	3.0±1.8
Wheatgrasses	7.1±3.5	65.5±6.6
Mustard species	20.2±3.0	0.4±0.3

greater on 3- and 5-year-old areas ($P<0.001$), whereas PSC of all forbs combined and yellow sweetclover was greater on 2-year-old areas ($P<0.001$). Total PSC of leguminous forbs, especially alfalfa, was greater on 3- and 5-year-old areas ($P<0.001$). The PSC of forbs in general was greater on the 3-year-old area (161.4±18.5 g/m²) than on the 5-year-old area (106.0±18.5 g/m², $P=0.046$).

The proportion of the total PSC consumed by deer mice, as estimated from average daily food consumption in 1981, was negligible (Table 4). Adding ground squirrels and harvest mice, which were far less abundant than deer mice, still results in total consumption of less than 1% of PSC. However, deer mice and other rodents consumed a relatively large proportion of the PSC of sainfoin, especially on 3- and 5-year-old reclaimed areas. Larger proportions of the PSC of fireweed summercypress and mustard species were consumed on 3- and 5-year-old reclaimed areas than on 2-year-old areas. On 2-year-old areas, a relatively large proportion of PSC of fourwing saltbush was consumed compared with

Table 4. Percent of peak standing crop consumed by deer mice during the growing season on reclaimed land in northeastern Wyoming.

Species	Reclamation Age	
	2 Years	3-5 Years
Total	0.10±0.02%	0.12±0.02%
Alfalfa-sweetclover	trace	trace
Fourwing saltbush	2.05±0.95%	0.01±0.01%
Sainfoin	6.20±2.08%	13.60±1.55%
Fireweed summer-cypress	0.05±0.01%	2.40±0.96%
Common Russianthistle	0.06±0.04%	0.07±0.03%
Wheatgrasses	0.01±0.01%	trace
Mustard species	0.04±0.03%	0.47±0.23%

consumption of other species.

Discussion

Food Preferences of Deer Mice

Deer mice are opportunistic omnivores, feeding on the more abundant, efficiently digested available food (Whitaker 1966, Williams 1959). Compared with results of previous studies on undisturbed rangelands (Williams 1959, Johnson 1961, Flake 1973), diets of deer mice on reclaimed land, especially in late summer, consisted of more vegetative material and fewer seeds. A native legume, sainfoin, and an annual forb, fireweed summercypress, were preferred food species in both years. Sainfoin frequently occurred in the diet of deer mice early in the growing season. Everett et al. (1978) have reported a preference by deer mice for seeds of sainfoin, but a preference for green vegetative parts of this species has not been reported. The prevalence of annuals such as fireweed summercypress and common Russianthistle in the diet is consistent with previous food habitat studies of deer mice (Flake 1973, Kritzman 1974). Everett et al. (1978) ranked seeds of alfalfa intermediate in preference and seeds of fourwing saltbush among the least preferred as food for deer mice. Deer mouse consumption of fireweed summercypress, common Russianthistle, mustards, and fourwing saltbush was not a direct response to the amount present and may reflect a need to supplement a "monotonous diet" (Andrzejewska and Gyllenberg 1980).

Energetics

Estimates of total food consumption derived from the dry-weight composition of the diet are higher than those reported by Johnson and Groepper (1970), who found that deer mice required 1.9 g/day of food averaging 5.57 kcal. Schreiber (1979) estimated that deer mice (males 1.2 g, females 16.8 g) required 2.9 g/day of a diet with a mean caloric value of 5.75 kcal/g, averaged over the entire year, but indicated that consumption during the growing season may average only 2.7 g. The consumption estimates for ground squirrels are minimum estimates because they do not reflect the costs of reproduction or that 50% of the individuals were juveniles with additional requirements for growth.

Impact of Small Mammals on Revegetation

The pattern of consumption of higher proportions of plant species where they are less abundant indicates the potential of small mammals to alter plant communities. Although the proportion of total PSC consumed is small, the proportion of sainfoin consumed, may affect the establishment of that species. Considering the entire small-mammal community and the scope of their activities, potential exists for small mammals to alter subsequent plant communities. On the basis of estimated consumption by reestablished small mammal populations, the greatest problems for reclamation specialists would be establishing leguminous forbs and shrubs. The established vegetation is the net result of the seeding mixture, prevailing abiotic conditions, and the effects of reinventing herbivores. Given sufficient data on the preferences of

herbivores, legumes could be screened for nonpreference (Hewitt et al 1982), alternative foods could be provided (Sullivan and Sullivan 1982), or preferred species could be seeded at higher rates. The most suitable management alternative will depend on the levels of herbivory and the projected uses as grazing land and wildlife habitat.

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Grazing Management Impacts on Quail During Drought in the Northern Rio Grande Plain, Texas

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Abstract

Relationships between the abundance of 2 quail species and range site and grazing management during drought were evaluated in the northern Rio Grande Plain of Texas. Clay loam range sites provided better nesting cover and greater abundance of forbs for quail than sandy loam and shallow ridge range sites. Foliar cover and aboveground standing crop of grass were greater on the 3 range sites within the short duration and deferred rotation systems as compared with the yearlong system. During drought, grazing systems provided better nesting and protective cover for quail than yearlong grazing.

Recent grazing studies have shown that the primary values of grazing systems are increased forage production and range improvement (Heady 1961, Mathis et al. 1974, Kothmann 1975, Pieper et al. 1978). Many questions remain concerning effects of specialized grazing systems on wildlife populations.

Wildlife has always been a primary product of rangeland, and in recent years the economic value of game animals has become increasingly important to landowners in Texas. A growing interest in quail among Texas hunters points to the desirability of understanding effects of grazing management on quail populations. The objective of this study was to evaluate bobwhite (*Colinus virginianus*) and scaled (*Callipepla squamata*) quail indices of abundance in relation to vegetation parameters affected by grazing management and range site.

Study Area

The study was conducted from March through December 1980 on the Rio Grande Plain Experimental Ranch. The 4,228-ha ranch, located about 55 km west-southwest of Uvalde, Texas, is operated by the Texas Agricultural Experiment Station.

The area has a subtropical steppe climate characterized by mild winters and hot summers. The average annual rainfall is about 50 cm, and periodic droughts are common. Over a 75-year period, 53% of the annual rainfall has been below average with 1 of 4 years having less than 40 cm (Waldrip 1957). The frost-free period lasts about 285 days. Mean air temperatures range from -4° C in January to 42° C in July.

Total rainfall for 1980 was 48 cm, with major storms in May (18 cm), August (11 cm) and November (7 cm), contributing 75% of the annual total. Only about 4 cm of precipitation fell during January through April, so spring vegetative growth and most quail breeding activity were delayed until after the May rainfall. Above average temperatures were recorded during June and July, with total rainfall during this period of only 2 cm. Rainfall received in August

and November as a result of hurricanes relieved drought effects on vegetation.

The topography of the ranch is flat to gently sloping. Soils are clays (Entic Pellusterts), clay loams (Aridic Haplustolls, Aridic Calcicustolls), sandy loams (Aridic Paleustalfs, Ustollic Calciorthids), and shallow gravelly loams (Petrocalcic Calcicustolls, Ustollic Paleorthids). Located in the South Texas Plains Vegetational Area (Gould 1975), the ranch is typical of the mixed brush country of south Texas.

Methods

The grazing systems were initiated in 1975 and include a 6-pasture, 1-herd short duration system, a 4-pasture, 3-herd deferred rotation system, and a 1-pasture, 1-herd yearlong system (Fig. 1). Pastures 9 and 11 of the short duration system, pasture 10 of the deferred rotation system, and pasture 12, grazed yearlong, comprised the study areas. These pastures were chosen because they included mixtures of the various range sites in somewhat equal proportions.

All grazing systems were stocked with Hereford \times Brahman, Angus \times Brahman, and Santa Gertrudis cows. The cattle under yearlong grazing were drylot fed from March 23–May 24 because of lack of forage and critical weight loss by animals due to drought.

The average 1980 yearlong stocking rates were 7.2, 9.0, and 9.4 ha/AU for the short duration, deferred rotation, and yearlong grazing systems, respectively. Actual stocking rates for each study pasture are shown in Figure 1. The short duration system was stocked 25% heavier than the other 2 systems. Of pastures used in the study, pasture 11 of the short duration system had the highest stocking rate during 1980. Stocking densities (AU/ha during the grazing period) were greater for short duration pastures and least for the pasture grazed yearlong.

Clay loam, sandy loam, and shallow ridge range sites were sampled within each pasture in which they occurred. Thirty-four transects, each 150 m in length, were located randomly on each range site in each pasture. Ten, 0.25-m² plots, randomly located along each transect, were used to sample herbaceous vegetation in March, May, August, and December. Foliar cover was estimated for grass species using a gridded sampling frame with adjustable legs. A measure of forb abundance was determined by recording the number of 10-cm² grid areas, within the 0.25 m² frame, in which each forb species occurred. Current standing crop of grasses and forbs was clipped at ground level for each plot and weighed in the field during each sampling period. Samples of clipped vegetation were oven dried to determine moisture content and dry weight of field samples.

Three methods were used to index quail abundance. Visual counts from horseback were made from May through December. Two permanent transects, each about 1.6 km long, were established in each of pastures 9, 10, and 11, and 4 transects were placed in pasture 12. Transects were located across the 3 range sites in each pasture as equally as possible (Table 1). The transects were ridden monthly during morning and afternoon. Quail sightings were

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Table 2. Average number of quail/32 km seen on monthly counts from a vehicle on the Rio Grande Plain Experimental Ranch from 1976 through 1980.

Year	Bobwhite Quail	Scaled Quail
1976	18	4
1977	52	9
1978	15	2
1979	19	5
1980	3	1

approximated (Miller 1981, p. 70).

Results and Discussion

Quail populations were low throughout the study period due to drought conditions beginning in 1979 and continuing through April 1980.

Foliar cover of grasses was significantly greater on clay loam

sites compared to sandy loam and shallow ridge sites during each sampling period and over all sampling dates in each of the 4 pastures (Table 3). Clay loam sites in pastures 9 of the short duration system and 10 of the deferred rotation system had greater grass cover than the same range site in pasture 12, grazed yearlong.

Aboveground standing crop of grass was significantly greater on clay loam sites compared to sandy loam and shallow ridge sites during each sampling period and over all dates in each of the pastures (Table 3). Short duration pasture 9 had greater grass weights on clay loam sites compared to other pastures. Trends showed that pasture 12, grazed yearlong, had the lowest grass weights on each of the 3 range sites. Pasture 9 had the lowest stocking rate at 11.8 ha/AU and short duration pasture 11 the highest at 9.4 ha/AU.

Forb abundance was generally higher on clay loam sites, although there were few significant differences (Table 3). Forbs were most abundant on clay loam sites in pasture 12 of the yearlong system.

Although Chi-Square analysis showed that bobwhite use of at least one of the pastures was significantly different than expected ($\alpha < .025$), use of Bonferroni *t*-statistic showed that quail occurred in each pasture with expected frequency (Table 4). Scaled quail

Table 3. Differences in grass cover, weights and forb abundance for range sites by dates and pastures.

Range site	Date ¹				Pasture ²				Avg.
	March	May	Aug.	Dec.	9 SD	10 DR	11 SD	12 Y	
Grass cover (m ² /ha) × 10 ⁻²									
Clay loam	2.6 ^a	3.5 ^a	4.4 ^a	3.4 ^a	3.9 ^a	4.2 ^a	3.3 ^{ab}	2.7 ^b	3.5 ^a
Sandy loam	1.0 ^b	1.0 ^b	1.3 ^b	1.1 ^b	—	1.1 ^c	1.4 ^c	0.7 ^c	1.1 ^b
Shallow ridge	0.7 ^b	0.7 ^b	1.0 ^b	0.7 ^b	1.2 ^c	0.8 ^c	0.7 ^c	0.4 ^c	0.8 ^b
Grass weights (g/m ²)									
Clay loam	24.0 ^a	39.2 ^a	77.2 ^a	50.1 ^a	72.6 ^a	45.7 ^b	41.8 ^b	32.7 ^b	48.2 ^a
Sandy loam	9.3 ^b	10.2 ^b	19.0 ^b	14.0 ^b	—	15.7 ^c	13.2 ^c	10.1 ^c	13.0 ^b
Shallow ridge	8.7 ^b	4.9 ^b	9.7 ^b	8.1 ^b	10.1 ^c	8.0 ^c	7.3 ^c	5.3 ^c	7.7 ^b
Forb Abundance ³									
Clay loam	6.5 ^a	10.2 ^a	12.5 ^a	27.7 ^a	10.2 ^{bcd}	15.7 ^{ab}	14.8 ^{abc}	16.7 ^a	14.3 ^a
Sandy loam	3.7 ^a	8.6 ^a	9.6 ^b	22.9 ^b	—	11.0 ^{bcd}	8.6 ^d	13.3 ^{abcd}	11.0 ^a
Shallow ridge	5.6 ^a	7.3 ^a	7.7 ^b	20.6 ^b	9.4 ^{cd}	9.9 ^{cd}	11.2 ^{abcd}	10.7 ^{bcd}	10.3 ^a

¹Data are compared by column. Means followed by the same letter do not differ significantly at the 5% level by Duncan's new multiple range test.

²Means followed by the same letter do not differ significantly at the 5% level by Duncan's new multiple range test. SD-Short Duration, DR-Deferred Rotation, Y-Yearlong.

³Average number of 10cm² grid areas in which forb species occurred (based on 10, 0.25m² plots/transect or 250 grid areas).

Table 4. Occurrence of quail in each pasture on the 1359 ha study area from May through December 1980.

Species	Pasture and grazing system	Proportion of total transect length (Pi ₀)	Number of quail observed	Expected number ^b of quail observed	Proportion observed in each pasture (Pi)	Confidence interval on ^c proportion of occurrence (95% family confidence coefficient)
Bobwhite	9 (SD)	.197	14	23	.118	0 ≤ P ₁ ≤ .236
	10 (DR)	.199	29	24	.244	.086 ≤ P ₂ ≤ .402
	11 (SD)	.201	17	24	.143	.014 ≤ P ₃ ≤ .272
	12 (Y)	.403	59	48	.496	.312 ≤ P ₄ ≤ .680
Total		1.00	119	119		
Scaled	9	.197	33	10	.623	.356 ≤ P ₁ ≤ .890
	10	.199	8	11	.151	0 ≤ P ₂ ≤ .348
	11	.201	4	11	.075	0 ≤ P ₃ ≤ .220
	12	.403	8	21	.151	0 ≤ P ₄ ≤ .348
Total		1.00	53	53		

^aProportions of total transect length represent expected quail observation values as if quail occurred in each pasture in exact proportion to availability.

^bCalculated by multiplying proportion Pi₀ × n; i.e., .430 × 119 = 48.

^cPi represents theoretical proportion of occurrence and is compared to corresponding Pi₀ to determine if hypothesis of proportional use is accepted or rejected, i.e., Pi = Pi₀.

Table 5. Occurrence of quail on each range site on the 1359 ha study area from May through December 1980.

Species	Range site	Proportion of total transect length (Pi _o)	Number of quail observed	Expected number ^b of quail observed	Proportion observed in each range site (Pi)	Confidence interval on ^c proportion of occurrence (95% family confidence coefficient)
Bobwhite	Clay loam	.426	96	51	.807	.646 ≤ P ₁ ≤ .968
	Sandy loam	.358	14	42	.118	0 ≤ P ₂ ≤ .250
	Shallow ridge	.216	9	26	.076	0 ≤ P ₃ ≤ .184
Total		1.00	119	119		
Scaled	Clay loam	.426	23	23	.434	.130 ≤ P ₁ ≤ .738
	Sandy loam	.358	2	19	.038	0 ≤ P ₂ ≤ .155
	Shallow ridge	.216	28	11	.528	.222 ≤ P ₃ ≤ .834
Total		1.00	53	53		

^a Proportion of total transect length represent expected quail observation values as if quail occurred in each range site in exact proportion to availability.
^b Expected number of quail = proportion Pi_o × n; i.e., .216 × 119 = 26.
^c P_i = observed proportion of occurrence and is compared to corresponding Pi_o to determine if hypothesis of proportional use is accepted or rejected, i.e., P_i = Pi_o.

were observed more frequently than expected in short duration pasture 9, i.e., expected use of pasture 9 was .197 while confidence intervals on observed use were .356 ≤ Pi < .890. Scaled quail use of pasture 12, grazed yearlong was less than expected. Pasture 9 consisted of 61% shallow ridge range site, whereas pasture 12 contained only 7% shallow ridge site.

Clay loam range sites were used significantly more frequently by bobwhite quail, while both sandy loam and shallow ridge sites were used less frequently than expected (Table 5). Scaled quail were observed on shallow ridge range sites significantly more often than expected, whereas sandy loam sites were used less frequently. Scaled quail were observed on clay loam sites with expected frequency.

Whistle count data showed that 81% (155) of the bobwhite whistling cocks recorded in pastures 10, 11, and 12 from April through September were on clay loam sites. These sites provided the greatest perennial grass cover. Sandy loam and shallow ridge sites had 18% and 1% of the bobwhites, respectively. The importance of grass cover to nesting bobwhites has been reported by Lehmann (1946), Parmalee (1955), and Jackson (1972) in Texas. Scaled quail differed from bobwhite with 37, 49 and 14% of the calls being recorded on clay loam, sandy loam, and shallow ridge sites, respectively. In west Texas, Wallmo (1956) observed that calling scaled quail males wandered extensively from one elevated perch to another. This behavior may be reflected in this study. Although scaled quail frequently were observed on shallow ridge sites, the lack of herbaceous cover on these sites probably prevented their use as nesting habitat.

A number of significant correlations were seen between bobwhite quail indices and vegetation parameters (Table 6). Both horseback and whistle indices showed significant positive relationships

between cover and weight of grasses and bobwhite abundance. Correlation coefficients were highest for the whistle index as compared with the horseback index. There were significant positive relationships between bobwhite quail and forb abundance and weight in pastures 11 (short duration) and 12 (yearlong). Forb height was also significantly related to bobwhite abundance in pasture 12 (Table 6).

Few significant correlations were found between scaled quail indices of abundance and vegetation parameters. Perhaps scaled quail were less specific in their habitat preferences under the environmental conditions of this study, and were therefore less likely to show relationships.

Conclusion

The clay loam range site was most important in providing adequate nesting and screening cover and a greater abundance of forbs for quail during the drought year of 1980. Bobwhite quail were particularly dependent upon this habitat type. The more moist clay loam sites may be analogous to bottomlands, identified by Jackson (1972) as "key" habitat for bobwhite quail in the Rolling Plains of Texas. Vegetation on both habitat types was more stable than on other sites during drought. The preference of bobwhite quail for greater herbaceous cover, provided by the clay loam site during the nesting season, was shown by whistle counts.

In southwestern Texas where periodic droughts are common, fluctuations in bobwhite populations are expected. Land managers interested in maintaining highest quail populations during drought years should consider quail habitat requirements when planning practices which affect clay loam range sites. The trend toward greater grass cover and weight within short-duration and deferred rotation pastures showed these grazing systems to be more valuable.

Table 6. Correlation coefficients of bobwhite quail abundance indices and vegetation parameters.

Vegetation parameters	Horseback index				Whistle index			
	Pastures				Pastures			
	10	11	12	Total	10	11	12	Total
Grass cover	0.84*		0.78*	0.47**	0.88*	0.96**		
Grass weight	0.80*	0.74*	0.88**		0.89*	0.89*	0.87*	
Forb abundance		0.70*					0.87*	0.85**
Forb weight			0.89**				0.97**	0.70**
Forb height			0.80**				0.85*	

*Significant at P < 0.05 level.

**Significant at P < 0.01 level.

Correlations that were not significant are not shown.

ble than continuous grazing in providing adequate nesting and protective cover for bobwhites during a drought year. The higher abundance of forbs and lower cover and weight of grasses under yearlong grazing also indicated range deterioration compared to use of a rotational grazing system. Chamrad et al. (1982) showed 5-year average beef production and net income per hectare highest for short duration grazing and lowest for yearlong grazing. Hence, better grazing management for cattle was also best for quail production under drought conditions.

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The Effect of Phytophagous Nematode Grazing on Blue Grama Die-off

NANCY L. STANTON, DENNIS MORRISON, AND WILLIAM A. LAYCOCK

Abstract

Nematode populations were sampled in ungrazed and heavily grazed areas in northeastern Colorado under patches of healthy, senescing, and dead blue grama to test the hypothesis that phytophagous nematodes may cause the senescence. Densities of plant parasites were significantly different under the 3 plant types. Live blue grama supported the highest numbers ($1.2 \times 10^6/m^2$) and dead blue grama, the lowest ($2 \times 10^5/m^2$). Bacterial feeding nematodes also varied significantly with plant type. Highest densities were found under senescing plants ($2.4 \times 10^6/m^2$) and lowest densities were under dead plants ($7 \times 10^5/m^2$). Total densities were slightly but insignificantly lower in the heavily grazed area. Scarlet globemallow and fringed sagewort supported lower populations of both plant parasites and bacterial feeders than did live blue grama. The densities under live blue grama were not unusually high and well within the values reported in the literature for arid grasslands. Thus, nematode root grazing may decrease net primary production but we conclude that nematodes themselves were not the major cause of the die-off.

Blue grama (*Bouteloua gracilis* (H.B.K.) Griffiths) is the dominant plant species on the shortgrass plains in eastern Colorado. In the early to mid 1970's large patches of senescing and dead blue grama plants were observed. By 1977 the Central Plains Experimental Range, the Pawnee National Grasslands, and other shortgrass areas in northeastern Colorado had large areas of dead and dying blue grama (Weiner and Capinera 1980). Initially, nothing was known about the cause of the die-off. However, large numbers of white grubs, the larvae of a May beetle (*Phyllophaga fimbripes* LeConte), were found in the die-off areas. White grubs are root feeders which were suspected to be the cause of the blue grama die-off (Weiner and Capinera 1980). The present study of nematode populations was one of the several investigations to study other possible causes of the damage to blue grama.

Nematodes are a major faunal component in grassland soils and some studies have suggested that they are one of the major herbivores (Scott et al. 1979). In short-grass and mixed-grass prairies, nematodes may significantly reduce both shoot (Smolik 1974, 1977) and root production (Stanton et al. 1981, Stanton 1983) anywhere from 13 to 60%. If further work confirms these results, plant parasitic nematodes will be established as a major factor affecting primary production and vitality of native grasslands. Therefore, in 1978, in conjunction with the study of white grubs, we sampled patches of blue grama in various states of health to determine if root grazing by phytophagous nematodes might be contributing to the die-off.

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Methods

Study Site

The study was conducted on the Central Plains Experimental Range (CPER) operated by the USDA Service, Agricultural Research, 18 km NE of Nunn, Colo. The vegetation is shortgrass prairie dominated by blue grama with other grasses, sedges, forbs, and pricklypear cactus (*Opuntia polyacantha* Haw.) also present. The mean annual precipitation at CPER is 31 cm, based on 30 years of data. May through August are the wettest months, accounting for more than 50% of the annual precipitation. Monthly mean temperatures vary from a high of 22°C in July to a low of -2°C in January.

Sampling Areas

Two areas were selected for sampling. One was in the Environmental Stress Plot (ESA) initially established by the Grassland IBP. The site we selected was adjacent to areas previously manipulated but it had not received any treatment other than relief from ungulate grazing pressure. The other site had been heavily grazed by cattle during summers since 1939. In both areas, soil is an Ascalon sandy clay loam and blue grama was the dominant species.

Both areas could be characterized by numerous patches of senescing and dead blue grama. The most prevalent pattern was apparently healthy blue grama surrounded by senescing plants that could be identified by the mixture of dead and live leaves. In the center of these patches were dead blue grama plants. Most dead plants were widely spaced. Thus it appeared that the die-off began in the center and moved outward in all directions.

A large representative patch in each area was selected for sampling and was divided into 4 quarter circle quadrants. Two cores, randomly selected, were taken from each quadrant within each of the 3 plant types for a total of 8 replicates taken each time of sampling. Cores were 4.8 cm in diameter and 10 cm deep. In 1978 the ungrazed plot was sampled on June 5, June 27, and August 4, and the grazed plot was sampled on June 27 and August 4.

Vegetation was not sampled on the plots where the soil samples were taken; but adjacent dead patches, senescing areas, and healthy areas were sampled on .09 m² quadrats. Weight of individual species was estimated and converted to oven-dry weights based on clipped samples.

The dead patches were dominated by annual forbs in both areas (Table 1). Pricklypear cactus and scarlet globemallow (*Sphaeralcea coccinea* (Pursh) Rydb.) were the main perennial species occurring in the dead patches in both areas. Fringed sagewort (*Artemisia frigida* Wild.) was also abundant within the dead patches in the ungrazed area. Additional cores for nematode extraction (8 replicates in each area) were taken within the quadrants of the dead patches only to include the roots of scarlet globemallow in the grazed area and the roots of fringed sagewort in the ungrazed area.

Each soil core was returned to the laboratory, suspended in cold water, and the suspension sieved (No. 325 sieve) to remove nema-

Table 1. Peak aboveground standing crop (Kg/ha, oven dry) on dead blue grama patches and adjacent live blue grama in areas similar to those where soil samples were extracted to determine nematode densities.

Species	Dead blue grama patches		Adjacent live blue grama	
	Not grazed	Heavily grazed	Not grazed	Heavily grazed
<i>Bouteloua gracilis</i>	52	18	308	155
Other perennial grasses and sedges	15	24	51	111
<i>Ariemisia frigida</i>	141	0	27	0
<i>Sphaeralcea coccinea</i>	317	214	141	12
Other perennial forbs	4	48	24	15
Total perennial herbaceous	529	304	551	293
<i>Chenopodium</i> spp. (mainly <i>C. leptophyllum</i>)	124	201	35	125
<i>Salsola kali</i>	336	48	138	11
Other annuals	187	86	100	41
Total annuals	647	337	273	177
Shrubs	138	0	34	0
<i>Opuntia polyacantha</i>	402	1084	409	1042
Total standing crop	1716	1084	1267	1512

todes. The material retained by the sieve was put on a Baerman funnel for 48 hours (Christie and Perry 1951). The number of nematodes in each sample (and their trophic category) was determined by counting individuals present in each of 3 1-ml subsamples of a 50-ml suspension as described by Smolik (1974). All counts were corrected for extraction efficiency, which averaged 60% for bacterial feeding nematodes, 46% for Dorylaimida, and 59% for the plant parasites. These were the 3 dominant trophic groups. The Dorylaimida consists of species which are plant parasites, predators and omnivores. But they were not assigned to trophic groups since species determination was not possible within the scope of this study.

Laboratory Experiments

To determine nematode response to different moisture levels, wet or dry, 16 senescent and 16 live blue grama plants were dug up from the ungrazed area and potted in 10 by 10-cm plastic pots in the field on August 4, 1978. They were returned to the laboratory and placed in an environmental chamber which was set to duplicate both summer temperature and light regimes of the Central Plains Experimental Range. Half of the senescing plants and half of the live plants were watered every 2 days (wet treatment) and the remaining half were watered every 4 days (dry treatment) to field capacity. On November 4, the nematodes were extracted and counted as described above.

Analysis

Logarithmic transformations of nematode counts were accomplished to provide normally distributed data for analysis of variance. The model for the field study was a stratified random design with 2 factors: date and plant type. There were 8 replicates for each of 4 plant types on each of 2 or 3 sampling dates. Differences between means were compared by Least Significant Range (LSR, Sokal and Rohlf 1969).

The laboratory data were also log transformed for ANOVA. The model is a completely randomized design with 2 factors: plant type and moisture regime.

Results

Field Study

On the ungrazed plot there was both a significant date ($\alpha \leq .001$) and plant ($\alpha \leq .01$) effect on plant parasites (Fig. 1). On all sampling dates, densities were highest under live blue grama, intermediate under senescing blue grama, and lowest under fringed sagewort and dead blue grama. Densities of plant parasites were high in the spring, low in late June, and intermediate in August under live and senescing blue grama and under the fringed sagewort. Plant parasites under dead blue grama declined in mid-season but did not

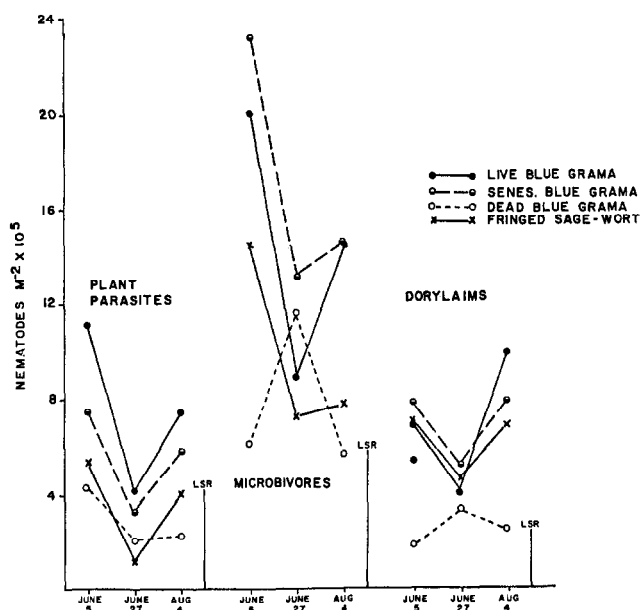


Fig. 1. Densities of plant parasites, microbivores, and Dorylaimida under live, senescing, and dead blue grama and under fringed sagewort sampled to a depth of 10 cm in the ungrazed area.

increase in August.

Densities of bacterial feeders (microbivores) averaged about twice those of the plant feeders and there was also a significant date ($\alpha \leq .005$), plant ($\alpha \leq .001$) and interaction effect ($\alpha \leq .001$). As with the plant parasites, under the live and senescing blue grama and fringed sagewort, an early season high was followed by a significant mid-season decline ($\alpha \leq .05$) with a subsequent increase in August (Fig. 1). The significant date-treatment interaction was caused by this mid-season high sandwiched between early and a late season low densities under dead blue grama. It is also interesting to see that on all dates there were more microbivores under senescing than under live blue grama.

The Dorylaimida (Fig. 1) (which includes omnivores, plant parasites and predators) experienced a significant treatment effect ($\alpha \leq .001$) and a significant date-treatment interaction ($\alpha \leq .05$). Generally, the changes reflect those of the microbial feeders except that the August densities for Dorylaimida were higher or equal to the spring densities. The Dorylaimida population under dead blue grama also appeared to have a mid-season high, but

there was no significant difference in density among the 3 sampling dates.

The heavily grazed plot was sampled only in late June and early August. For the plant parasites (Fig. 2) there were significant date ($\alpha \leq .001$) and treatment effects ($\alpha \leq .05$). As in the ungrazed plots, a late June low was followed by a significant increase in August under the live and senescing plants.

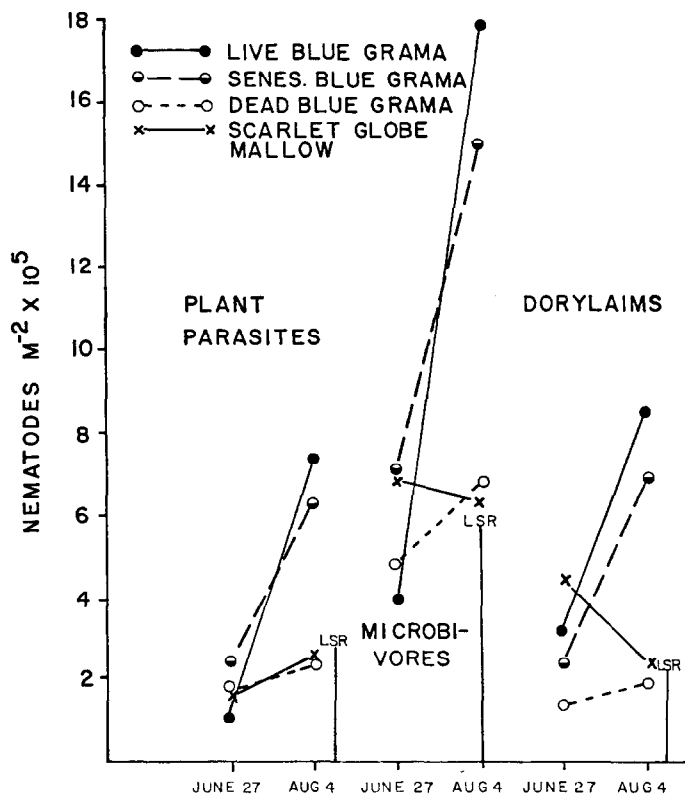


Fig. 2. Densities of plant parasites, microbivores, and *Dorylaimida* under live, senescing, and dead blue grama and under scarlet globemallow sampled to a depth of 10 cm in the heavily grazed area.

A similar pattern was exhibited by some of the microbivores (Fig. 2) with a significant date ($\alpha \leq .001$) and interaction effect ($\alpha \leq .001$). The most notable change was an increase in densities in the live and senescing plots from June 27 to August 4. The other treatments did not change significantly.

For the *Dorylaimida* the date ($\alpha \leq .001$), treatment ($\alpha \leq .001$) and interaction ($\alpha \leq .01$) effects were all significant. Again, there was an increase under live and senescing plants from June to August. The scarlet globemallow population declined and the populations under dead blue grama increased but neither change was significant.

Although the ANOVA was significant in all cases, a comparison of individual mean densities at each date, usually revealed a significant difference only between the extreme values; e.g., in Figure 1 on August 4, the plant parasites were significantly different only under live blue grama (the highest density) and dead blue grama (the lowest density). Further individual comparisons may be made by the LSR values indicated in each Figure.

Laboratory

The nematode densities from pots of live and senescing blue grama exposed to wet and dry treatment in the environmental chamber are shown in Figure 3. For the plant parasites and *Dorylaimida* there was no significant effect of either plant status or moisture. Although the live plants in the wet treatment supported twice as many nematodes on the average as the other 3 treatments, no significant difference emerged because of the high variance among pots.

For the microbivores there was a significant plant type ($\alpha \leq .05$) and moisture effect ($\alpha \leq .05$). The senescent plants in the dry treatment had significantly more microbivores than either of the wet

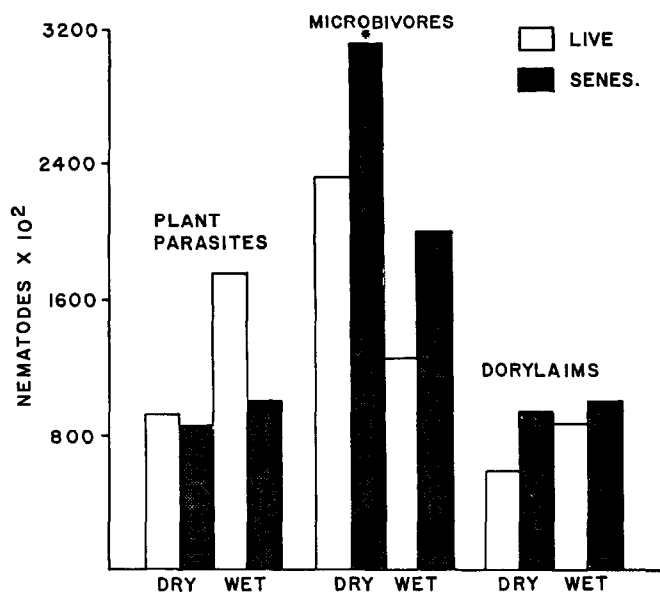


Fig. 3. Average densities of plant parasites, microbivores, and *Dorylaimida* extracted from pots of live and senescing blue grama subjected to either dry or wet moisture regimes in an environmental chamber. The only significant difference appeared with microbivores whose density under dry-senescent plants (*) was significantly higher than the other treatments.

treatments ($\alpha \leq .05$), and the live plants in the wet treatment supported the fewest numbers.

The mean number of microbivores per treatment was inversely, but not significantly (because of small sample size), correlated with the mean number of plant parasites per treatment ($r = .87$ in a simple linear regression); i.e., the senescent plants in the dry treatment had the largest density of microbivores and the smallest density of plant parasites. Likewise, the live plants in the wet treatment had the most plant parasites and the fewest microbivores.

Discussion

Both field and laboratory studies have shown that control of nematodes from shortgrass and mixed grass prairies could significantly increase net primary production (NPP) over the short term. Smolik (1977) found that nematicide application to mixed grass prairie vegetation increased harvestable herbage by 29–59%. Stanton et al. (1981) applied nematicide to plots on the Central Plains Experimental Range and root production increased about 25%. In additional laboratory experiments to measure blue grama response to both above- and below-ground grazing, Stanton (1983) indicated that populations of one species of plant parasite feeding on blue grama for 140 days reduced NPP about 13%. The experimental densities were lower than field densities by at least one-half and were far less species rich (one blue grama plant in the field may host several species of plant parasites). Thus, even at normal field densities, nematodes may exert strong grazing pressure on blue grama roots.

Phytophagous nematodes probably influence plant growth; conversely, changes in root biomass may also affect nematode density. The seasonal pattern in density (early high, mid-season low, late season high) is probably a response to new roots and changes in soil moisture. Field observations, through windows placed on excavations at the Central Plains Experimental Range (Ares 1976), revealed that root growth began a short time before leaf growth in the spring. However, mid-season soil desiccation resulted in the death of 30–60% of the new roots. Late in the season with high water potential, roots again increased in length. However, it is uncertain whether the nematodes die with root die-off or enter anhydrobiosis. Anhydrobiosis is a quiescent state induced by

lowering of soil moisture. This phenomenon has been described in a number of species (see review by Demeure and Freckman 1981) and is probably one of the reasons nematodes are so abundant in arid grasslands. They can essentially wait through periods of low soil moisture with little or no metabolic activity. When conditions become favorable, the nematodes again become active. Plant parasites were most abundant under live, healthy plants because they prefer to feed on new roots. Surprisingly, plant parasite densities under dead blue grama and fringed sagewort did not differ. Fringed sagewort generally supports fewer plant parasites than blue grama (Stanton et al. 1981). Volatile compounds such as terpenes are present in the root exudates of fringed sagewort which may deter belowground herbivores. Scarlet globemallow, also with low nematode densities, has a long, deep tap root so it probably provides fewer feeding sites than the shallow fibrous roots of blue grama. Thus, these 2 plant species do not support as large a population of nematodes as blue grama and might be at a selective advantage under stress conditions when nematode populations are high.

Microbivores were the most abundant trophic class, varying from .4 to $2.2 \times 10^6 \text{ m}^{-2}$, and populations were highest under senescing plants. Microbivores feed on bacteria and the dying roots probably provided more resources for the microbial populations. Another major carbon source for bacteria is root exudates. High exudation rate probably correlates with new root growth. Thus, with favorable moisture regimes in the spring and high root exudation, microbial populations should be high.

In the ungrazed plot the microbivore densities under dead blue grama reached a maximum in mid-season probably because the dead roots provided a large source of carbon. This is consistent with findings from our laboratory experiment in which the highest microbivore densities were from drought-stressed senescing plants.

The Dorylaimida densities were within the range of the plant parasites, and the seasonal trends in their density almost paralleled those of the microbivores. Since many of the Dorylaimida species are predators, they may use the very abundant bacterial-feeding nematodes as a major prey item.

In summary, plant parasitic densities on both the grazed and ungrazed plots under live blue grama varied from 1×10^5 to $1 \times 10^6/\text{m}^{-2}$, well within the range reported from other areas of the Central Plains Experimental Range (R. Anderson personal com-

munication, Stanton et al. 1981). Since these densities are not abnormally high, it is unlikely that nematodes were the cause of the die-off, although they certainly may have been a contributing factor. It is also possible that plant species invading the die-off patches (e.g. fringed sagewort and scarlet globemallow) are successful in part because of chemical or morphological traits that make them resistant to nematode and white grub feeding. Since nematodes may remain viable but inactive in the soil for many years, plant species which provide a root system that is palatable and accessible to nematodes may be difficult to establish even with proper climatological conditions. This idea is speculative but certainly should be investigated further.

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Spatial and Seasonal Variability of Field Measured Infiltration Rates on a Rangeland Site in Utah

MOUJAHED ACHOURI AND GERALD F. GIFFORD

Abstract

This study was conducted to examine both spatial and temporal variability of infiltration rates on a rangeland site in west-central Utah. The experiment utilized a grid 20 m long and 18 m wide in both grazed and ungrazed sites with a sample spacing of 2 m within the grid. To investigate the seasonal effect on variability of infiltration rates, data were collected for 3 seasons (summer, fall, and spring). Measured infiltration rates at 10 and 30 min during all seasons and under grazed versus ungrazed conditions were all found to approximate a two-parameter log normal distribution. Regionalized variable theory was applied to the data through the development of autocorrelograms and semivariograms, revealing a complete lack of variance structure among the infiltration rates. This finding excluded the possibility of using the Kriging technique for interpolation. Seasonal effect was found to be very important in influencing infiltration rates. The difference between the measured infiltration rates at both grazed and ungrazed sites was very significant for the 3 seasons under study.

Variability is considered one of the most important aspects of the infiltration process. Many difficulties arise due to natural variability which is characteristic of all field studies. This characteristic complicates analytical expressions developed to describe and predict the infiltration process. In this matter, Vieira (1980) stated, "To estimate the infiltration rate of a given field, the variance structure of the observations throughout the field must be identified in order to appropriately analyze each set of measurements, and obtain the best estimate of the expected mean value". Also, Nielsen et al. (1973) emphasized that it is important to assess to some degree the confidence that can be attached to predictions made by models.

Though many factors contribute to variability of infiltration rates, they can often be expressed simply in terms of time and space. The variation can be attributed to source combination of experimental error, time variations, and spatial variation (Campbell 1978).

Several studies have investigated the spatial variability relationships among measured infiltration rates; however, there has been little attempt to investigate seasonal changes. In addition, most studies of spatial variability of infiltration rates have been conducted on agriculture lands.

This study examines both spatial and temporal variability on a rangeland site in Utah. The study uses regionalized variable theory to assess the spatial relationships of field measured infiltration rates on a seasonal basis. The experiment had 4 objectives: first, to study seasonal infiltration rates; second, to determine the approximate frequency distribution of measured infiltration rates on a seasonal basis; third, to determine the spatial variability

relationships among measured infiltration rates by using semivariograms and autocorrelograms; and last, to compare infiltration rates from grazed and ungrazed pastures.

Concept of Regionalized Variables

The term *regionalized* was proposed by Matheron (1971) to describe a phenomenon distributed in space (and/or time) which exhibits a specific structure. A variable which characterizes such a phenomenon is called a regionalized variable. Almost all variables describing subsurface water movement or atmospheric water movement may be considered regionalized variables (Delhomme 1976).

From the mathematical viewpoint, a regionalized variable is simply a function $x(z)$ which gives the value at point z (in a 1, 2, or 3-dimensional space) of a characteristic x of the natural phenomenon being studied. Regionalized variable theory is used for the analysis of the spatial variation of infiltration rates. Autocorrelograms and semivariograms are used to identify the degree of dependence (zone of influence) of infiltration rates on the distance between pairs of measurements.

The Autocorrelogram

If $x(z)$ is the value of the regionalized variable x at a point z , and $x(z+h)$ is the value of x at a point $z+h$ at a distance h from z , the autocovariance between $x(z)$ and $x(z+h)$ for a given h is (Rendu 1978):

$$\sigma(h) = E \{ [x(z) - E[x(z)]] [x(z+h) - E[x(z+h)]] \}$$

where E denotes expected value.

The function $\sigma(h)$ is the autocovariogram of the regionalized variable x . Assuming σ_1^2 to be the variance of $x(z)$ and σ_2^2 variance of $x(z+h)$:

$$\sigma_1^2 = E \{ [x(z) - E[x(z)]]^2 \}$$

$$\sigma_2^2 = E \{ [x(z+h) - E[x(z+h)]]^2 \}$$

The coefficient of correlation between $x(z)$ and $x(z+h)$ is:

$$\rho(h) = \sigma(h) / \sigma_1 \sigma_2$$

The function $\rho(h)$ is the autocorrelogram of the regionalized variable x .

The autocorrelogram is a process of self-comparison that expresses the linear correlation between a spatial series and the same series at a further interval of space (Davis 1973). Webster and Cuanalo (1975) and Webster (1978) stated that the zone of influence corresponds to one-half the lag where the autocorrelogram flattens after a steady decay. Webster et al. (1975) defined the autocorrelation analysis as an alternative way of examining the relationships between sampling points in a spatial series. It measures the relationship as a function of the distance separating the

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sampling points rather than on the absolute position of them. The serial correlation of lag K is given by:

$$r_k = \frac{[1/(n-k) \sum_{i=1}^{n-k} (u_i - \bar{u})(u_{i+k} - \bar{u}_{i+k})]}{[1/(n-k) \sum_{i=1}^{n-k} (u_i - \bar{u})^2 [1/(n-k) \sum_{i=1}^{n-k} (u_{i+k} - \bar{u}_{i+k})^2]^{1/2}}$$

where:

$$\bar{u}_i = [1/(n-k) \sum_{i=1}^{n-k} u_i] \quad \bar{u}_{i+k} = [1/(n-k) \sum_{i=1}^{n-k} u_{i+k}]$$

r_k is the autocorrelation at lag K

n is the number of observations

u_i is the value of the observation at the i th portion

u_{i+k} is the value of the observation at the $(i+k)$ th portion

Autocorrelations can be calculated for lags $k=1, 2, \dots, m$ to give an ordered set of coefficients. A graph of these plotted as ordinate against lag is known as a correlogram. Clearly, when the lag is zero ($k=0$), $r_k=1.0$. As the value of lag k is increased, the correlation may drop possibly to zero, which means one element is changing inversely with relation to other elements being compared.

The Semivariogram

Another way of analyzing the spatial dependency between neighboring observations is the semivariogram. By definition, the value of the semivariogram (h) for a given distance h is one-half the expected squared difference between the values of the samples separated by h , as defined by Rendu (1978).

$$\gamma(h) = 1/2 E[(x(z) - x(z+h))^2]$$

If the experimental points are at a regular spacing on a line, the variogram may be calculated for values of h multiples of the step, using the formula:

$$\hat{\gamma}(h) = \frac{1}{2n(h)} \sum_{i=1}^{n(h)} [x(z_i) - x(z_i + h)]^2$$

$x(z)$ = the data

z = the points for which the data are available both in z and $z+h$

$n(h)$ = the number of pairs of points separated by a distance h .

A variogram or semivariogram is a plot of the variance $\gamma(h)$ along the ordinate against the distance measured in multiples of h along the abscissa. For large distances h such that $x(z)$ and $x(z+h)$ are not correlated, the semi-variogram $\gamma(h)$ will reach a value equal to the variance σ^2 . This limiting value is called the sill of the semivariogram, and the distance at which $\gamma(h)$ reaches the sill is called the range. The range of the semi-variogram obtained from a given type of sample corresponds to the distance of influence of these samples (Rendu 1978).

The regionalized variables, by use of the variogram, characterize the spatial variability of a phenomenon. The connection with problems of estimation is done by Kriging.

Methods

Study Area

The study was conducted approximately 3.20 km southwest of Eureka, Utah, in the west-central area of the state, within Utah State University experimental pastures. In 1957, the pastures were plowed and seeded and then fenced into 24 28-ha units. Two experimental areas within a pasture seeded to crested wheatgrass (*Agropyron desertorum*), one moderately grazed (1.5 ha/AUM) for several years during parts of June, July or August by cattle and the other ungrazed for over 20 years, were utilized in this study.

Average annual precipitation for the area is 20-30 cm, most of which falls in the winter months. The taxonomic soil classification for both experimental sites is: coarse-loamy, mixed, mesic, torri-

fluentic hafloxeroll. Surfaces are generally free of coarse fragments and surface textures are generally loamy. Cracks 0.5 to 1.5 cm wide, 1 to 2 cm deep with pentagonal configurations 10 to 15 cm in diameter are common in relatively undisturbed areas.

Experimental Design

The experiment utilized a grid 20 m long and 18 m wide in both grazed and ungrazed sites (Fig. 1). A sample spacing of 2 m was

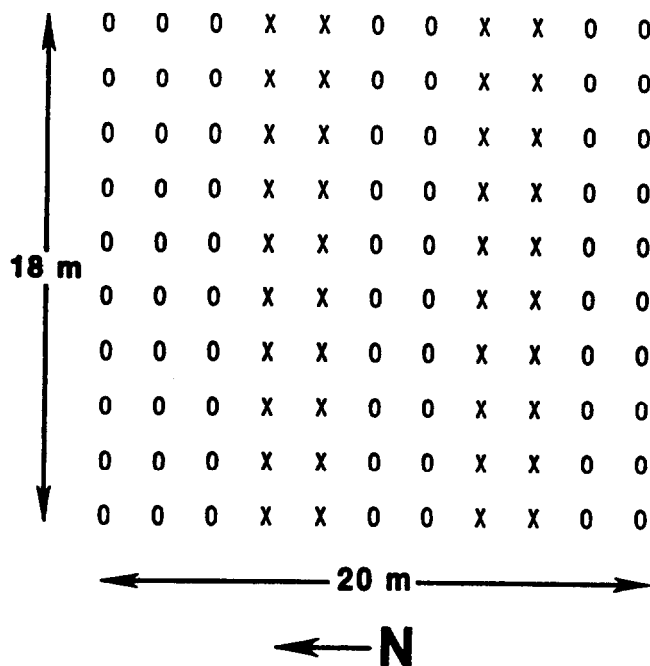


Fig. 1. Layout of the experimental design with 0 representing measured values and X representing values to be Kriged (interpolated) later. Distance between points is 2 m.

used within the grid. The data were collected in 7 columns in the east-west direction with 10 samples per column, and 70 samples in total per sampling data per site.

To investigate the seasonal effect on variability of infiltration rates, data were collected for 3 seasons (summer, fall, and spring).

Procedures

Infiltration data were collected during the months of July (during grazing) and October (after grazing) for the summer and fall of 1981, respectively, and during the month of April (before grazing) for the spring of 1982.

A double ring infiltrometer was used to minimize the effect of lateral water flow in measurement of infiltration rates. The inner ring diameter was 30.48 cm (12 inches) and the outer ring diameter was 45.72 cm (18 inches). The infiltrometer was inserted to a depth of 10 cm in the soil with a minimum of disturbance. Before measurements were taken, all plots were pre-wet with 5.08 cm (2 inches) of water and covered for a period of 3 hours to minimize confounding effects of antecedent moisture. Infiltration rates were measured using a 7.62-cm (3 inch) constant head for 32 minutes and rates were determined at 10 min (measured over the period 8-12 min) and 30 min (measured over the period 28-32 min).

Results and Discussion

Distributions

Visual (fractile diagrams) and statistical (goodness-of-fit test) methods were used to distinguish between normal and log-normal distributions in this study. Fractile diagrams were constructed for the 10- and 30-min infiltration rates measured on both grazed and ungrazed sites for 3 seasons. The fractile diagrams were con-

structured using the method described by Biggar and Nielsen (1976). Examination of the fractile diagrams (Fig. 2-4 are typical examples) suggests a lognormal distribution for the infiltration rates (straight-line fit). A goodness-of-fit test described by Ryan and Joiner (undated) was utilized to decide between the normal and

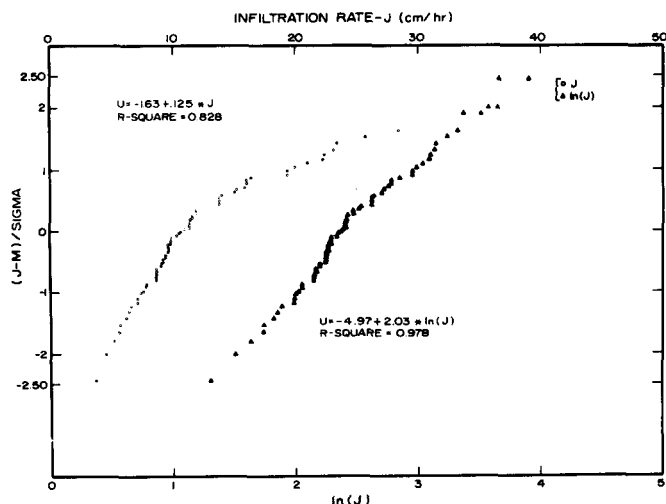


Fig. 2. Fractile diagram of the 10 min measured data from the ungrazed pasture during the summer. Ungrazed period in excess of 20 years.

lognormal distributions. The correlation coefficients (Table 1) indicate that measured infiltration rates closely approximate a two-parameter lognormal distribution. The statistics for the 3

Table 1. Correlation coefficients for goodness-of-fit test of measured infiltration rates from grazed and ungrazed sites at Tintic, Utah.

Season, site and time	Distribution	
	Normal	Lognormal
Summer		
Ungrazed site		
t=10 min	0.910	0.989*
t=30 min	0.919	0.994*
Grazed site		
t=10 min	0.943	0.990*
t=30 min	0.937	0.991*
Fall		
Ungrazed site		
t=10 min	0.943	0.996*
t=30 min	0.960	0.994*
Grazed site		
t=10 min	0.841	0.973**
t=30 min	0.860	0.984**
Spring		
Ungrazed site		
t=10 min	0.969	0.981**
t=30 min	0.972	0.983**
Grazed site		
t=10 min	0.974	0.995*
t=30 min	0.973	0.990*

*Data are lognormally distributed at = 0.10 level of probability.
 **Data are lognormally distributed at = 0.01 level of probability.

season infiltration rates from the grazed and ungrazed sites at t=10 min and t=30 min are presented in Table 2. The parameter estimates were calculated using the formulas given by Yevjevich (1972).

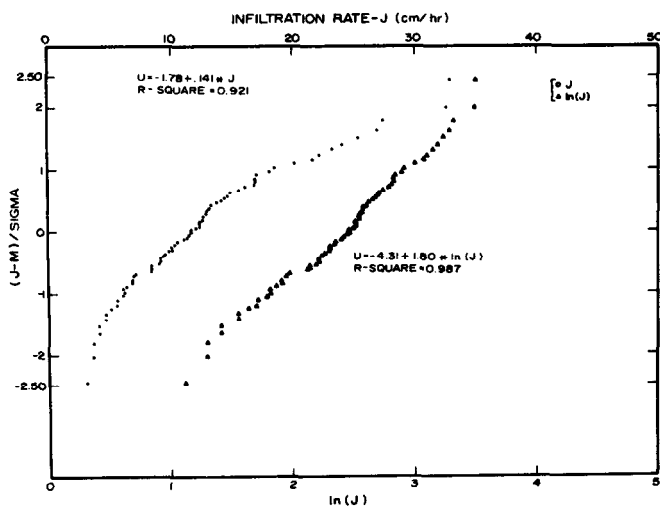


Fig. 3. Fractile diagram of the 30 min measured data from the ungrazed pasture during the fall. Ungrazed period in excess of 20 years.

Statistical Analyses

A 3 (seasons) by 2 (grazing treatments) by 2 (time intervals) factorial analysis of variance was performed to analyze the seasonal effects on infiltration rate, to compare ungrazed and grazed measured infiltration rates, and to differentiate between the 10- and 30-min measured infiltration rates. Season of the year (spring vs. summer, fall) was found to be very significant in influencing infiltration rates (Table 2). Pooled over sites and time intervals, the

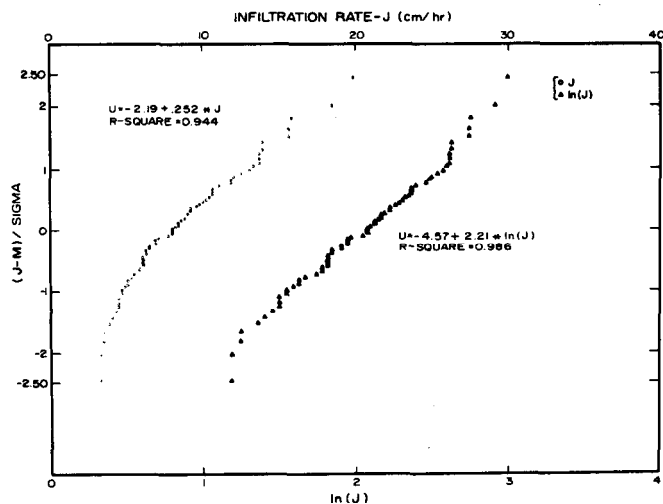


Fig. 4. Fractile diagram of the 10 min measured data from the grazed pasture during the spring. Pasture grazed moderately for several years by cattle during late spring.

mean infiltration rate for summer was 8.42 cm/hr, for fall 9.11 cm/hr, and for spring 15.67 cm/hr. The difference between summer and fall was not significant. These results agreed with the results found by Schumm and Lusby (1963) and Tricker (1981). In both papers, infiltration rates were reported to be maximum during early spring. Specific reasons for the seasonal changes are not known. However, field observations indicate that it is probably due to frost action and soil biological activity, which makes the soil surface more permeable. Seasonal changes should be considered an important factor in determining infiltration rates in future investigations (Gifford 1979).

The grazed and ungrazed measured infiltration rates were also

Table 2. Statistics for three seasons infiltration rates from the grazed and ungrazed sites at t=10 min and t=30 min.

Season, site and time	No. of samples	Log mean (μ_n)*	Log variance (σ_n^2)	Median (M)	Mode (m)	Mean (μ)	Variance (σ^2)	C.V. (n)	Skewness (γ)
Summer									
Ungrazed site									
t=10 min	70	2.42	0.23	1.25	8.93	12.63	40.74	0.50	1.64
t=30 min	70	2.32	0.26	1.29	7.84	11.62	40.12	0.54	1.77
Grazed site									
t=10 min	70	1.53	0.10	1.11	4.17	4.90	2.64	0.33	1.02
t=30 min	70	1.44	0.12	1.13	3.74	4.52	2.68	0.36	1.12
Fall									
Ungrazed site									
t=10 min	70	2.49	0.27	1.31	9.20	13.93	61.55	0.56	1.85
t=30 min	70	2.39	0.30	1.35	8.08	12.69	56.64	0.59	1.97
Grazed site									
t=10 min	70	1.44	0.26	1.29	3.25	4.94	7.07	0.54	1.77
t=30 min	70	1.47	0.22	1.24	3.49	4.87	5.86	0.49	1.58
Spring									
Ungrazed site									
t=10 min	70	2.99	0.42	1.53	13.06	24.74	326.16	0.73	2.58
t=30 min	70	2.86	0.42	1.53	11.47	21.62	248.06	0.73	2.58
Grazed site									
t=10 min	70	2.06	0.20	1.22	6.42	8.70	16.72	0.47	1.51
t=30 min	70	1.93	0.19	1.20	5.69	7.62	12.18	0.46	1.47

* μ_n , μ , M, and m in cm/hr; σ_n^2 and σ^2 in (cm/hr)²

compared, and ungrazed site infiltration rates were significantly higher (16.21 cm/hr) than grazed site (5.92 cm/hr) infiltration rates. The high infiltration values on the ungrazed site are probably due to better soil structure, less compaction by grazing animals, and increased accumulation of litter on the soil surface.

The difference between the 10- and 30-min infiltration rates, pooled over sites and seasons, was found to be significant. The mean infiltration rate for 10 minutes was 11.64 cm/hr and for 30 minutes 10.49 cm/hr.

Interactions among seasons and sites, season and time intervals, sites and time intervals, and among seasons and sites and time intervals were not significant.

Spatial Variability

To examine relationships between the measured infiltration rates at various grid points, autocorrelograms and semivariograms were constructed for the 10- and 30-min measured infiltration rates from both and ungrazed pastures during the summer, fall, and spring. The interpretation of the autocorrelograms (Figure 5 is a typical example) based upon Webster and Cuanalo (1975) and Webster's (1978) concept suggests no linear correlation with the 2-m spacing. Autocorrelograms drop rapidly from 1.0 at 0 lag, then fluctuate near zero. This indicates no significant trend exists in the measured infiltration rates. Examination of the isotropic empirical semivariograms (Figure 6 is a typical example) shows that the semivariance values, for the 10- and 30-min observed infiltration rates during the summer, fall, and spring from both grazed and ungrazed sites, center about the sill value. This also indicates that the infiltration rates are randomly distributed, which means that the covariance between the measured values is zero for all distances h . This is the case of a pure nugget effect described by Rendu (1978), a case where infiltration values are uncorrelated. The results obtained from both autocorrelograms and semivariograms reveals the absence of continuity between plots.

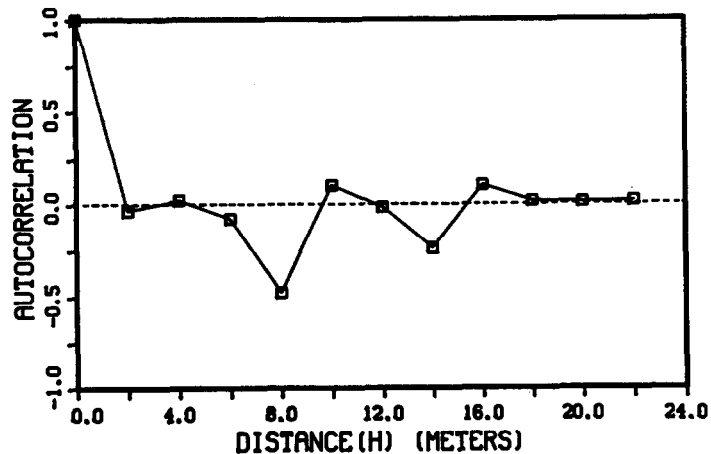


Fig. 5. Autocorrelogram for the 10 min measured infiltration rates within the ungrazed pasture during the summer. Ungrazed period in excess of 20 years.

Conclusions

Measured infiltration rates at 10 and 30 min during all seasons and under grazed versus ungrazed conditions were all found to approximate a two-parameter lognormal distribution. Springer and Gifford (1980) found that infiltration rates on a plowed sagebrush site in Idaho could be adequately represented by either a normal or lognormal distribution. However, smaller sample numbers were used in the Idaho study than in the current study; a rainfall simulator was also used versus a ring infiltrometer in this study. Assuming that instrument type makes no difference, the larger sample sizes indicate that lognormal distributions should be assumed when analyzing infiltration data.

Autocorrelograms and semivariograms showed a complete lack of variance structure among the infiltration rates, indicating that measured data were randomly distributed within the 2-m grid

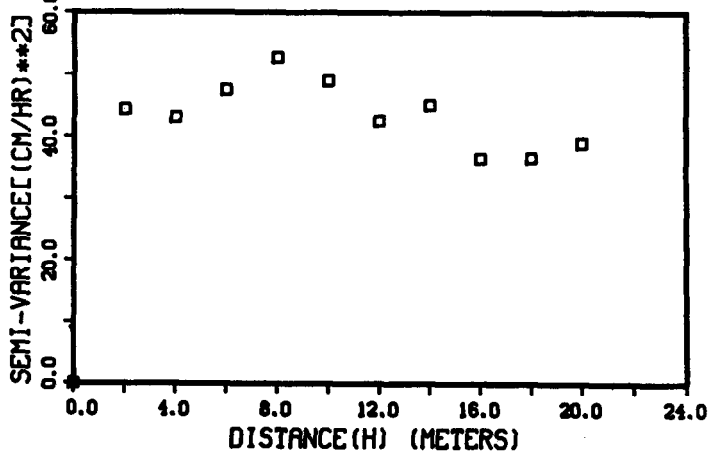


Fig. 6. Semivariogram for the 10 min measured infiltration rates within the ungrazed pasture during the summer. Ungrazed period in excess of 20 years.

spacing. These results, which relate to the zone of influence of individual measures, contrast with distances of 5.3 m and 50 m found by Wagenet (1981) and Vieira et al. (1981), respectively, on agricultural soils. The complex nature of rangeland soils undoubtedly accounts for the difference.

Significant seasonal trends in infiltration rates indicate the need for a better understanding of the winter recovery process. Such information is currently lacking.

The reduction in infiltration rates on the moderately grazed area was perhaps more than might have been expected based on the model presented by Gifford and Hawkins (1979). However, evaluations with a sprinkling device should be conducted before any conclusions are made regarding increased runoff potentials.

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Vegetation of Two Relict Mesas in Zion National Park

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Abstract

Twelve permanent vegetation sampling plots were established on Greatheart and Church mesas in Zion National Park, Utah. Both relict mesas are surrounded by cliffs but contain the same variety of soil conditions as the nearby "mainland." The mesa vegetation was segregated into the following broad community types: mixed conifer forest, ponderosa pine savanna, Gambel oak woodland, pinyon woodland, snowberry-sagebrush steppe, and oak-sagebrush shrubland. Cover of all species was measured in the plots, in addition to tree stem density. Relationships of each community type to topo-edaphic factors and response to fire are noted. The mesa ecosystems can be used as standards to gauge the various effects of resource exploitation on analogous "mainland" areas.

Relict areas are of value to wildland managers as points of reference against which to gauge successional changes induced by land use activities. Perceptions of the degree of human modification are sharpened by such comparison, which lends an important historical perspective to the land quality evaluation process. Changes in ecosystem structure have a direct bearing on the amount of forage produced, in addition to affecting other wildland values such as watershed quality, timber production, and wildlife habitat. Knowledge of relict ecosystems can assist managers in planning activities by illustrating different resource levels than are found in the more prevalent, modified landscapes. Potential for range improvement can be predicted with greater accuracy if careful consideration is given to relict areas within the region of interest.

The relicts under consideration in this paper, Greatheart and Church Mesas, are but 2 of nearly 40 mesas in the high dissected confines of Zion National Park, Utah (Fig. 1). All of these mesas have a fairly level, vegetated summit related to the presence of the Temple Cap and/or Carmel Formation (Hamilton 1978).

Zion National Park lies on the western margin of the Colorado Plateau, a region that contains many isolated, and hence pristine, mesas. However, most studies of relict mesas in the Colorado Plateau have focused on ecosystems more typical of lower elevations, i.e., pinyon-juniper woodland, sagebrush shrubland, or desert grassland (Jameson et al. 1962; Schmutz et al. 1967; Mason et al. 1967; Kleiner and Harper 1972, 1977a, 1977b). Studies of relict mixed conifer (*Abies-Pseudotsuga-Pinus*) forest, ponderosa pine (*Pinus ponderosa*) forests or savannas, and Gambel oak (*Quercus gambelii*) woodlands have apparently been limited to Mason and West's (1970) report of a brief visit to Timber Top Mesa inside the Kolob Section of Zion National Park (Mason and West 1970). These authors reached this heretofore inaccessible mesa by helicopter and noted fire evidence in the mountain brush community (dominated by Gambel oak), ponderosa pine forest, and Douglas fir (*Pseudotsuga menziesii*) forest. No wildlife species larger than a chipmunk (*Eutamias* sp.) were seen on the mesa. Since Timber Top Mesa is bounded on all sides by sheer cliffs, it is apparently unvisited by large herbivores like mule deer (*Dama*



Fig. 1. Church Mesa as seen from the southern tip of the Horse Pasture Plateau. The vegetated summit is encircled by 150-300 m high cliffs.

hemionus hemionus (Rafinesque)). This situation lowers the value of the vegetation structure for comparison purposes, since it did not develop with the type of browsing pressure that characterized normal "mainland" systems in pre-European times. Mule deer signs have been observed on both mesas in our study.

This paper describes the vegetation on Greatheart and Church mesas. Its purpose is to provide a clearer picture of presettlement conditions of mid-elevation plateaus of southwestern Utah.

Description of Study Area

Greatheart and Church mesas are located in the center of Zion National Park (Fig. 2). Greatheart Mesa is 1 km west of the Horse Pasture Plateau and is 85 ha (210 acres) in size. Church Mesa (an unofficial name not yet on USGS maps) lies 2 km south of the Horse Pasture Plateau and 2 km west of the Zion Lodge. Church Mesa is 150 ha (370 acres) in size.

The vegetated summits of Greatheart and Church mesas lie between the elevations of 2,160 m (7,092 ft) and 2,259 m (7,410 ft), and 2,150 m (7,058 ft) and 2,254 m (7,395 ft), respectively. The higher parts of the mesa tops are capped with limestone from the Carmel Formation. The remainder of each vegetated summit is underlain by sandstone and shales of the Temple Cap Formation (Hamilton 1978). The sheer 150- to 300-m (500 to 1,000 ft) cliffs that circumscribe the 2 relicts are carved from Navajo sandstone.

Soils on the ridgetops are in the Paunsaugunt gravelly silt loam series, while the slopes are covered by the deeper Kolob-Detra association. Level areas near the rim of the mesas feature Kinesava fine sandy loam (Madany 1981). Soils of Zion National Park are described in more detail by Mortensen et al. (1977).

The mesas are covered by vegetation quite similar in general composition to that of the nearby Markagunt Plateau. Ponderosa

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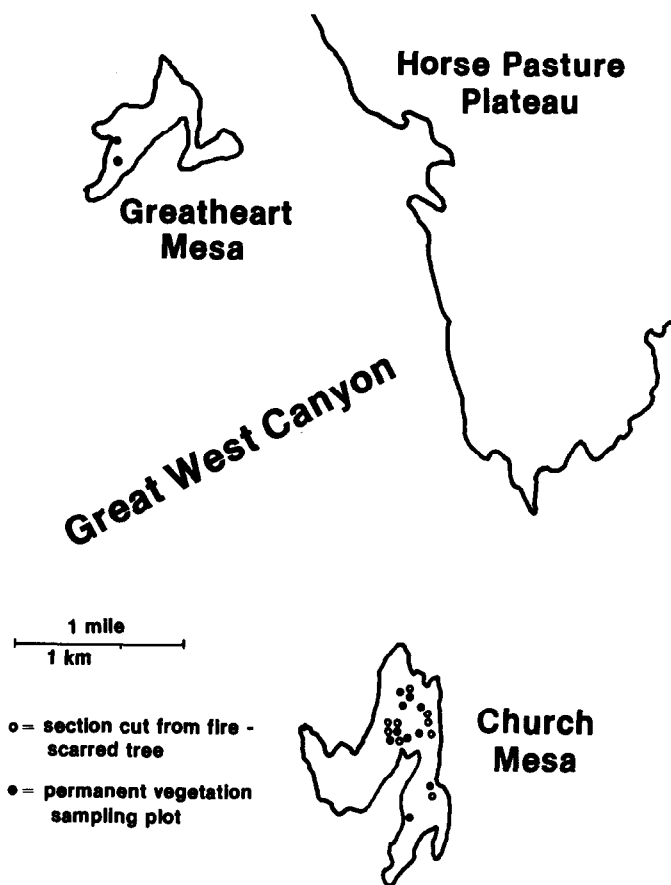


Fig. 2. Location of sampling points for vegetation plots and fire scarred trees in the study area.

pine, Gambel oak, Douglas fir, pinyon pine (*Pinus edulis*), white fir (*Abies concolor*), Rocky Mountain juniper (*Juniperus scopulorum*), and bigtooth maple (*Acer grandidentatum*) are the major trees in the study area. Common shrubs are Utah serviceberry (*Amelanchier utahensis*), greenleaf manzanita (*Arctostaphylos patula*), mountain snowberry (*Symphoricarpos oreophilus*), and big sagebrush (*Artemisia tridentata*). Important grasses include muttongrass (*Poa fendleriana*), Indian ricegrass (*Oryzopsis hymenoides*), squirreltail (*Sitanion hystrix*), needle-and-thread (*Stipa comata*), Letterman needlegrass (*Stipa lettermanii*), and blue grama (*Bouteloua gracilis*). Nomenclature for vascular plants follows Nelson (1976).

Mule deer droppings, tracks, and antlers were seen on both mesas. Cougar (*Felis concolor kaibabensis* (Nelson and Goldman)) tracks, and a possible den, were found on Church Mesa. No permanent water was found on either mesa, although a seepage spring was seen on Church Mesa. Presumably, large mammals would have to leave the mesa regularly to obtain drinking water. The high elevation precludes year-round use by mule deer. The presence of large mammals in these relict areas adds to the comparison value of the vegetation since they developed under browsing pressure from the same species as on the "mainland." Diggings of what were presumed to be pocket gophers (*Thomomys* sp.) were also seen on Church Mesa.

Methods

Greatheart Mesa was visited by helicopter on November 4, 1978. Thus, the vegetation sampling that took place there did not register the presence of some of the more ephemeral forb species. Three days were spent on Church Mesa (August 15-17, 1979) when a

much higher proportion of the flora was in identifiable condition.

Two permanent vegetation sampling plots were established on Greatheart Mesa and 10 were placed on Church Mesa (Fig. 2). All plots had a metal reinforcement bar placed at the northeast corner. Each 20×15-m plot was subjectively located in a homogenous portion of vegetation. All plots were chosen to correspond with the physical variables of objectively chosen sampling points on the nearby Horse Pasture Plateau (Madany 1981, Madany and West 1983). At each plot, the physical environment was quantified by measuring elevation and slope and assigning various categories such as topographic position, bedrock, and soil type. All tree stems greater than 5-cm dbh were recorded by species and size class for the entire plot. Cover of saplings, shrubs, forbs, and graminoids was visually estimated by species in each of 4 5×5-m subplots at the corner of the main plot. Increment cores were taken from several trees in each plot.

Nine partial cross-sections of fire-scarred ponderosa pine were cut on Church Mesa using the methods outlined by Arno and Sneek (1977). Descriptive notes were made concerning ecological conditions of the 2 mesas. Numerous color slides and black-and-white photographs were taken to document conditions.

Results and Discussion

The 12 sampling plots were subjectively grouped into 5 cover types based on the dominant species in the upper-most strata of the community. These units are mixed conifer forest, ponderosa pine savanna, Gambel oak woodland, pinyon pine woodland and snowberry-sagebrush steppe. For each of these units, the constancy (where more than 1 plot was sampled), average cover, and density (for trees) will be presented. Remarks are also made pertaining to edaphic affinities, response to fire, and general structure.

Mixed Conifer Forest

Table 1 summarizes vegetation data for this very limited vegetation unit found only on shaded northern and eastern slopes. In the sample plot, white fir was the only conifer; however, in other locations Douglas fir and ponderosa pine made up part of the canopy. Three white fir and 1 Gambel oak were cored, giving the following ages: 102, 125, 173, and 116 years, respectively. There was no direct evidence that the most recent fire of 1964 had burned this particular stand. The understory of this stand was dominated by small Gambel oak and mountain snowberry. For details on the effects of fire in an extensive area of mixed conifer forest on a mesa just north of Church Mesa, see Madany (1981). Mixed conifer forest stands on the Horse Pasture Plateau tend to occur in similar topo-edaphic situations.

Ponderosa Pine Savanna

All communities dominated by ponderosa pine that were visited on Church and Greatheart mesas possessed a savanna physiognomy with a discontinuous canopy and a herbaceous-dominated groundlayer (Fig. 3). No closed forests were seen in contrast with the prevalent situation on the nearby Horse Plateau (Madany 1981, Madany and West 1983). A variety of edaphic conditions support ponderosa pine savanna. These include level areas near the rims of both mesas on soils (probably Kinesava fine sandy loam) derived from Temple Cap sandstones and shales; a north-facing slope of 15–20° on Church Mesa on soils of the Kolob-Detra association; and shallower, gravelly sites on Paunsaugunt gravelly silt loam along the central ridgetop of Church Mesa underlain by limestone of the Carmel Formation.

The canopy was composed almost entirely of ponderosa pine ranging in age from 100 to 360 years. A few scattered Rocky Mountain or Utah junipers, white firs, or Douglas-firs were seen occasionally. Several regeneration groves of ponderosa pine of approximately 60 years of age were seen on Church Mesa. These presumably date from the 1919 generation that is so widespread throughout the Southwest (Arnold 1950). However, nowhere was

Table 1. Species contributions to constancy (%), cover (%) and tree density (stems/ha) for five plant community types on two isolated mesas in Zion National Park.

Growth form Species	Plant Community Types											
	Mixed conifer forest (1 plot)			Ponderosa pine savanna (7 plots)			Gambel oak woodland (2 plots)			Pinyon woodland (1 plot)		Snowberry-sage- brush steppe (1 plot)
	constancy	cover	density	constancy	cover	density	constancy	cover	density	cover	density	cover
Trees												
<i>Abies concolor</i>		75	400	14	3	14						
<i>Quercus gambelii</i>		30	333	14	1	5	x ²	76	617			
<i>Juniperus osteosperma</i>				14	1	5						
<i>Juniperus scopulorum</i>				14	4	10						
<i>Pinus ponderosa</i>				100	33	129						
<i>Acer grandidentatum</i>								15	233			
<i>Pinus edulis</i>										30	200	
Saplings/Shrubs												
<i>Symphoricarpos oreophilus</i>		42		86	9			x	42			20
<i>Quercus gambelii</i>		29		71	14		x	25		22		1
<i>Acer grandidentatum</i>		8		14	T			1				
<i>Amelanchier utahensis</i>		1		29	1			T		30		
<i>Pachistima myrsinites</i>		1		14	T						1	
<i>Prunus virginiana</i>		T ¹		29	T			3				2
<i>Berberis repens</i>				71	1			T				
<i>Juniperus scopulorum</i>				14	T					1		
<i>Abies concolor</i>				14	2			T				
<i>Artemisia tridentata</i>				14	2							14
<i>Chrysothamnus viscidiflorus</i>				29	2							11
<i>Petradoria pumila</i>				29	2							
<i>Pinus ponderosa</i>				14	T							
<i>Chrysothamnus nauseosus</i>				14	T							
<i>Rosa woodsii</i>				14	T							
<i>Chrysothamnus depressus</i>				14	T							
<i>Ceanothus fendleri</i>				14	T							
<i>Purshia tridentata</i>				43	1							
<i>Yucca augustissima</i>				14	1							
<i>Arctostaphylos patula</i>				29	2					34		
<i>Cercocarpus montanus</i>										18		
<i>Opuntia basilaris</i>										2		
Graminoids												
<i>Bromus ciliatus</i>		T		43	T							
<i>Carex praegracilis</i>				14	1			T				2
<i>Poa fendleriana</i>				100	9			2		T		2
<i>Sitanion hystrix</i>				86	5			1				1
<i>Stipa lettermanii</i>				57	3		x	2				3
<i>Oryzopsis hymenoides</i>				29	1					T		
<i>Muhlenbergia montana</i>				29	6							7
<i>Stipa comata</i>				57	4							47
<i>Bromus tectorum</i>				14	2							
<i>Koeleria cristata</i>				14	T							
<i>Agropyron riparium</i>								8				5
Forbs												
<i>Disporum trachycarpum</i>		T										
<i>Phacelia heterophylla</i>		T		43	1				T			
<i>Lathyrus leucanthus</i>		1		43	1				T			
<i>Stellaria jamesiana</i>		1		29	T		x	4				T
<i>Polygonum douglasii</i>				71	2		x	T				4
<i>Solidago multiradiata</i>				43	6			3				2
<i>Artemisia ludoviciana</i>				43	2			1				1
<i>Artemisia dracunculus</i>				29	2			4				5
<i>Phlox austromontana</i>				43	1					T		
<i>Senecio multilobatus</i>				29	1			1		T		
<i>Macheeranthera linearis</i>				57	1			T				
<i>Eriogonum racemosum</i>				57	1		x	T				T
<i>Vicia americana</i>				43	2							2
<i>Cirsium pulchellum</i>				43	1							
<i>Arabis holboellii</i>				43	T							
<i>Linum lewisii</i>				43	T							
<i>Lomatium nuttallii</i>				29	2							
<i>Chrysopsis villosa</i>				29	1							
<i>Thermopsis montana</i>				29	1			1				2
<i>Comandra umbellata</i>				29	T							
<i>Arenaria macredenia</i>				29	T							

Table 1. Continued.

Growth form Species	Plant Community Types												
	Mixed conifer forest (1 plot)			Ponderosa pine savanna (7 plots)			Gambel oak woodland (2 plots)			Pinyon woodland (1 plot)		Snowberry-sage- brush steppe (1 plot)	
	constancy	cover	density	constancy	cover	density	constancy	cover	density	cover	density	cover	
<i>Calochortus nuttallii</i>				29		T							
<i>Frasera speciosa</i>				29		T				T			
<i>Lithospermum ruderale</i>				29		T				T			
<i>Streptanthus cordatus</i>				29		T							
<i>Viguera multiflora</i>				29		T				3			
<i>Eriogonum subreniforme</i>				14		T				T			
<i>Hackelia micrantha</i>				14		T				T			
<i>Achillea millefolium</i>				14		T							
<i>Arabis perennans</i>				14		T							
<i>Cryptantha jamesii</i>				14		T							
<i>Cymopterus fendleri</i>				14		T							
<i>Delphinium scaposum</i>				14		T							
<i>Erigeron divergens</i>				14		T							
<i>Helianthella quinquerevis</i>				14		T							
<i>Penstemon</i> sp.				14		T							
<i>Mertensia fusiformis</i>				14		T							
<i>Chenopodium</i> sp.							x		1			1	
<i>Agastache urticifolia</i>									1				
<i>Phacelia heterophylla</i>									T				
<i>Oenothera caespitosa</i>										T			
<i>Lupinus sericeus</i>												2	

¹T indicates a trace (less than 0.5% cover)

²x indicates presence in both plots



Fig. 3. The ridge crest on Church Mesa is covered by ponderosa pine savanna featuring a grass-dominated groundlayer. Squirreltail is visible in the foreground.

the continuous layer of pine stems of that age seen that characterize the understory of ponderosa pine forests on the mainland (Madany and West 1983).

As indicated in Table 1, only Gambel oak and mountain snowberry have a considerable amount of coverage in the shrublayer of this community type. A wide diversity of shrubs (17 species) were present, but nearly all had less than 2% cover. The effects of the most recent fire (in 1964) on the Church Mesa stands were quite evident. Utah serviceberry was diminutive in stature and only rarely were individuals seen that were over a meter in height. Greenleaf manzanita had not yet recovered even 50% of its pre-fire coverages, as evidenced by the comparison between skeletons killed by the 1964 fire and existing shrubs. Most oak and maple clones that had their aerial portion killed in the 1964 fire were vigorously resprouting. Fendler buckbrush (*Ceanothus fendleri*), while only occurring in 1 of the 7 plots, appears to be much more

widespread and vigorous than on the Horse Pasture Plateau (Madany and West 1983)—a condition quite possibly linked with the 1964 fire. Tree saplings are scattered throughout the shrub-layer, with white fir being locally common on the north slope of the central ridge on Church Mesa. These saplings presumably date from after 1964. A fire frequency interval of 69 years (with a range of 56 to 79) was determined from analysis of the 9 partial cross-sections cut from fire-scarred pines. This is much lower than the 4 to 7 years frequency interval for the "mainland" Horse Pasture Plateau (Madany and West 1980).

The most important grasses, in terms of cover, are nearly all of the cool-season growth habit: muttongrass, squirreltail, needle-and-thread, and Letterman needlegrass. Mountain muhly (*Muhlenbergia montana*) is the only warm-season grass of note. In contrast to the above-mentioned cool season grasses, mountain muhly is quite rare on the nearby Horse Pasture Plateau (Madany and West 1983). Among forbs, low goldenrod (*Solidago multiradiata*) is notable in its relatively high coverage. Cheatgrass (*Bromus tectorum*) was restricted in its occurrence to areas beneath juniper trees killed in the 1964 fire. Presumably, there were few herbs directly below the juniper before 1964. Following the intense heat generated by the burning juniper, the cheatgrass apparently invaded to occupy the sterilized soil. The appearance of this alien, several kilometers from the nearest mainland seed source can be either attributed to animal vectors or wind dispersal.

Gambel Oak Woodland

This widespread community type covered at least 50% of both mesas and was found in the same general range of sites, and on similar soils, as the ponderosa pine savanna. As on the "mainland" (Madany and West 1983), the reasons why a particular spot is dominated by Gambel oak rather than ponderosa pine are unclear. The clonal habit of the oak produces a complex community patterning with mottes of the small tree interdigitating with grassland and savanna in intricate mosaic (Fig. 4). Sampling such a community was difficult since conditions directly beneath the canopy tended to be quite different (both physically and biotically) from the small openings that separate each motte. As a rule, shrubs and



Fig. 4. Interspaces between mottes in the Gambel oak woodland are dominated by perennial bunchgrasses. The large tree in the background is an isolated specimen of ponderosa pine.

certain forbs are more prominent in the direct shade of the clone interior, while grasses dominated the interspaces. From the 3 oaks and 1 maple cored in the 2 stands (both on Church Mesa), the following ages were derived: 62, 64, 113, and 65 years, respectively.

This woodland community is not as flammable as the savanna and snowberry-sagebrush steppe. On Church Mesa, a variety of responses of Gambel oak to fire were observed. Isolated clones surrounded by grass were killed to the ground and were vigorously resprouting. Areas of woodland that bordered on savanna or snowberry-sagebrush steppe showed evidence of burning with many of the lower branches being killed on the oak. Losses of entire mature stems ranged from about 10–30%. Areas further away from more flammable communities did not appear to have burned. The presence of large stems of presumably more sensitive species like big-tooth maple and chokeberry (*Prunus virginiana*) in burned stands indicates that fires were both patchy and of low intensity. Fires probably burn into the Gambel oak woodland along the grassy interspaces, but eventually burn out in the moist fuels of the interior of oak mottes.

As can be seen in Table 1, the most prominent shrubby associate of Gambel oak in the shrublayer is mountain snowberry. A variety of herbaceous species is present, reflecting the physiognomic heterogeneity of the community. Streambank wheatgrass (*Agropyron riparium*), muttongrass, and Letterman needlegrass are especially characteristic graminoids. Tarragon (*Artemisia dracunculus*), tuber starwort (*Stellaria jamesiana*), low goldenrod, and showey goldeneye (*Viguiera multiflora*) are the most prevalent forbs.

Pinyon Woodland

This community occupies the driest sites on both mesas, favoring southern and western exposures, often in areas with bedrock outcrops. The sole stand sampled in our study was on a west-facing slope of 26° on Greatheart Mesa. A fire had probably not burned the locale for a century or more. One pinyon was cored and yielded an age of 210 years. The dense understory was made up of Gambel oak, Utah serviceberry, greenleaf manzanita, and true mountain mahogany (*Cercocarpus montanus*). Since sampling was done in early November, the cover and number of herbaceous species is doubtless under-represented (Table 1). Nevertheless, the conclusion can be drawn that the pinyon woodland, like the mixed conifer forest, lacks a sizeable herbaceous groundlayer.

Unfortunately, a sample plot was not placed in this vegetation type on Church Mesa. However, several observations can be made. A number of mature pinyons killed in the 1964 fire were seen in both level, grassy, and steeper, rockier sites. Also, true mountain mahogany is lacking on Church Mesa. This anomaly is curious, as

the shrub is found on both Greatheart Mesa and Burnt Mountain (a mesa 14 km to the northwest). The pinyon woodland type on Church Mesa is generally restricted to steeper sites than Greatheart Mesa, with corresponding sparser understory and groundlayer vegetation. The different fire histories of the 2 mesas may be one factor in effecting this condition.

Snowberry-Sagebrush Steppe

One plot was established in this community type on Church Mesa. The proper topographic conditions conducive to low shrub steppe development are apparently not found on Greatheart Mesa. This community type occupies a well-defined alluvial depression at the north end of Church Mesa that is between 5 and 10 ha in area. While an intermittent stream channel is shown dissecting this community on the official USGS topographic map (see Zion National History Association 1977), we did not find any visible channel at any point in the entire valley. By contrast, gullying and deeply incised channels are common phenomena in analogous valleys on the Horse Pasture Plateau.

Big sagebrush, mountain snowberry, and sticky-leaf rabbitbrush (*Chrysothamnus viscidiflorus*) are all present in youthful vigor. The sagebrush presumably has reproduced from seed following the 1964 fire that burned the entire valley, while the other 2 shrubs have resprouted. However, due to their low stature, the visual dominance is usurped by the grasses. From Table 1, one can see that needle-and-thread contributes nearly half of the cover of the community. The species richness and high coverage of the mesa community (when contrasted with similar sites on the plateau) is a situation which can probably be attributed to the better water relations of the undissected soil.

Oak-Sagebrush Shrubland

Unfortunately, no plots were established in this community type on either mesa. While being quite similar to an analogous community sampled on the Horse Pasture Plateau (Madany 1981), the mesa communities seemed to have a much higher grass component. This shrubland is restricted to level sandy soils near the rim of the mesa on areas underlain by the Temple Cap Formation. Dominance appeared to be shared between shrub form (usually less than 2 m) Gambel oak, big sagebrush, needle-and-thread, and blue grama. This community occasionally merged into Gambel oak woodland or ponderosa pine savanna. The relative abundance of shrubs vis-a-vis grasses would seem to be mediated by the frequency of fire.

Conclusion

The results of the vegetation sampling conducted on the 2 mesas show the importance of perennial herbaceous species in the groundlayer of all but 2 rather minor vegetation types. This contrasts with conditions on the formerly grazed Horse Pasture Plateau (Madany 1981, Madany and West 1983). The savanna physiognomy of the ponderosa pine stands is quite similar to conditions described by Rummell (1951) and Franklin et al. (1982) on Meeks Table in central Washington. Accounts of various early explorers in the West give the impression that the typical structure of ponderosa pine communities was indeed savanna (Cooper 1960).

The results of studies of lower elevation mesas in Arizona and Utah (Jameson et al. 1962, Mason et al. 1967, Schmutz et al. 1967) were similar to those of our study. In fact, many of the same species of grass are dominant on the mesas they studied and this study area. The presence of these relicts complements and corroborates the historical accounts of the pristine vegetation before impacts of livestock grazing, logging, and fire control began. Declines in forage production, wildlife habitat quality, and watershed characteristics may be gauged by the careful comparison of these mesas and adjacent "mainland" areas. See Madany and West (1983) for a discussion of these issues.

Current National Park Service policy regarding land management objectives is to restore, through a variety of approaches, ecosystems that have been affected by European man (Bonnicksen and Stone 1982). The data presented here can contribute to a comprehensive effort to restore pre-settlement conditions in the modified upper elevation ecosystems of Zion National Park.

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Effects of Temporary Dehydration on Growth of Green Needlegrass (*Stipa viridula* Trin.) Seedlings

TIMOTHY E. FULBRIGHT, A.M. WILSON, AND E.F. REDENTE

Abstract

Green needlegrass (*Stipa viridula* Trin.) has been variously rated as "extremely" to "fairly" drought tolerant. This study was conducted to determine the capacity of green needlegrass seedlings for emergence and root growth following temporary dehydration. Germinating seeds were exposed to dehydration treatments of 0, -4, -10, -22, and -37 megapascals (MPa) and then planted in soil-filled pots for a 10-day growth performance test. Exposure of germinating seeds to temporary dehydration treatments of -10 MPa and lower reduced subsequent seedling emergence. When the seminal primary root of germinating seeds was excised or injured by dehydration, seedlings developed up to 3 seminal lateral roots. No additional seminal roots were developed if the seminal primary root was undamaged. Germinating seeds of green needlegrass have relatively low tolerance to dehydration possibly as a result of a low latent potential for development of seminal lateral roots and low tolerance of the embryo and developing tissues to dehydration. Sites to be seeded and planting dates should be selected so as to insure adequate soil moisture for seedling development.

Green needlegrass (*Stipa viridula* Trin.) is a native, cool-season perennial bunchgrass that ranges from Alberta and Saskatchewan south to New Mexico and Arizona. Considerable use of this species has been made in range seedings and mined-land reclamation plantings in the northern Great Plains (Thornburg 1982).

Green needlegrass is referred to by several authors as a species that often occurs abundantly on sites such as swales and low lying areas that receive greater moisture than the surrounding area (North Dakota Agricultural Experiment Station 1941, Wright and Wright 1948, Donahue et al. 1956, Coupland and Johnson 1965). Vallentine (1971) rated green needlegrass as "fairly" drought tolerant. In contrast, Judd (1938) had reported that green needlegrass was found to be extremely drought resistant in studies in the northern Great Plains region. Seedlings of green needlegrass are resistant to drought according to Hoover et al. (1947) and Donahue et al. (1956).

Periods of high soil water potentials are often of short duration on semiarid rangelands and are separated by longer periods of much lower water potentials (Bokhari et al. 1975). Sala et al. (1981) reported that soil water potential at a depth of 5 cm decreased as low as -6 megapascals (MPa) during a 56-day drying cycle in north-central Colorado. Wilson (1973) measured soil water potentials as low as -600 bars (-60 MPa) at a depth of 2.5 cm in eastern Washington.

Seedling emergence and establishment on semiarid rangelands may depend on the ability of germinating seeds to tolerate extremely low water potentials and recover during subsequent periods of higher water potentials (Hassanyar and Wilson 1978).

The ability of plants to tolerate low water potential is related to the ability of their tissues to endure dehydration without undergoing destructive changes in cell structure and chemistry. The capacity for root growth following temporary dehydration of germinating seeds is particularly important for survival and initial growth of grass seedlings. Seminal lateral root primordia at the scutellar node of germinating seeds of crested wheatgrass (*Agropyron desertorum* (Fisch.) Schult.) and Russian wildrye (*Elymus junceus* Fisch.) remain quiescent for several days or weeks after planting, during which time they are less susceptible to dehydration injury than the apex of the actively growing seminal primary root. Because actively growing seminal primary roots may be killed by temporary dehydration prior to development of adventitious roots, growth and survival of seedlings may depend on the development of seminal lateral roots. However, many grass species lack the capacity to develop seminal lateral roots (Hoshikawa 1969). Those species that lack seminal lateral roots entirely are less tolerant of low soil water potentials (Hassanyar and Wilson 1978).

The objective of the present study was to determine the capacity of green needlegrass seedlings for emergence and root growth following temporary dehydration.

Materials and Methods

Accession SD-93 and Lodorm, a variety of green needlegrass with reduced seed dormancy, were the seed sources used in this study. Both were obtained from the USDA Soil Conservation Service Plant Materials Center at Bismarck, N. Dak. The study was conducted in 3 sequential steps: (1) germination of seeds under darkness in a seed germinator adjusted for a 20-15°C (16 hours-8 hours) temperature regime, (2) exposure of germinating seeds to dehydration treatments, and (3) a 10-day seedling growth period.

Seeds were germinated in closed plastic boxes on top of substrata moistened with 100 ml tap water. Dehydration treatments were imposed on germinating seeds when seminal primary roots reached 2-5 mm in length by placing them in constant humidity trays. Saturated solutions of K₂SO₄, Na₂SO₄, KCl, and NaCl were used to maintain water potentials of -4, -10, -22, and -37 MPa, respectively, in the constant humidity trays (Hassanyar and Wilson 1978). Seeds were allowed to lose moisture to the constant humidity environment without touching the salt solution. Seeds were exposed 4 days to constant humidity environments of each water potential. Gravimetric determination of seed water content by Hassanyar and Wilson (1978) indicated that seeds of crested wheatgrass and Russian wildrye equilibrated with constant humidity environments in about 2 days. Seminal primary roots of half the seeds in each dehydration treatment and in the control treatment were excised to simulate conditions under which the seminal primary root was killed by drought.

Seeds were removed from the constant humidity trays following the 4-day dehydration treatment and planted at a depth of 1.5 cm in plastic pots (15 cm diameter by 15 cm deep) filled with autoclaved sandy loam soil. Pots were placed in a growth chamber adjusted for a daily temperature and light regime of 25-20°C (15 hours with

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light-9 hours with dark). Light intensity was $450 \mu\text{E m}^{-2} \text{sec}^{-1}$ of photosynthetically active radiation. Pots were watered when needed to maintain a soil water potential of approximately -0.03 MP a.

The seedlings that emerged were counted after a 10-day period in the growth chamber. Five of the seedlings that emerged in each pot were randomly selected and marked. Soil was then removed from the pots and washed from seedling roots with a fine spray of water. Data for (1) number of seminal roots, (2) number of adventitious roots, (3) length of longest seminal root, (4) length of longest adventitious root, and (5) shoot length per seedling were based on averages of the 5 marked seedlings in each pot.

A randomized complete-block experimental design with a factorial arrangement of treatments was used in the experiment. Five replications were conducted sequentially over time. Data were analyzed by analysis of variance, and Duncan's new multiple range test was used at the 0.05 level to identify significantly different means. All differences discussed in the following section were significant at $P < 0.05$ unless otherwise stated.

Results

Increasing severity of dehydration of germinating seeds resulted in a corresponding decrease in subsequent seedling emergence (Table 1). Emergence of SD-93 and Lodorm seedlings was reduced by temporary dehydration treatments of -10 MP a and lower. No seedlings emerged following the -37 MP a dehydration treatment. Percent emergence of seedlings with seminal primary roots excised was not different from those with intact roots. There was no difference in percent emergence between the 2 seed sources.

Total number of roots per seedling decreased with each increase in severity of dehydration treatment (Table 2). Number of seminal roots per seedling did not differ between the 0 and -4 MP a treatments, but was reduced by the -10 MP a dehydration treatment. There was an interaction of seed sources with dehydration treatments for percent of seedlings with at least 1 seminal root. Lodorm seedlings had a higher percent of seedlings with at least 1 seminal root than did SD-93 for the -10 MP a treatment, but not for the 0 and -4 MP a treatments. Length of longest seminal root per seedling was reduced by the -4 and -10 MP a dehydration treatments.

Length of longest adventitious root per seedling was not affected by the dehydration treatments (Table 2). Number of adventitious roots per seedling was lower for the -4 MP a dehydration treatment than for the 0 and -10 MP a treatments.

Table 1. Effects of temporary dehydration (MP a) and seminal primary root excision of germinating seeds on subsequent percent emergence of 2 sources of green needlegrass.

Source	Dehydration treatment (MP a)	Percent emergence for seminal primary root treatment		
		Nonexcised	Excised	Means
SD-93	0	99.2	98.4	98.8a ¹
	-4	93.6	93.6	93.6a
	-10	87.2	79.2	83.2b
	-22	0.8	0.0	0.4d
	-37	0.0	0.0	—
Lodorm	0	99.2	98.4	98.8a
	-4	96.0	94.4	95.2a
	-10	76.0	64.8	70.4c
	-22	0.8	0.0	0.8d
	-37	0.0	0.0	—
Root treatment means		55.3y	53.0y	

¹Means presented at the end of each column and at the end of each row that are followed by the same letter are not significantly different at the 0.05 level of probability according to Duncan's multiple range test.

Shoot length (length from the scutellar node to the tip of the longest leaf) per seedling decreased with each increase in severity of dehydration treatment (Table 2). Shoot length was the only seedling characteristic measured for which a significant difference existed between seed sources. Lodorm seedlings had longer shoots than did SD-93 seedlings.

Excision of the seminal primary root, when averaged over all dehydration treatments, did not affect total number of roots, number of seminal roots, or number of adventitious roots per seedling. Excision of the seminal primary root did reduce the length of seminal roots and shoots and increased the length of the longest adventitious roots. There was an interaction of root treatment with dehydration treatment for total number of roots, number of seminal roots, and shoot length per seedling. Seedlings with excised seminal primary roots had greater total number of roots, number of seminal roots, and shorter shoots for the control (0 MP a) treatment than seedlings with intact seminal primary roots. No difference existed between seedlings with the seminal primary root excised and those with the seminal primary roots intact for treatments other than the control.

Table 2. Effects of temporary dehydration (MP a) and seminal primary root excision of germinating seeds on subsequent root and shoot development (cm) of 2 sources of green needlegrass.

Source and dehydration treatment (MP a)	Seedling characteristic and seminal primary root treatment											
	Total number of roots		Number of seminal roots		Length of longest seminal root		Number of adventitious roots		Length of longest adventitious root		Shoot length	
	N ¹	E ²	N	E	N	E	N	E	N	E	N	E
SD-93												
0	1.7	2.1	1.0	1.4	11.9	10.1	0.7	0.7	1.3	3.3	12.3	10.3
-4	1.6	1.4	1.1	1.0	5.8	4.4	0.4	0.4	2.5	3.6	7.7	7.0
-10	1.3	1.2	0.5	0.5	6.6	5.0	0.8	0.7	2.3	3.4	6.8	6.4
Lodorm												
0	1.8	2.0	1.0	1.2	12.0	9.9	0.8	0.8	1.5	2.1	13.3	11.1
-4	1.5	1.2	1.1	1.1	8.4	7.4	0.4	0.2	1.0	5.2	10.1	9.1
-10	1.3	1.2	0.8	0.6	4.1	5.1	0.4	0.6	1.2	2.2	7.3	7.4
Root treatment means	1.5y ³	1.5y	0.9y	1.0y	8.2y	7.0z	0.6y	0.6y	1.6y	3.3z	9.6y	8.5z

¹N refers to seminal primary root not excised.

²E refers to seminal primary root excised.

³Means under each seedling characteristic followed by the same letter are not significantly different at the 0.05 level of probability. The main effect of seed source was significant ($P < 0.05$) only for shoot length per seedling. Main effects of dehydration treatments were significant ($P < 0.01$) for all seedling characteristics except length of longest adventitious root per seedling. There was a significant ($P < 0.01$) interaction of seed source with dehydration treatment for length of longest seminal root per seedling. There was a significant ($P < 0.05$) interaction of root treatment with dehydration treatment for number of roots per seedling, number of seminal roots per seedling, and shoot length per seedling.

Seedlings in the nonexcised control treatment developed only the seminal primary root and often an adventitious root during the 10-day growth period. Seedlings in the control treatment with the seminal primary root excised developed up to 3 seminal lateral roots (average of 1.3 per seedling) and often 1 (rarely 2) adventitious root. Adventitious roots developed from the coleoptilar node of all seedlings (with and without seminal primary root excision) in the control treatment. In the -10 MP a dehydration treatment, adventitious roots developed from either the coleoptilar node or the subcoleoptile internode.

Discussion

Germinating seeds of green needlegrass are apparently less tolerant of temporary dehydration than germinating seeds of crested wheatgrass and Russian wildrye. Emergence of green needlegrass seedlings following the -22 MP a dehydration treatment was 0.6% compared to 88% for Russian wildrye seedlings under the same experimental conditions (T.E. Fulbright and A.M. Wilson, unpublished data). Temporary dehydration treatments of -10 MP a and lower reduced the percent of green needlegrass seedlings that developed a seminal root. In comparison, Hassanyar and Wilson (1978) reported that the percent of crested wheatgrass and Russian wildrye seedlings that developed a seminal root was reduced by temporary dehydration treatments of -91 and -37 MP a and lower, respectively.

Development of seminal lateral roots by green needlegrass during early seedling growth is apparently an adaptation that provides an alternate source of water and nutrients if the seminal primary root is killed or injured by environmental stress. Development of adventitious roots from the subcoleoptile internode is apparently also a response to environmental stress. If seedlings are not subjected to environmental stress during the early stages of growth, they develop only the seminal primary root from the embryo and adventitious roots from the nodes of shoots.

The number of adventitious roots per seedling was greater following the -10 MP a treatment than following the -4 MP a dehydration treatment. That result was not expected because root growth generally decreases with increasing severity of the dehydration treatment. The increase in number of adventitious roots per seedling at -10 MP a resulted from the sampling procedures used in the study. Growth characteristics were measured for emerged seedlings only. The -10 MP a dehydration treatment was severe enough to kill the seminal primary root of many seedlings (45% of the seedlings in the -10 MP a treatment lacked seminal roots entirely). Generally seedlings did not emerge unless they had developed at least 1 seminal root or 1 adventitious root. Therefore, when the morphology of emerged seedlings only was investigated, there was an apparent increase in number of adventitious roots per seedling at -10 MP a as compared with -4 MP a.

Apparent discrepancies in the literature regarding the drought tolerance of green needlegrass may be partly explained by the

results of this study. Lack of tolerance of germinating seeds to temporary dehydration may cause green needlegrass to be abundant only on more mesic sites. Once the adventitious root system is established, the plant probably exhibits the drought tolerance noted by some authors.

Results of this study suggested that lack of tolerance to dehydration of germinating seeds of green needlegrass may result from (1) a low latent potential for development of seminal lateral roots and (2) low tolerance of the embryo and of developing tissues to dehydration of germinating seeds should be taken into consideration when using green needlegrass in revegetation. Sites to be seeded and planting dates should be selected so as to insure adequate soil moisture for germination and seedling development.

low latent potential for development of seminal lateral roots and (2) low tolerance of the embryo and of developing tissues to dehydration. The low tolerance to dehydration of germinating seeds should be taken into consideration when using green needlegrass in revegetation. Sites to be seeded and planting dates should be selected so as to insure adequate soil moisture for germination and seedling development.

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Seasonal Variation in Total Nonstructural Carbohydrate Levels in Nebraska Sedge

JUDITH M. STEELE, RAYMOND D. RATLIFF, AND GARY L. RITENOUR

Abstract

Seasonal variation in total nonstructural carbohydrate (TNC) levels in rhizomes and shoots of Nebraska sedge (*Carex nebraskensis* Dewey) suggest that grazing too early or too late or both may be detrimental. Samples were collected from a natural population of Nebraska sedge growing in Tule Meadow at 2,170 m elevation in the Sierra Nevada, Calif. TNC reserves in rhizomes decreased to 7.5% of the dry weight during early shoot growth, and reached a peak level of 17.4% in the fall. TNC levels in shoots ranged from a low of 10.6% in the spring to a high of 16% in August, after flowering. TNC levels in emerging shoots averaged 16.4% in September and 19.1% at the end of October.

Nebraska sedge (*Carex nebraskensis* Dewey) is a perennial species common in mountain meadows of the Western United States. Frequently heavily grazed by cattle and horses, it is considered a valuable late-season sedge (Hermann 1970). However, the effects of grazing on Nebraska sedge are not known. Knowledge of its seasonal fluctuations in carbohydrate levels would aid in evaluating the effects of defoliation on its energy reserves and health.

Total nonstructural carbohydrate (TNC) levels provide an estimate of the amount of energy available for plant growth (Weinmann 1947, Smith 1969). A pattern of storage and use of TNC reserves has been noted in many perennial species. Reserve carbohydrate levels in storage organs generally decline to a seasonal minimum upon initiation of spring growth. Reserves are then replenished during the summer, and a high level of TNC is attained before dormancy in the fall (Humphreys 1966).

Carbohydrate reserves in rhizomes of Bigelow sedge (*Carex bigelowii* Torr.) were high in the spring and fell sharply when early shoot growth began (Fonda and Bliss 1966). These reserves were rapidly replaced and peaked after seed dispersal. A similar trend in carbohydrate storage was noted in river sedge (*Carex lacustris* Willd.) (Roseff and Bernard 1979). Total nonstructural carbohydrate levels were low early in the growing season and were at a high level in the fall.

This paper reports a study of seasonal carbohydrate levels in Nebraska sedge in the Sierra Nevada, Calif.

Methods

A site at Tule Meadow, a wet meadow, on the Sierra National Forest, Fresno County, Calif., was selected for this study. Tule Meadow, at 2,170 m elevation, lies in a swale formed by moraines (Wood 1979). Soils of the meadow have not been classified. Generally, however, beneath a sod surface is an organically rich top soil, which extends to depths of 90 cm to 120 cm. Soil texture ranges from sand to silt loam. Inorganic, grayed material then extends to 275 cm (the depth sampled by Wood).

The specific site selected falls into the Nebraska sedge class (Ratliff 1982) or the Nebraska sedge wet meadow association (MW19 11) of Hall (1979). Other species of some importance on

the site included beaked sedge (*Carex rostrata* Stokes) and tufted hairgrass (*Deschampsia caespitosa* (L.) Beauv.). Soil at the site is typical of Nebraska sedge sites in the Sierra Nevada. Such sites have a loam texture, a strongly acid reaction, and more than 20% organic matter at the 10 to 20 cm depth (Ratliff 1982).

On April 10, 1980, snow was 1.5 m deep over the site. By May 8 snow was melting and some ground could be seen. The site was fully accessible on May 22. As is usual in the Sierra Nevada, little precipitation occurred during the summer (Table 1). Minimum air temperatures were above freezing only from mid-July to about mid-August. Soil temperatures were above freezing at all times. Free surface water remained into August, and soil water content was at or near saturation level even when surface water was not present. Rain in early September caused a temporary return of free surface water and was associated with a hard freeze. Hot weather in late September and early October produced a temporary warming.

Samples were collected at 2-week intervals from May 22 through October 23, 1980. All sampling was done before noon so as to reduce any variability due to time of day. Three samples were taken from an ungrazed native population of Nebraska sedge on each date. Intact blocks of sod (about 30 cm thick and 30 cm in diameter) were removed from near the centers of randomly selected 0.5-m² (0.5 × 1.0 m) quadrats in a 12 × 6-m study plot. Care was taken not to disturb adjacent quadrats during block extraction. The wet sod blocks were set in plastic bags to reduce loss of soil moisture. That care and the block size should have minimized respirational degradation of TNC during transportation.

At the laboratory sod blocks were washed to remove soil and separate Nebraska sedge from any other plant material present. Established shoots, rhizomes, and new shoots (without unfolded leaves) of Nebraska sedge were then separated. New shoots began to appear in abundance in the fall and were separated from other plant parts on September 11 and 25 and on October 9 and 23 only. While rhizomes of sedges (*Carex*) are important, their roots comprise relatively small proportions of the underground biomass and are relatively unimportant as storage organs (Fonda and Bliss 1966). Root material, therefore, was not saved for analysis.

Plant parts were washed thoroughly in tap water. To facilitate drying, shoots and rhizomes were cut into short segments (4 to 6 cm). They were oven dried for 1 hour at 100° C and then dried to a constant weight at 70° C (Raguse and Smith 1965). The dried materials were ground to pass a 40-mesh (0.42-mm opening) screen and stored at room temperature in sealed bottles until TNC analysis.

To remove total nonstructural carbohydrates from the plant tissue samples, we followed the takadiastase enzyme method (Smith 1969). After digestion by takadiastase, fructosans and other sugars were hydrolyzed to monomers with 0.1 N sulfuric acid. Reducing power of the resulting solutions was measured by the Shaeffer-Somogyi copperiodometric titration method (Heinze and Murneek 1940, Smith 1969).

Sample weights used for analysis ranged from 100 to 200 mg, depending on the type of plant tissue and the date of sampling.

Data were analyzed following analysis of variance procedures for the randomized complete-block, fixed effects experimental

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Table 1. Precipitation, maximum and minimum air temperatures, soil temperatures, and surface water depths at Tule Meadow (June 19 to October 23, 1980).

Sampling date	Precipitation cm	Air temperatures		Soil temperatures		Surface Water Depth cm
		Maximum Degrees C	Minimum Degrees C	0-10 cm Degrees C	10-20 cm Degrees C	
June 19	Note taken		Not taken	13.9	13.9	10.4
July 3	0.0	24.7	-1.1	14.2	14.4	8.8
17	0.0	24.4	-2.2	15.6	13.6	4.4
31	0.3	29.7	3.1	17.5	15.6	1.5
Aug. 14	0.0	26.7	5.0	15.0	14.7	0.0
28	0.0	22.8	-4.4	12.2	12.5	0.0
Sept. 11	3.6	25.6	-11.7	10.0	9.7	1.7
25	0.1	25.0	-4.4	11.1	10.8	0.0
Oct. 9	Trace	28.3	-2.2	11.7	10.8	0.0
23	1.7	17.8	-12.8	6.1	5.8	0.3

design. Means were separated by Duncan's multiple-range test.

Results and Discussion

The TNC cycle of Nebraska sedge is similar to that of other species and follows closely the generalized cycle characterized by Humphreys (1966). Carbohydrate levels in the rhizomes were low at the beginning of the season and dropped sharply when shoot growth began. Levels of TNC in the rhizomes and shoots rose significantly during the short maturation period. Shoot TNC levels declined with the onset of shoot senescence.

Total nonstructural carbohydrate levels for shoots averaged 10.6% on May 22, the first sample date (Fig. 1), and were statistically constant until the period of full bloom. Anthesis began about

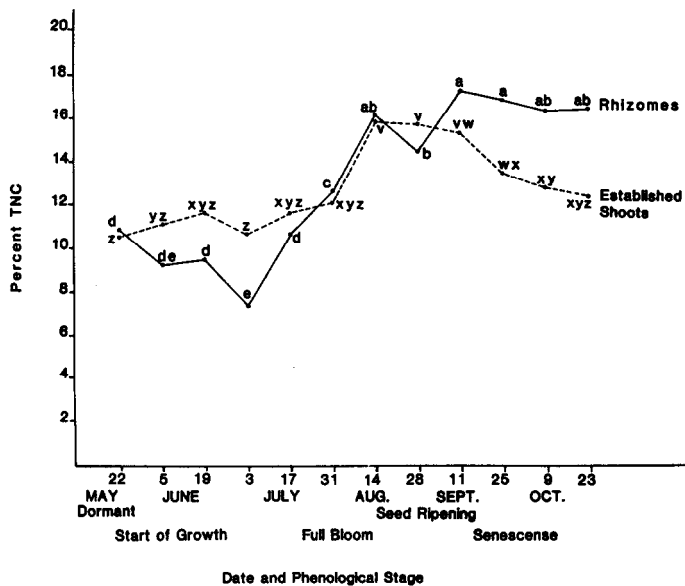


Fig. 1. Seasonal variation in levels (expressed as percentage of dry weight) of total nonstructural carbohydrate (TNC) in established shoots and rhizomes of Nebraska sedge, as related to reproductive shoot phenology. Data points followed by the same letter within plant parts are not significantly different at the .05 level.

July 17, and shoots were in full bloom by July 31. Shoot TNC levels reached a peak of 16% on August 14, shortly after the full bloom period, and then slowly declined to 12.5% by the final sample date (October 23).

Rhizome TNC level averaged 10.8% on May 22 (Fig. 1). It declined significantly and reached a seasonal low of 7.5% on July 3, just before the early bloom period. The rhizome TNC level rose steadily from that period until August 14, when it reached 16.1%. It reached a seasonal high of 17.4% on September 11, and then remained statistically constant. Nevertheless, a tendency of rhi-

zome TNC levels to decline late in the growing season is seen.

Carbohydrates were transferred from rhizomes to actively growing shoots of Bigelow sedge, and rhizome reserves declined to 9.6% in the spring (Fonda and Bliss 1966). Nebraska sedge shoot TNC levels were constant, while rhizome TNC levels decreased to 7.5% during early shoot growth. Photosynthesis by the shoots was evidently insufficient for shoot growth and to replenish rhizome reserves until after the start of anthesis. Therefore, as with Bigelow sedge, depletion of rhizome TNC in Nebraska sedge early in the growing season may be due to carbohydrate translocation from rhizomes to shoots.

Total nonstructural carbohydrate levels in Nebraska sedge were lower than those reported for river sedge (Roseff and Barnard 1979), although the same analytical methods were used. While actual levels in the 2 species differed, the variations in carbohydrate levels during the growing season did not. High rhizome TNC levels (44.9%) were recorded for river sedge in the fall and low levels (29.2%) in the spring.

A significant interaction occurred between the sampling dates and the carbohydrate levels of mature shoots, rhizomes, and emerging new shoots of Nebraska sedge (Fig. 2). The new shoots

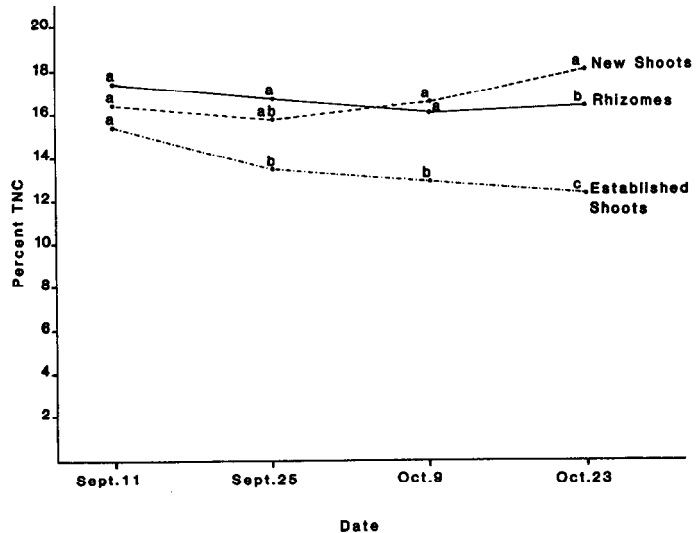


Fig. 2. Total nonstructural carbohydrate (TNC) levels (expressed as percentage of dry weight) in new shoots, established shoots, and rhizomes of Carex nebraskensis from Sept. 11 through Oct. 23. Means followed by the same letter within each date are not significantly different at the .05 level.

contained a relatively high level (16.4%) of TNC on September 11. By then, the TNC level of established shoots had begun to decline, while the rhizome TNC level was at its seasonal peak. On Sep-

tember 11, we found no significant differences among the TNC levels of the 3 plant parts.

On October 9, the TNC level in the new shoots was 16.6%, and that of established shoots was 12.9%, a significant difference. Rhizome TNC levels had gradually declined to 16.2%, a value similar to the level in new shoots. On October 23, TNC levels in plant parts were: new shoots—19.1% (the highest level recorded during this study), established shoots—12.5%, and rhizomes—16.3%.

The high accumulation of carbohydrates in new shoots in the late fall may account for the significant TNC decrease in established shoots. Carbohydrates appeared to be transferred to the young shoots from mature shoots and (perhaps to a lesser extent) from rhizomes. We suggest that during the fall period new shoots are carbohydrate sinks. In a concurrent study, 79 new Nebraska sedge shoots were observed September 11 through November 20, 1980. Of the new shoots 11, 27, 22, and 25% were first observed on September 11 and 25 and October 8 and 22, respectively. The other 15% were first observed on November 5 and 20. Photosynthesis by newly emerged shoots could explain their increased TNC levels, but it seems likely that such activity was minimal. The new shoots began to appear as reproductive shoots became senescent and older vegetative shoots became quiescent. Very few of those shoots (even among the earliest ones) had advanced beyond the first phenological stage by November 20. While environmental conditions following the September freeze were not prohibitive, photosynthetic activity by established shoots was clearly declining. And, there was an abundance of developing unemerged shoots.

Attaining a high concentration of TNC in the fall may be necessary for the survival of the new shoots during the winter and/or upon emergence in the spring. Data on overwinter survival of fall emerging shoots of Nebraska sedge have not yet been analyzed. However, they appear to overwinter at least as successfully as mature vegetative shoots, for which a 95% overwinter survival rate is indicated (Ratliff 1983).

Management Consideration

Based upon the results from this study we hypothesize that at Tule Meadow the optimum grazing period for maintenance of Nebraska sedge is from about mid-August to mid-September, when shoots and rhizomes attain their highest TNC levels. We suggest that it is best to not graze or defoliate Nebraska sedge until

after anthesis, when seed is ripening and peak TNC levels have been reached and after the onset of senescence. Rhizome reserves are at a minimum during early shoot growth. At this point in its seasonal growth Nebraska sedge may not be able to recover from significant loss of photosynthetic tissue. This premise is supported by responses in grasses defoliated when carbohydrate reserves were low (Donart and Cook 1970). Late defoliation may adversely affect overwinter survival of fall emerging shoots by reducing TNC accumulation in those tissues.

Effects of grazing at times other than the optimum grazing period will, of course, depend upon the degree and frequency of defoliation and the regrowth opportunity for restoration of TNC reserves.

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Reliability of Captive Deer and Cow In Vitro Digestion Values in Predicting Wild Deer Digestion Levels

HENRY CAMPA, III, DAVID K. WOODYARD, AND JONATHAN B. HAUFLE

Abstract

The in vitro dry matter digestibility (IVDMD) values of 9 forages were compared using rumen fluid collected from wild white-tailed deer (*Odocoileus virginianus*), captive white-tailed deer, and a Holstein cow. Five of the 9 forages analyzed displayed significantly different ($P < 0.05$) IVDMD between wild deer and captive deer inocula and between wild deer and cow inocula. Differences were attributed to the diet differences of the donor animals, which may have influenced the composition of microorganisms within the rumen. In vitro dry matter digestibility of all 5 forages considered together decreased significantly ($P < 0.05$) when rumen inocula were stored at various intervals. This study indicates that IVDMD values obtained using inoculum from captive and domestic animals on commercial diets should only be used by researchers to make comparisons of forages, not to predict actual digestibility levels by wild animals. In addition, in vitro samples should be inoculated as soon after collection as possible in order to obtain reliable data.

The quantity and quality of available forage is a major factor affecting the quality of rangelands for wildlife. Biologists have attempted to determine the nutritional quality of various forages and to evaluate digestibility by different animals. In order to determine how well selected wildlife species, such as ruminants, can utilize various forages, researchers have conducted digestibility experiments. Traditionally, digestion trials involving the feeding of animals were used. However, researchers encountered problems using this technique including expense, time, and difficulties in obtaining large amounts of forage (Palmer 1976). Because of such problems, in vitro procedures have been developed to estimate the degree of forage digestion by ruminants (Tilley and Terry 1963, Pearson 1970).

The advantage of using in vitro procedures is that they are relatively inexpensive and a large number of forage samples can be analyzed at one time using only a small amount of sample. Like conventional digestion methods, however, in vitro digestibility procedures also have their limitations in practice and application. Because it is often impractical to obtain inoculum from the wild ruminant under investigation, researchers have substituted, using inoculum from captive animals of the same species, or of a different species, in an attempt to quantify how well free ranging animals are using various forages (Palmer et al. 1976, Blankenship et al. 1982). However, because the composition of microorganisms within the rumen is dependent on the diet of an animal (Church 1969, Maynard et al. 1979), differences in diets may influence an animal's ability to digest a forage. Some researchers have documented that the use of inoculum from different ruminant species, on various diets, affected the IVDMD of various forages (Robbins et al. 1975, Horton et al. 1980). Welch et al. (1983), however, found no significant difference in the IVDMD of 25 forages among 6 ruminant species. Conflicting results may have been caused by differences in

the chemical composition of test forages or in differences in laboratory procedures.

This study investigated the feasibility of using cow and/or captive white-tailed deer (*Odocoileus virginianus*) as the inoculum source for estimating in vitro digestion in wild white-tailed deer. In addition, the effect that the time interval between collection of rumen fluid and inoculation of samples has on in vitro dry matter digestibility (IVDMD) levels was also investigated.

Methods

To investigate the effects various inoculum sources have on IVDMD of selected forages, rumen fluid was collected from wild white-tailed deer, captive white-tailed deer, and a nonlactating rumen-fistulated Holstein cow. Captive deer were fed commercial deer pellets. The Holstein cow was maintained on a diet of good quality alfalfa hay.

Three replicate trials were conducted using captive deer and cow inoculum and duplicate trials were run using wild deer rumen fluid. Rumen fluid for cow replicates was obtained from 1 animal on 3 different days in March, 1983. To obtain inoculum from captive deer, three 7-8 month old, male deer were sacrificed from the Houghton Lake Wildlife Experiment Station, Houghton Lake Heights, Mich., in February, 1983. Inoculum from wild deer was obtained by sacrificing 2 adult does: 1 in October, 1982, from an aspen (*Populus* spp.) clearcut, where vegetation samples were collected in Montmorency County Mich., and 1 in February, 1983, from an agricultural area in Ingham County Mich. The food habits of these 2 deer were not determined but, based on studies conducted in similar areas, their diets were assumed to be fairly diverse (Rogers et al. 1981).

Rumen fluid from all 3 sources was strained through 4 layers of cheesecloth into an Erlenmeyer flask and placed in a waterbath (39°C) for transportation to the laboratory. Inoculum was kept in a waterbath maintained at 39°C and flushed with CO₂ until inoculation. All samples, except those used in the inoculum storage test, were inoculated within 1 hr of obtaining rumen fluid. Analytical procedures used were described by Tilley and Terry (1963), modified by Michigan State University, Department of Dairy Science. Modifications included the use of a phosphate-carbonate buffer solution (Table 1) and using a ratio of 12 ml of rumen fluid to 10 ml buffer solution.

The plant samples used for digestion trials included orange-hawkweed (*Hieracium aurantiacum*), wild strawberry (*Fragaria virginiana*), panic grass (*Panicum virgatum*), and separate leaf and twig samples from 3 woody species: black cherry (*Prunus serotina*), trembling aspen (*Populus tremuloides*), and big-tooth aspen (*P. grandidentata*). Vegetation samples were collected in June, 1982, from a 10-year-old aspen clearcut. Tissues collected were restricted to the current annual growth of randomly selected individuals. These samples were dried at 60°C and ground in a Wiley mill to pass a 1.0-mm screen.

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Table 1. Composition of in vitro buffer solution.

Ingredient	g/L
Na ₂ HPO ₄	8.72
KH ₂ PO ₄	4.08
MgSO ₄ •7H ₂ O	1.5
KCl	0.5
CaCl ₂	0.1
Na ₂ S•9H ₂ O	0.025
Na ₂ CO ₃ solution, 15.73g/ 100 ml	20(ml/L)
Urea solution, 8.0g/ 100 ml	10(ml/L)

Statistical analysis of the data was with analysis of variance and Duncan's new multiple-range test. Barlett's test was conducted on all data to test for homogeneity of variance. Data which had heterogeneous variances were subjected to an arc sine transformation (Steel and Torrie 1980).

Tests for effects of storage time of inoculum on IVDMD from 3 captive adult male deer from the Houghton Lake Wildlife Experiment Station and the Holstein cow were conducted. In vitro digestion trials were initiated 40 minutes after rumen fluid collection, with subsequent samples inoculated at 7, 20-minute intervals, with the final inoculation at 3 hr. Vegetation samples for this phase of the project consisted of cherry (*Prunus* spp.) leaves, cherry twigs, sedge (*Carex* spp.), orange-hawkweed, and panic grass collected from a 5-year-old jack pine (*Pinus banksiana*) clearcut. Subsamples of each of the 5 vegetation samples were used in all 8 time periods. Vegetation was dried, separated, and ground by methods stated earlier.

Regression equations were calculated to determine the relationship between IVDMD and storage time of the rumen fluid.

Results

Of the 6 samples from the 3 woody species analyzed, only 2 showed significantly different digestibility levels among inoculum sources (Table 2). Black cherry twigs and trembling aspen leaves had IVDMD levels which were significantly different between wild deer and captive deer and between wild deer and cow. Black cherry leaves were the only species which displayed significantly different IVDMD levels among all combinations of inoculum sources. Two of the 3 herbaceous species analyzed show significantly different IVDMD values between wild deer and captive deer inoculum sources and between wild deer and cow (Table 2). There were no significant differences in IVDMD between individual wild deer and individual captive deer.

Results of inoculum storage time trials showed that IVDMD of all species combined significantly decreased ($P<0.05$) over 3 hr using both captive deer and cow inoculum (Fig. 1). The IVDMD of

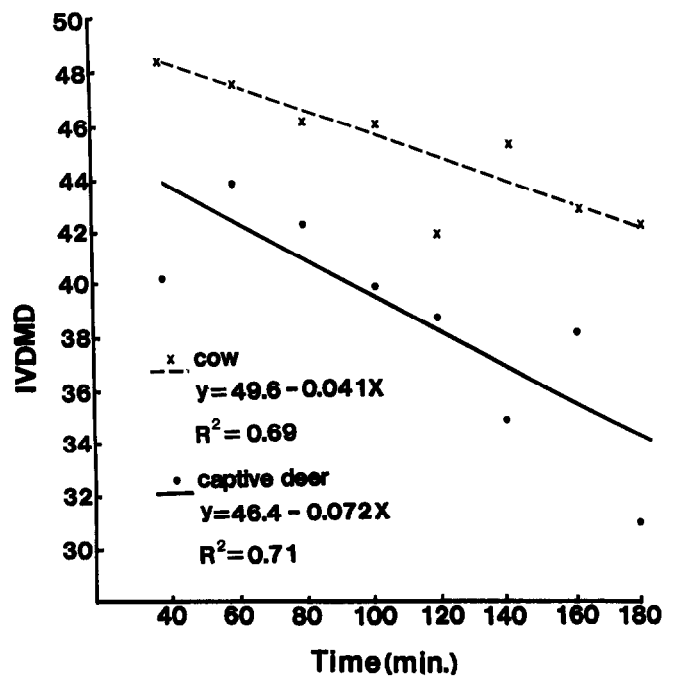


Fig. 1. Effects of time prior to inoculation on the in vitro dry matter digestibility of forages (mean values of 5 forages at each time) using cow and captive deer inoculum.

individual forage species did not show a significant decline over time using captive deer inoculum. Using cow inoculum, however, cherry leaves, panic grass, and orange-hawkweed all showed a significant decrease in IVDMD ($P<0.05$) (Fig. 2).

Discussion

Results indicate that of the forages used for the in vitro digestion comparison trials, 5(56%) had significantly different IVDMD values between wild deer and captive deer and between wild deer and cow. These data suggest that in vitro digestion of some forages by wild deer differed significantly from both captive deer and cow. This dissimilar capability to efficiently utilize the selected forages may have been caused by differences in the diet composition of the respective donor animals. Since the captive deer and cow were fed a homogeneous ration of good nutritional quality, the diversity of microorganisms which inhabit the rumen may have been limited. Robbins (1983) stated that the inoculation of bacteria into the

Table 2. Mean IVDMD of forage species from three inoculum sources. Number of animals used for each inoculum source is indicated in parentheses.

Forage species	Inoculum sources		
	Wild deer (2)	Captive deer (3)	Cow (3)
<i>Fragaria virginiana</i> (wild strawberry)	68.8a ¹	30.9b	45.4b
<i>Hieracium aurantiacum</i> (orange-hawkweed)	63.6	56.3	57.8
<i>Panicum virgatum</i> (panic grass)	54.5a	31.8b	38.9b
<i>Prunus serotina</i> (black cherry) leaves	34.2a	44.5b	51.3c
<i>P. serotina</i> (black cherry) twigs	52.7a	26.9b	33.1b
<i>Populus tremuloides</i> (trembling aspen) leaves	50.3a	26.7b	28.9b
<i>P. tremuloides</i> (trembling aspen) twigs	47.6	39.7	41.9
<i>Populus grandidentata</i> (big tooth aspen) leaves	41.9	47.9	49.3
<i>P. grandidentata</i> (big tooth aspen) twigs	56.3	43.2	53.2

¹Any two means within a row with different letters indicate a significant difference ($P<0.05$).

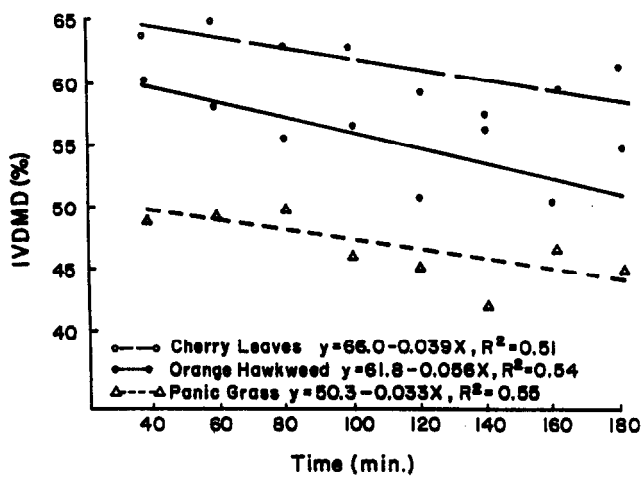


Fig. 2. Effects of time prior to inoculation on the in vitro dry matter digestibility of 3 forages using cow inoculum.

neonate rumen is often dependent on such factors as the feed handled by the mother or maternal feces touched. Therefore, if wild deer have the opportunity to feed on a variety of forages, it is more likely they are in contact with a greater diversity of microorganisms and therefore may be more capable of utilizing a greater diversity of forages than domestic or penned individuals (Blankenship et al. 1982). Good populations of microorganisms can also be influenced by the nutritional quality of the diet of an animal (Church 1969), so poor quality diets could also influence IVDMD, regardless of the likely diversity of microorganisms present. However, all individuals used in this study were in excellent condition and assumed to be on a diet of good nutritional quality. Therefore, differences in rumen microorganisms appear to be responsible for the differences in IVDMD for some forages. The forage species which exhibited nonsignificantly different IVDMD between inoculum sources could be attributed to a possible dissimilarity in the chemical composition of these forages to the diets of one or more of the donor animals.

The results from the time trials for both captive deer and cow inoculum paralleled the results by Schwartz and Nagy (1972) using mule deer (*Odocoileus hemionus*). In vitro dry matter digestibility significantly decreased after approximately 2 hr of storage. In addition, IVDMD levels became more variable at times beyond 2 hr.

The nonsignificant results obtained for time trials when considering individual forage species and using captive deer inoculum may be attributed to the diet composition of donor animals. Because captive deer were fed a high protein pelleted ration, instead of a forage fed to the cow, appropriate microorganisms may not have been present to digest forages adequately enough to detect changes in digestibility of individual species over time, given the variance associated with digestion trials of one sample at each time. Using cow inoculum, however, significant decreases in IVDMD were detected with cherry leaves, panic grass, and orange-hawkweed. Those results may be attributed to possible similarities, such as nutrient content and/or stage of maturity, between the 3 forage species and the alfalfa hay the cow was fed. Previous analysis conducted on the 3 forage species indicated crude protein contents ranged from 17 to 23% while lignin content was 5.6 to 8.5% (Campa 1982). These crude protein values are similar for the protein content (18.1%) of second cutting alfalfa hay reported by Crampton and Harris (1969). According to Van Soest (1975) lignin must compose at least 40% of the total cell-wall constituents for the

digestion of the cell-wall constituents to cease. Lignin content for these 3 species was below this level (only 11 to 27%), therefore cell-wall constituents were able to be partially digested. Cherry twigs and sedge did not show the significant decreases in IVDMD over time using cow inoculum, possibly due to the low protein and high fiber contents of these species. The cell-wall constituent values for these 2 species were 66 and 72% respectively, while crude protein contents for the 2 species were 9 and 12%, respectively (Campa 1982). These cell-wall values are considerably higher than crude fiber content (31.2%) of alfalfa hay reported by Crampton and Harris (1969) and crude protein values are considerably lower. Because lignin may hinder the utilization of vegetation by ruminants (Van Soest 1965, Milchunas and Baker 1982) by binding to other fiber constituents, sedge and cherry twigs may not have been digested sufficiently to detect changes in IVDMD over time.

From these results it appears that inoculum from captive deer and cows cannot be used to accurately estimate IVDMD in wild deer if animals are fed dissimilar diets. However, the relative values from in vitro digestibility trials using captive deer or cows as the inoculum source can still provide useful comparisons of the utilization of forages.

The length of storage time between collection of rumen fluid and the inoculation of samples is a variable researchers should consider before conducting any in vitro digestion trial. If laboratory facilities are not in close proximity to donor animals, one may obtain depressed values and variable data. Therefore, researchers should attempt to minimize inoculum storage time by inoculating samples as soon after collection as possible.

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Estimating Grazingland Yield from Commonly Available Data

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Abstract

Range managers must often estimate or predict annual forage yield at a distance, from minimal data, or for a variety of sites. This study compared and modified 6 simple formulas potentially useful for this purpose. The grazingland data that were used represented 44 sites on 5 continents. Soil texture at site affected accuracy of all formulas. Shrubiness affected accuracy of formulas based on evapotranspiration. Some formulas modified to include past-year yield as a variable were fairly accurate over a variety of grazinglands. An equation based only on past-year yield predicted yield within an average of 34% at new sites. Equations that incorporated past-year yield, used a measure of current effective moisture, and had a limiting-factor approach estimated current yield within an average of 18–19% at new sites.

Attempts to estimate forage production of particular grazinglands have resulted in hundreds of mathematical models (Van Dyne et al. 1977). The general relation between forage yield and climate has also occupied researchers (Coupland 1979, Lauenroth 1979, Singh et al. 1980). However, range managers and resource planners concerned about carrying capacity must often estimate a year's production for an unmodeled site or for a variety of sites. They may have available only such data as precipitation, temperature, and possibly past yield. But differences in the performance of yield models that claim some generality and require only readily available data have not been investigated systematically for a variety of rangeland sites.

In this study the ability of 6 sample formulas to estimate grazingland yield for specific years for a variety of sites was tested, and the formulas were modified. This paper compares the equations and suggests that some modified versions could be used to estimate a year's aboveground dry-matter production on grazinglands where detailed data are scarce.

Formulas, Data, and Methods

Six published formulas (Table 1) that were intended to be large-area plant production models and required minimal climate data were chosen for testing. Each related annual yield to precipitation, temperature, or variables derived from these, through coefficients estimated by regression. Two formulas had the same structure; they were designed to estimate aboveground standing dry matter on rangelands of 2 regions, the Sahel-Sudan and the Mediterranean Basin (Le Houerou and Hoste 1977). The other 4 formulas

(by Czarnowski 1973; Lieth 1973, 1975; Lieth and Box 1972; and Rosenzweig 1968) were designed to estimate net primary productivity of any vegetation type. Estimates of the Czarnowski, Lieth, and Lieth-Box formulas, all for total plant production, were halved to apply to aboveground production, a relation common for rough conversion (e.g., Lieth 1973).

Data on climate and concurrent aboveground dry matter production came from grazinglands at 28 locations in North America, Asia, Africa, Australia-New Zealand, and Europe. Sites differing in physical characteristics or sampling method were available for some locations and consecutive data years were available for most, for a total of 194 years of climate and yield data at 44 sites (Table 2). Nearly all sites were exclosures on native grazed range.

Basic variables chosen were those thought likely to affect accuracy of simple rangeland yield models. Variables included 3 qualitative ones derived from site descriptions:

- (1) dominant vegetation type—perennial herb using the "C4" photosynthetic pathway (Downton 1975, Moore 1977, Waller and Lewis 1979), perennial herb using the "C3" pathway, annual herb, or shrub;
- (2) soil texture—sand, loam, clay, or silt, based on particle size and proportion (Soils Survey Staff 1951);
- (3) method of sampling yield—peak standing crop, end-of-season crop, sum of peak crops by species, or sum of crop increments (Kelly et al. 1974, Singh et al. 1975).

Numeric variables totaled 104. Basic ones were latitude, elevation, precipitation, temperature, growing-season length and temperature, water-balance variables, a moisture index, yield, and past-year yield. Annual water-balance variables were derived from monthly water balances based on precipitation and temperature (Thorntwaite and Mather 1955, 1957) and calculated by computer programs (Wisioł 1981). These variables included actual and potential evapotranspiration, ratio of actual to potential evapotranspiration, and ratio of precipitation to potential evapotranspiration. A moisture index (Thorntwaite 1948) was calculated as: annual surplus minus 0.6 times deficit, the difference taken as a percent of potential evapotranspiration. Other variables included past-year values, ratios, reciprocals, logarithms, and products of basic variables.

The study compared annual yields estimated by models with reported yields, with error expressed as a percent of yield. Variables not used in the formulas were tested for effect on accuracy, often graphically. Logarithmic transformation helped normalize distributions for parametric analysis. Regression, covariance, and time series methods (Johnston 1972) were used to test effect of variables on accuracy as well as to modify original formulas. Tests used a single year of data per site except where multiple-year data were appropriate. Details are given by Wisioł (1981). Spearman rank correlations (Snedecor and Cochran 1967) were taken as primary measures of association.

Modified formulas, built using data from some of the sites, were tested on data from the remaining sites. Versions based on identical rangeland data were derived (in logarithmic form) for all the original formulas, to focus on differences due to structure or

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Table 1. Published yield equations tested.

Source	Equation ¹	Climate variables ²
Czarnowski 1973	$y = 0.176(V)(L)(1 - e^{-P/PE})$	P/PE = precipitation ÷ potential evapotranspiration V = saturated vapor pressure, mm Hg, for mean temperature T of growing season (monthly T > 3°C) L = length growing season, hrs. daylight
Lieth 1973	y = minimum of (Y1, Y2) Y1 = 15000 (1 - e ^{-0.000664P}) Y2 = 15000 / (1 + e ^{1.315 - 0.119T})	P = precipitation, mm T = mean temperature, °C
Lieth & Box 1972	y = 15000 (1 - e ^{-0.0009695(AE - 20)})	AE = actual evapotranspiration, mm
Le Houerou & Hoste 1977 (Mediterranean model)	y = 3.89 (P ^{1.09})	P = precipitation, mm
Le Houerou & Hoste 1977 (Sahel-Sudan model)	y = 2.643(P ^{1.001})	P = precipitation, mm
Rosenzweig 1968	y = 10(10 ^{1.66(log₁₀AE-1)})	AE = actual evapotranspiration, mm

¹y = annual aboveground dry matter yield, kg/ha; e = base of natural logarithms, 2.718. Form, units, and symbols are those allowing easy comparison. Czarnowski, Lieth, and Lieth-Box estimates were intended for total vs. aboveground yield and are shown halved here. Rosenzweig model was published in logarithmic form: log y = 1 + 1.66(log AE - 1), where y was in g/sq m.

²Annual totals except for temperature (mean).

Table 2. Grazingland sites, with annual climate and yield. Mean ± standard deviation is given if data covered a series of years. AE and PE = actual and potential evapotranspiration. Yield = aboveground dry matter.

Location	Latitude (deg.)	Longitude (deg.)	Elevation (m)	Site ¹	Temp. (°C)	Precip. (mm)	AE (mm)	PE (mm)	Yield (kg/ha)
Aiken (AEC Plant), SC, USA	33.6 N	81.7 W	161	1	17	1013	668	901	5855
				2	17	1013	668	901	4851
Ale IBP Site, Richland, WA, USA	46.4 N	119.5 W	365	3	12 ± 0.4	190 ± 14	168 ± 14	748 ± 4	1500 ± 396
Armidale, N.S.W., Australia	30.6 S	151.5 E	1046	4	12 ± 0.1	868 ± 182	595	650 ± 4	6320 ± 1541
				5	12 ± 0.1	868 ± 182	595	650 ± 4	9405 ± 3444
Cañas, Costa Rica	10.3 N	85.2 W	45	6	28	2044	1352	1787	9676
				7	28	2044	1352	1787	13870
Claresholm, Alberta, Canada	50.0 N	113.7 W	1018	8	4.7 ± 1.1	458 ± 93	385 ± 46	535 ± 23	2755 ± 493
				9	4.8 ± 1.2	462 ± 102	387 ± 50	533 ± 24	3364 ± 485
Craigmyle, Alberta, Canada	51.6 N	112.2 W	841	10	2.6 ± 1.3	392 ± 81	379 ± 33	520 ± 26	6734 ± 1727
Desert Exptl. Range, Utah, USA	38.6 N	113.8 W	1600	11	9.9 ± 0.8	170 ± 53	170 ± 52	711 ± 42	249 ± 103
Dickinson, ND, USA	46.9 N	102.8 W	750	12	4.4 ± 0.3	420 ± 73	373 ± 46	560 ± 35	2237 ± 734
				13	4.4 ± 0.3	420 ± 73	373 ± 46	560 ± 35	2671 ± 489
Dissa, Tunisia	33.9 N	9.9 E	61	14	19 ± 0.6	208 ± 48	189 ± 20	994 ± 60	333 ± 71
Gabes, Tunisia	33.9 N	10.0 E	56	15	20 ± 0.8	227 ± 69	191 ± 64	1019 ± 54	269 ± 123
Gellap-Ost, SW Africa (Namibia)	26.4 S	18.1 E	1040	16	20 ± 0.6	218 ± 154	216 ± 149	1031 ± 53	433 ± 237
Kalahari, SW Africa (Namibia)	24.1 S	18.5 E	1200	17	19 ± 0.3	315 ± 149	300 ± 117	923 ± 25	766 ± 370
Kurukshetra, India	30.0 N	76.8 E	250	18	24	676	495	1421	19740
				19	24	676	495	1421	20466
				20	24	676	495	1421	26636
Lamto, Ivory Coast	6.2 N	5.0 W	120	21	27	1189	1089	1638	6940
				22	27	1189	1072	1638	7010
				23	27	1189	1072	1638	9880
				24	27	1189	1111	1638	11110
				25	27	1189	1111	1638	6960
				26	27	1189	1111	1638	8300
				27	27	1189	1111	1638	6890
				28	27	1189	1111	1638	13380
Lanzhot, Czechoslovakia	48.8 N	17.0 E	155	29	8.8	537	451	648	5270
				30	8.8	537	428	648	3940
Mandan, ND, USA	46.8 N	100.9 W	610	31	5.3 ± 1.2	394 ± 97	385 ± 74	604 ± 31	2345 ± 548
Manyberries, Alberta, Canada	49.1 N	110.5 W	934	32	3.8 ± 0.8	336 ± 89	323 ± 58	545 ± 24	1372 ± 257
Maraekakaho, N.I., New Zealand	39.6 S	176.3 E	120	33	14 ± 0.3	810 ± 45	615 ± 94	725 ± 27	7280 ± 915
Meekatharra, W.A. Australia	26.6 S	118.5 E	517	34	22 ± 0.7	306 ± 148	305 ± 152	1173 ± 72	268 ± 105
Migda, Israel	31.4 N	34.4 E	100	35	20 ± 0.2	289 ± 86	288 ± 83	992 ± 16	2644 ± 1081
Mt. Washington, NH, USA	44.3 N	71.3 W	1840	36	-2 ± 0.7	1620 ± 447	329 ± 61	367 ± 54	1938 ± 418
			1665	37	-2 ± 0.8	1609 ± 431	342 ± 70	404 ± 53	1167 ± 278
Osage (IBP), Pawhuska, OK, USA	36.9 N	96.5 W	380	38	15 ± 0.2	827 ± 157	633 ± 117	867 ± 10	5977 ± 1250
Rajkot, India	22.3 N	70.9 E	136	39	26	702	617	1562	3692
San Joaquin Exp. Range, CA, USA	37.1 N	119.7 W	370	40	15 ± 0.7	474 ± 154	300 ± 33	827 ± 54	2626 ± 830
Scotfield, Alberta, Canada	51.6 N	111.3 W	762	41	3.3 ± 0.1	317 ± 46	315 ± 37	558 ± 35	1374 ± 326
Squaw Butte Exp. Sta., OR, USA	43.5 N	119.7 W	1425	42	7.7 ± 0.5	291 ± 82	215 ± 39	577 ± 20	836 ± 313
Westport, S.I., New Zealand	41.8 S	171.6 E	60	43	12 ± 0.7	2178 ± 267	680 ± 46	684 ± 47	10922 ± 741
Winchmore, S.I., New Zealand	43.8 S	171.8 E	160	44	11 ± 0.3	724 ± 118	545 ± 49	633 ± 23	5867 ± 1111

¹Multiple sites for same location differed in at least vegetation type, soil texture, or method of sampling yield. Full descriptions and sources are given by Wisiol (1981). Maraekakaho data was used only as series data.

variables. Rangeland versions took this form, after back-transformation:

$$\text{Rangeland Yield} = a \cdot \text{Original Formula's Estimate}^b$$

where $\log a$ and b were estimated by regression.

Tests of estimates or of year-ahead predictions examined ability to estimate or predict a single year's yield at a variety of sites. Two indexes of accuracy were calculated for each model: (1) average percentage error over test sites; and (2) maximum percentage error for the 9/10 of the test sites at which model was most accurate, taken as a reasonable measure of the maximum error to be expected at most new sites.

Results

Accuracy of Original and Rangeland-based Formulas

The 6 published formulas erred by an average 67% to 128% in estimating annual yields for grazingland sites (Table 3). All tended strongly to overestimate, as much as several hundred percent, except the 2 Le Houerou-Hoste equations. The Sahel-Sudan equation showed the smallest error and range of error. Each formula was able to estimate yields within 5% or better at some sites.

Basing equations on global rangeland data decreased average error by 18 to 78 percentage points at new sites and, for all except the Sahel-Sudan equation, sharply reduced maximum error (Table 3). For the Czarnowski and Lieth rangeland versions, percentage error at new sites averaged less than 40% and maximum error at 9/10 of the new sites was less than 80%.

Effect of Site and Climate on Accuracy

When mean percentage errors were tabulated by classes of vegetation, soil, and sampling method, the published formulas except the Sahel-Sudan formula (and for a few classes the Mediterranean formula) overestimated yields for all classes. They all overestimated for shrubby sites, sandy sites, and sites sampled by summing increments, and all except the Sahel-Sudan showed maximum error at such sites. Equations derived from global rangeland data overestimated yield for shrubby sites but not for sandy sites, and errors were unrelated to sampling method.

Covariance analysis of original and modified equations using time series data (N=143) explored sensitivity to qualitative site factors, while adjusting for data-base and past-year effects. Soil texture significantly affected both average accuracy and relation of estimate to yield, except for year-ahead predictive equations based on the Le Houerou-Hoste formulas. Accuracy and relation of estimate to yield for clay and loam sites differed from those for sand and silt. For equations based on the Lieth-Box and Rosenzweig formulas, the relation of estimate to yield also differed for shrubs. Method of sampling yield did not significantly affect accu-

racy of any equation, and neither did any interaction of vegetation with soil or sampling method.

Spearman rank correlations quantified association of percentage error with numeric site and climate variables. For all formulas except the Sahel-Sudan and Rosenzweig formulas, errors showed a highly significant negative association with actual evapotranspiration. Errors of the Czarnowski, Lieth, and Lieth-Box formulas also showed such an association with the ratio of precipitation to potential evapotranspiration, ratio of actual to potential evapotranspiration, and Thornthwaite moisture index (itself significantly associated with the ratio of precipitation to potential evapotranspiration). Errors of the Czarnowski, Lieth, and Lieth-Box formulas were also negatively associated with precipitation. Latitude, temperature, potential evapotranspiration, and growing season temperature and length were associated with error only for the Rosenzweig equation. Elevation was associated with error only for the Lieth-Box equation.

Yield itself was associated with percentage error for all formulas except the Rosenzweig formula. The association was positive for the Sahel-Sudan equation and negative for the others. Variables showing significant Spearman correlations with yield were: past-year yield; estimates of all formulas; past-year Lieth, Lieth-Box, and Czarnowski estimates; actual evapotranspiration; precipitation; and past-year moisture index.

Numeric variables that boosted precision when added to formulas were past-year yield, for all formulas, and actual evapotranspiration, for formulas based on precipitation alone. Actual evapotranspiration itself could account for almost as much variation in yield (68%) as any equation lacking past-year yield. Adding variables based on latitude, elevation, or both made coefficients highly unstable. Graphically, the relation of annual yield to distance from the equator resembled a sine function, with 3 yield maxima: between 0° and 10°, near 30°, and near 40°.

Moisture index values were related to vegetation types. For the 189 annual index values calculated, the mean for sites dominated by shrubs was -44; C3 annual herbs, -23; C4 perennial herbs, also -23; and C3 perennial herbs, +15.

Effect of Past-year Values on Accuracy

Past-year yield level affected accuracy more than any other variable, except for the Sahel-Sudan equation in which errors were linked only to current yield levels. For the other formulas, percentage error was negatively associated with past-year yield with Spearman rank correlations ranging from -0.91 to -0.62. Yield itself showed a highly significant association with past-year yield at a Spearman rank correlation of 0.95 for raw values and Pearson linear correlation of 0.90 for logarithms. When past-year yield was included as a variable, formulas could account for 87% to 94% of

Table 3. Error as percent of yield, for original, rangeland-based, and time series rangeland equations. Absolute error is mean (\pm standard deviation) of absolute errors for all test sites. Maximum error for 9/10 sites is maximum of yield minus estimate for the best 9/10 of the sites.

Equation ¹	Absolute error (%) all site			Maximum error (%) 9/10 sites	
	Original equation ²	Rangeland version ³	Time series rangeland version ⁴	Original equation ²	Rangeland version ³
Czarnowski	117 (\pm 187)	39 (\pm 23)	19 (\pm 9)	-434	71
Lieth	97 (\pm 147)	35 (\pm 23)	18 (\pm 13)	-422	78
Lieth-Box	122 (\pm 170)	60 (\pm 32)	28 (\pm 20)	-432	-102
Le Houerou-Hoste Mediterranean	98 (\pm 176)	49 (\pm 21)	51 (\pm 64)	-302	87
Le Houerou-Hoste Sahel-Sudan	67 (\pm 40)	49 (\pm 21)	52 (\pm 73)	91	87
Rosenzweig	128 (\pm 120)	105 (\pm 70)	26 (\pm 20)	-258	-215

¹By source; Table 1 gives form.

²Error is for 43 test sites, for a single year's yield per site.

³Linear transformation of original to general rangeland equation, by regression of logarithmic values of yields on estimates, using 2nd year of data from 21 sites having more than 2 years' data. Error is for back-transformed estimates of a single year's yield at each of 22 other sites.

⁴Incorporating past-year yield. Equations were derived in logarithmic form by regression using series data from sites having more than 3 years' data (N=131) and were tested for estimation of a year's yield at each of 9 other sites.

variation (N=25, standard error of estimate = 3.8% to 5.4% of yield). Past-year yield used alone could account for 82% of variation (standard error = 5.9% of yield).

Equations built to include past-year yield were tested for estimation of a year's yield at a new group of sites. When past-year yield was the only variable, error averaged 34% and maximum error at the 9/10 of the test sites where the equation worked best was calculated at 50%. Year-ahead predictive equations that combined lagged yield with lagged reciprocal moisture index or lagged Lieth estimate showed average errors of only 26–27% but maximum errors about the same as for past-year yield used alone. Equations combining past-year yield with Lieth or Czarnowski estimates based on current climate showed errors averaging only 18–19%, with maximum errors for the best 9/10 of the test sites calculated at 30% and 24%, respectively.

Discussion

Data-base Effect

Data base had an overriding effect on accuracy for these simple formulas. All the original formulas except the Sahel-Sudan formula tended to overestimate rangeland yields grossly; this shows that, for most regions, rangeland sites produce less aboveground biomass than one would expect from general climate-vegetation relations. Basing equations on global rangeland data reduced error by reducing overestimation.

Structure and Type of Variables

Structure and type of variable governed differences in performance of equations based on global rangeland data. Equations having equivalent structure and variables, such as the 2 Le Houerou-Hoste equations, showed equivalent errors.

The rangeland-based Lieth and Czarnowski formulas outperformed the rest. Both formulas used information about moisture and energy simultaneously, the Lieth by alternate equations and the Czarnowski by multiplicative variables. Use of such approaches may enable general grazingland models to perform more accurately at sites outside their data base. Weekly climate data might represent moisture-energy relations more precisely than the monthly data used here, especially for water-stressed sites (Webb et al. 1983).

A more mechanistic approach did not ensure greater accuracy. Accuracy of the most mechanistic of the formulas, having the most variables and most elaborate theoretical basis (Czarnowski 1964), was matched by accuracy of the Lieth formula with one equation based on precipitation and another on temperature. Apparently either structure avoided the flaws which make most multiple-variable equations based on climate unreliable (Katz 1979). Inherent nonlinearity might also afford simple formulas like these an advantage in dealing with the heterogenous character of rangeland data. Neither the Lieth nor the Czarnowski formula could be transformed to a linear equation, and the nonlinear Lieth-Box equation was twice as accurate as the Rosenzweig equation using the same variable.

Analysis of errors according to vegetation, soil, and method of sampling suggests that if algebraic formulas of this type are designed for general vegetation, they will overestimate yield seriously for nearly all rangelands. The analysis by site factor also suggests that even if equations are based on global grazingland data, those lacking a past-yield term or a term taking vegetation or soil into account will overestimate yield for sites that are both shrubby and sandy.

The effect of soil texture on accuracy of estimation and prediction, confirmed by covariance analysis, suggests that soil texture or a correlated variable holds information about yield that is not captured by information about climate or previous year's yield. Both estimative and predictive general formulas might be improved by coding for soil. Adding percent clay or a correlate as a variable might improve general yield formulas.

The fact that shrubbiness influenced relation of estimates to yield only for equations based on actual evapotranspiration may mean that the relation of effective moisture to yield differs for woody and herbaceous rangeland vegetation. The relation of the Thornthwaite moisture index to dominant vegetation type, apparently reflecting plant ability to endure longterm water stress, confirms its utility as an indicator to sites suitable for different kinds of grassland vegetation (Thornthwaite 1952), an important consideration in revegetation studies. The study extends this concept to include photosynthetic type and also indicates that the ratio of precipitation to potential evapotranspiration could be used as an alternate.

Strong correlation between many of the site and climate variables in this study emphasizes the need for caution in use of stepwise and multiple regression to build forage-weather models (Katz 1979). Accidents of sampling are also a danger. Some researchers using data largely from northern hemisphere sites have postulated a negative exponential relation between degrees of latitude and aboveground yield (Caldwell 1975, Van Dyne et al. 1979). The more complex pattern of yield peaks and troughs suggested by these data might result in part from the joint latitudinal distribution of precipitation and potential evapotranspiration. Moisture supply exceeds demand poleward of 40° and below 10°, and supply is lowest while demand is highest between 20° and 30° (Sellers 1965).

Although this study confirmed traditional wisdom that rangeland yield is closely linked to moisture-based variables, especially effective or available moisture, nutrients can be decisive on some rangelands (Bremen and De Wit 1983, Van Keulen et al. 1976).

Past Yield Effect

The best single estimator and predictor of yield, and the variable having most effect on accuracy, was past-year yield, as might be expected. Although current climate information did cut average error in half, past yield remained critical information. Its addition improved accuracy of all equations at new sites. Certain equations including past yield estimated yield within an average 18%, while the closest estimation possible without use of past yield was 39%. When past-year yield was used alone in an equation to predict yield, error averaged only 34% at new sites. Even at a single site, where one would expect most information about yield variation by year to come from climate, 6% of variation can come from past-year yield (Hanson et al. 1982). Past yield may integrate factors determining potential yield, or range condition, while current effective moisture distinguishes one year's yield from another.

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Technical Notes:

An Improved Esophageal Fistula Bag for Sheep

D.M. CENTER AND M.B. JONES

Abstract

An improved bag for collecting samples from esophageal fistulated ewes was tested. The new bag reduced the time required to fit it to the animal and to remove the collected forage.

The use of esophageal fistulated animals is a preferred method of collecting samples representative of the diet of a grazing animal (Van Dyne and Torell 1964, Rice 1970, Vavra et al. 1978, Johnson and Pearson 1981, McInnis et al. 1983). The conventional collection bag, a square canvas bag attached around the neck by 2 straps, provides an adequate means of collecting esophageal extrusa (Fig. 1). However, these bags are time consuming to fit to the animal and

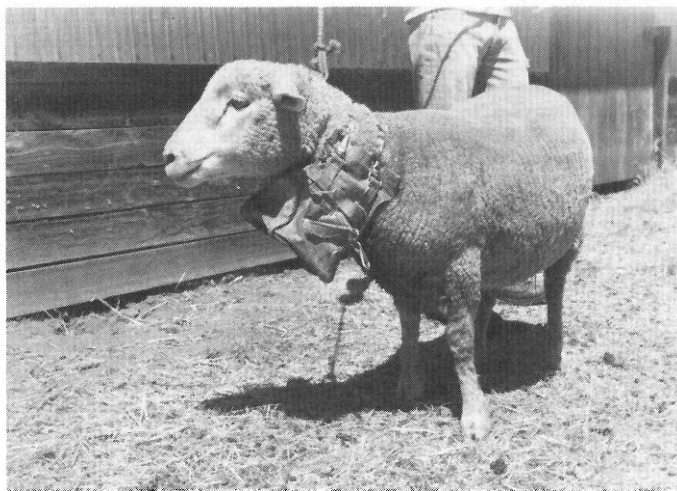


Fig. 1. Esophageal fistulated ewe with conventional collection bag.

transfer of the collected forage involves removing the bag from the animal. When taking repeated samples with several sheep, removing the bag, removing the sample from the bag, and finally replacing the bag can cause a delay in the sampling procedure. To reduce this delay a collection bag was developed that can be quickly fitted to the animal and allow for easy transfer of collected forage.

Procedure

The new collection bag consists of a fabric collar, which fits around the neck of the sheep, attached to a 2-cm wide ring made by sawing through a 10.2-cm dia. schedule 160 (5-mm wall thickness) PVC pipe (Figs. 2 and 3). A plastic bag is attached to the collar by placing the mouth of the bag around the PVC ring and sliding a second ring made of a 2-cm wide slice from the end of a 10.2-cm dia. PVC coupler over the plastic bag. The thickness of the plastic bag between the PVC ring and coupler provides a friction fit that will hold the bag in place. The fabric used in the collar in Figure 2 was 248 gm m^{-2} (8 oz yd^{-1}) urethane coated nylon pack cloth.

Figure 4 shows a cutting diagram for the fabric collar. All raw edges of the fabric are folded over 1 cm and stitched. Referring to Figure 4, end "A" is stitched to end "B" to form a ring. Inserts "D" are then stitched into the areas labeled "C" with the wide side to the top. All seam allowances are 1 cm. Flaps "E" are cut long enough

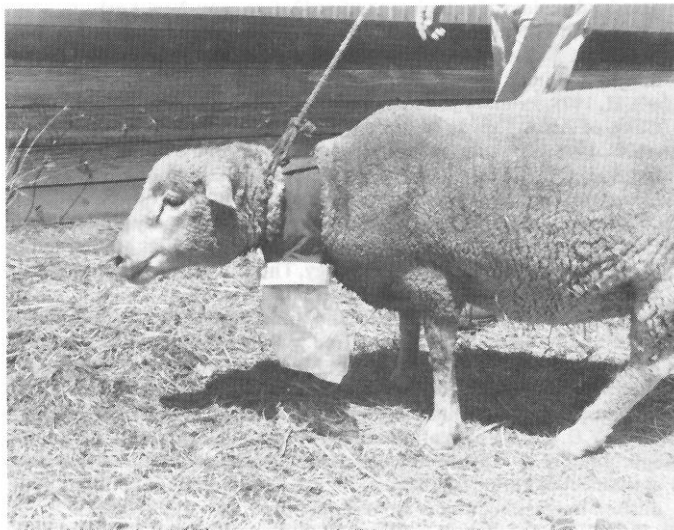


Fig. 2. Esophageal fistulated ewe with improved collection bag.



Fig. 3. Improved collection bag.

so they overlap each other by approximately 10 cm when wrapped around the neck of the sheep. Strips of hook and loop fastener (Velcro) are sewn to the ends of flaps "E" to provide a means of

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adjusting and closing the collar. In order to attach the PVC ring to the fabric collar, a 1-mm deep groove is cut in the outside of the ring 5 to 7 mm from one edge, and .5-mm dia. holes are drilled every 5 mm around the circumference of the ring along the groove. The fabric collar is stitched to the ring through these holes.

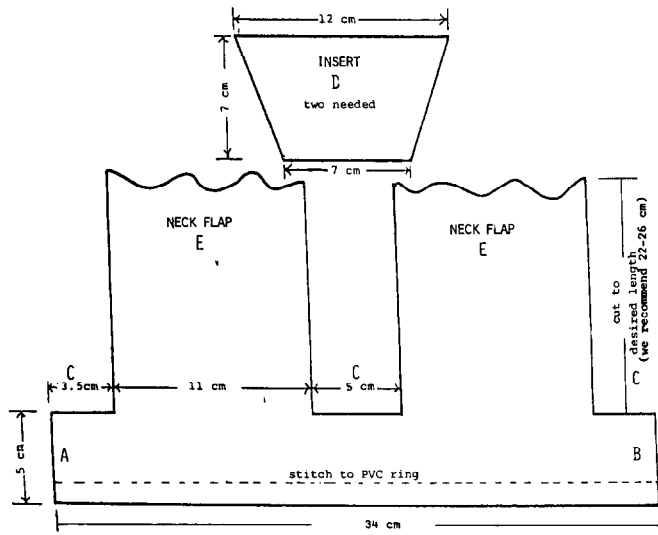


Fig. 4. Cutting diagram for fabric collar.

Discussion

This bag design requires less time to fit to the animal than the conventional bag. The collar is simply wrapped around the neck of

the sheep and is closed by means of the hook and loop closure. The clear plastic bag provides a convenient window through which to check the alignment of the bag with the fistula. To transfer collected forage the full plastic bag is removed by grasping the coupler ring with the fingers and sliding it off while pressing against the inner ring with the thumbs. An empty plastic bag can then be attached to the collar without removing the collar from the animal. If collection of saliva is not desired several holes punched in the bottom of the plastic bag will allow saliva to drain. The whole process takes 15 to 30 seconds. This bag design has worked well in open grassland. However, in brush areas the plastic bag may tear on the brush. In this situation a heavy weight plastic bag or a nylon mesh bag can be used to reduce the chance of losing a sample.

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Book Reviews

Management of Pastoral Development in the Third World.

By Stephen Sandford. 1983. John Wiley & Sons, One Wiley Drive, Somerset, New Jersey 08873. 316 p. \$34.95.

This book is one of a Wiley series on Public Administration in Developing Countries. The author is eminently well qualified to write on this subject. He is currently on the Staff of the International Livestock Center for Africa in Addis Ababa, Ethiopia. Also, he has worked with the British Overseas Development Institute, The Development Bank of Ethiopia, the Livestock and Meat Board of the Ethiopian Government, the British Government Ministry of Overseas Development, the Botswana Government, and the Canadian Government in Africa. A degree in Agricultural Economics, substantial research on arid and semiarid area management, field experience, economic advising, and a synthesis of contributions from a number of Mr. Sandford's associates have made this book possible.

The author treats the following topics in eleven chapters: (1) The Physical and Analytic Framework; (2) Objectives, Strategies and Instruments; (3) Management and Organization in Pastoral Development; (4) The Development of Pastoral Water Supplies; (5) The Scope of Range Management; (6) The Management of Land Allocation; (7) Managing the Improvement of Range Productivity; (8) Improvements in Animal Health and Husbandry; (9) Marketing and Processing; (10) Organizations of Pastoralists; and (11) The Organization of Governments. Each of the eleven chapters concludes with a summary, concluding comment or propositions arising out of the chapter content.

A bibliography of 301 entries reflects an excellent cross-section of writings by the international community of specialists and scholars concerned about pastoral development in the Third World. These are effectively interwoven with the text to broaden, reinforce or reference opposing views.

The author sets the stage of his presentation and discussion by challenging what he calls the "mainstream view." This is the view that "the world's rangelands are suffering severe and rapid desertification." He presents four causes or reasons for this generally held viewpoint. He then proceeds to challenge a number of the basic tenets and draws blunt attention to some of the unscientific half-truths and bits of misinformation or "non-information" that have contributed to the traditional view. In one instance he cites a case of unethical steps taken to support the "desertification" view in the face of opposing or neutral evidence. His assessment of the consequences of the "mainstream view" is enlightening and will challenge many to reassess their position. It may, in fact, open the minds of some pastoral technicians from the developed world to a new and different attitude from which to approach pastoral management and livestock or wild game production in arid regions of the Third World countries.

The author has done a very good job of presenting the evidence on both sides of controversial issues or viewpoints affecting pastoral development and management in Third World countries.

One of the appealing features is the author's persistent attempt to look for and identify the principles that should guide the decision process; that is, the setting of objectives and the establishment of priorities. One of the particularly beneficial aspects of this book is the author's definition of the criteria of choice between various alternatives. In this connection, emphasis is placed on understanding the pastoralist, communicating with him, involving him in the planning process and achieving a measure of agreement among the pastoralists; the proponent of development/management interventions and the government in the process of choosing alternatives. The author makes the basic assumption that pastoral areas will continue as such and that millions of people will continue to be involved in pastoralism as their primary way of life.

This book is a first and much needed, comprehensive treatment.

It does not tell how to do it. It is not a cookbook or prescription book; but it does an excellent job of telling what factors—economic, resource, technology and political—to bring into your thinking and analysis. It gives a new perspective as you make the decisions that are involved in planning and managing pastoral development projects.

In the reviewer's opinion, this book is an essential purchase for the library of anyone currently engaged or contemplating involvement as a rangeland, forestry, agricultural crops, livestock husbandry, veterinarian or wildlife advisor, project manager, or working technician in the developing countries. The book needs to be studied and contemplated in depth so that many of the excellent principles and concepts will become an integral part of one's own thinking and day to day "kit bag" of working tools.

Therefore, it should be obvious that the book is a mandatory acquisition for every college or university department offering training in the same spectrum of science and technology if they intend to be involved at all in training renewable natural resources and agricultural scientists for the global work and quality of professional performance that is required. This book could be a guide to the training of specialists to serve in the developing nations, once they have acquired their technical and scientific skills.

An excellent college course could be designed around this book and the excellent references incorporated into it. It is similarly appropriate for short courses. The purpose should be to establish the kind of understanding that is essential for everyone who intends to be an effective worker in technical assistance to developing countries and in training these people to help themselves.

One of the major reasons why this book is so potentially beneficial for grazing land management professionals and technicians who work in the developing world is the widespread recognition and easily documented fact of failure after failure of *developed world technology*, management systems and practices. This technology and management was interjected into the pastoral situation without questioning need or appropriateness—merely because it may have worked reasonably well in a high cash-flow, economically developed society. Attention to the ideas set forth in this book can help turn this situation around.—*Charles E. Poulton*, Santa Clara, Calif.

Oklahoma Beef Cattle Manual by Keith Lusby et al. 1983.

Oklahoma State University, Central Mailing Services, Stillwater, Oklahoma 74078. \$5.00 192 p.

Every cattle producer, and those working with ranchers, should have a copy of this inexpensive manual. The manual has practical, state-of-the-art information and contains quick reference guides. It is designed to be a complete reference guide for the cattle producer. It is intended to be a how-to-do-it guide for the novice and an update on the latest information for the experienced cattle raiser.

The manual is written in a style easily read by laymen. Technical and medical terms are defined so that the subject matter can be understood by people with limited training in animal husbandry. Current information is provided on each subject.

The nine chapters cover virtually all aspects of cattle science, and the subdivision of subject matter throughout the book makes it easy to find a subject. Chapter I describes feeding the cow herd. It is divided into: nutritional requirements, feeding cattle in cold weather, the supplementation program, and limiting feed intake with salt. Each main topic is broken down into smaller, interrelated subjects. For example, the supplementation program is subdivided into: steps to building a supplement, meeting the protein requirement, meeting the energy requirement, how often supplements should be fed, high quality pasture as a supplement of phosphorus and vitamin A, and arithmetic of pricing supplements.

Chapter II describes managing the cow herd for reproduction, including the replacement heifer, rebreeding, early weaning, bull fertility and nutrition, and artificial breeding. Chapter III deals with stocker cattle management, including nutrition, rations, and

health. Chapter IV describes beef cattle breeding, including cross-breeding. Chapter V describes external parasites, toxicities, and pesticides; Chapter VI, discusses calving difficulties; Chapter VII, corrals and working facilities; Chapter VIII, silage fermentation and additives; and Chapter IX, implanting beef cattle.

Native forage and how it affects nutrition are discussed, but there is little discussion of range management. Perhaps the only weakness of this manual is that no chapter is written by a range scientist. This omission is not an oversight; the authors felt that range management is too broad a subject to be treated adequately in a single chapter and should be the subject of a separate publication (Lusby, personal communication).

Although the manual was written by 13 members of the faculty of Oklahoma State University, research from other states in the Great Plains is also cited. The book is designed for beef producers in the central United States. Most of the information, however, can be helpful to cattlemen everywhere. The manual could be used as a textbook for animal science classes.—*Patrick J. Broyles, Columbus, Kans.*

New Mexico Grasses: A Vegetative Key. By Carolyn M. Barnard and Loren D. Potter. 1984. The University of New Mexico Press, University of New Mexico, Albuquerque, New Mexico 87131. 157 p. Paper—\$8.95.

This publication includes 286 species and varieties of the grass family, Gramineae or Poaceae. This key deals only with grasses, but the Juncaceae (rushes) and Cyperaceae (sedges) appear in the first two key couplets to separate these sometimes confused families.

The key was developed because it is often necessary to identify grass species when they are not in bloom or fruit. Dealing with only the vegetative grass parts, allows this book to be used for identification during any season of the year.

Living plants and herbarium specimens were used to collect the descriptive data, and several keys were used to suggest important vegetative characteristics. However, some species could not be separated by vegetative characters; for example, five species of *Aristida*. In these cases, determinations should be narrowed by careful descriptive comparative. The key and descriptions are based on growth form, life-cycle, ligule, sheath, collar, auricles, vernation, median-line, and habitat/distribution.

The dichotomous key is 44 pages in length and is followed by 95 pages of illustrations consisting of three species per page arranged alphabetically from *Aegilops* to *Trisetum*; common names are included. The book concludes with a glossary, selected bibliography, and an index to scientific and common names.

I'm anxiously waiting to give the key a thorough field test.—*Ed.*

Pecora X

The Tenth William T. Pecora Memorial Remote Sensing Symposium
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