Journal of Range Management

Publication
of the
Society for
Range Management

The Trail Boss

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THE JOURNAL OF RANGE MANAGEMENT (ISSN 0022-409X) is published six times yearly for $56.00 per year by the Society for Range Management, 1839 York Street, Denver, Colorado 80208. SECOND CLASS POSTAGE paid at Denver, Colorado. **POSTMASTER:** Return entire journal with address change-RETURN POSTAGE GUARANTEED-to Society for Range Management, 1839 York Street, Denver, Colorado 80206.

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Effects of continuous grazing on habitat and density of ground-foraging birds in south Texas

DENISE L. BAKER AND FRED S. GUTHERY

Abstract

We analyzed the response of the key habitat features and ground-foraging birds to 2 intensities of continuous grazing on sandy loam and clay soils in the Texas Coastal Bend during 1984–1985. Heavy continuous grazing increased the dispersion but not necessarily the availability of bare ground in comparison with moderate continuous grazing. Responses of habitat features (structure of ground cover, key food plants) depended on soil type. Seasonal densities of eastern meadowlarks *(Sturnella magna)* were higher on clay than on sandy loam soils and higher under moderate than under heavy grazing. Mourning doves *(Zenaida macroura)* were more abundant on sandy loams than on clays and more abundant under heavy than under moderate grazing. Northern bobwhite *(Colinus virginianus)* abundance was uniformly low, regardless of grazing intensity and soil type.

Key Words: continuous grazing, eastern meadowlark, mourning dove, northern bobwhite, Texas

Among numerous approaches to grazing management, continuous, yearlong grazing remains one of the most common. This approach minimizes management input and may maximize livestock performance, depending on area (Holechek 1983). Further, continuous grazing has been more profitable than 4-pasture, deferred rotation and high intensity, low frequency grazing in the Texas Coastal Bend (Drawe 1988).

A primary decision in use of continuous grazing to manage wildlife habitat is livestock stocking rate (AU/ha). Different stocking rates (e.g., light, moderate, heavy) have different impacts on the structure and composition of vegetation, which in turn affect the distribution and abundance of wildlife (Robinson and Bolen 1984, Ryder 1986).

Despite the prevalence of continuous grazing, little research has analyzed the impacts of different stocking rates on wildlife populations. We determined the response of key habitat features and populations of northern bobwhites *(Colinus virginianus)*, mourning doves *(Zenaida macroura)*, and eastern meadowlarks *(Sturnella magna)* to 2 intensities of continuous grazing by cattle.

Study Area and Methods

The study took place on the Rob and Bessie Welder Wildlife Refuge, San Patricio County, Texas, from July 1984 through June 1985. The refuge has 3,158 ha of rangeland and wetlands adjacent to the Aransas River (Drawe et al. 1978). Elevation ranges from 1 to 4 m above mean sea level. Climate ranges from humid subtropical to subhumid subtropical with average winter and summer temperatures of 13.9 and 30.0° C, respectively (Guckian and Garcia 1979). Average annual rainfall is 89 cm with most occurring in late summer and fall (Drawe et al. 1978).

Data were collected on 4 experimental pastures established in 1982. Soils on 2 pastures consisted mainly of Odem fine sandy loam with outcroppings of Sinton loam (Guckian and Garcia 1979). Victoria clays occurred in the other 2 pastures. A pasture on each soil type received heavy (2.8 ha/AU) or moderate (5.6 ha/AU) continuous grazing treatments identified as follows: MS = moderately grazed sandy loam soils (221 ha), HS = heavily grazed sandy loam soils (163 ha), MC = moderately grazed clay soils (144 ha), and HC = heavily grazed clay soils (277 ha).

Eight 400-m line transects, oriented north-south and 400 m apart, were established in each treated pasture by selecting a random starting point. The transects were used for seasonal sampling of vegetation structure, selected forb and grass species, and bird abundance. Sampling took place in summer (July–Aug.), autumn (Oct.–Nov.), winter (Jan.–Feb.), and spring (May–June).

We indexed vertical structure of vegetation with a profile pole (Robel et al. 1970) with readings at 13 points on each of the line transects. The first point was at the beginning of a transect and the remainder were 30.7 m apart. At each point we estimated percent visual obstruction (Guthery et al. 1981) for 1-dm strata on the profile pole from a distance of 4 m (kneeling position) up to a height of 1 m. Seasonal sample size was 104/treated pasture except in winter 1985 when flooding prevented data collection at 7 points.

We used cluster analysis (FASTCLUS procedure, SAS 1982:433) to identify types of structural profiles of vegetation based on strata screening. Examination of the dendogram of profile types indicated observations could be classified into 2 general types: profiles with high screening below and sparse screening above 2 dm and profiles with high screening at heights up to 1 m (Fig. 1). The shapes of profiles differed slightly among seasons (Baker 1988).

Because of their importance as food to the bird species under

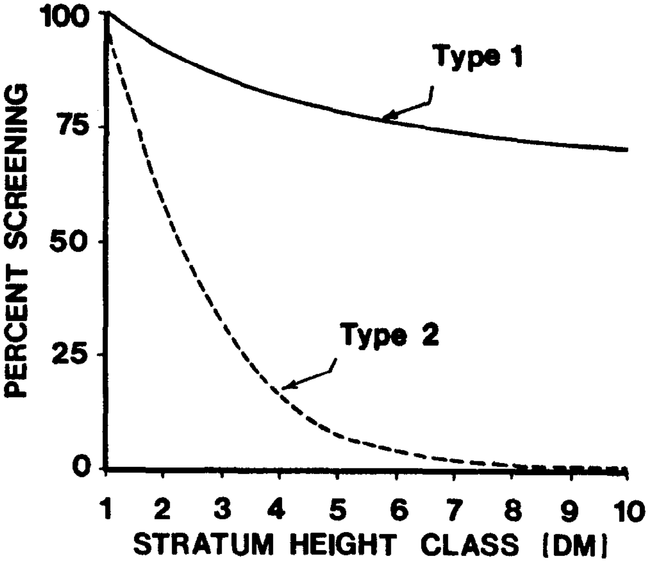

Fig. 1. Schematic representation of vegetation profile types identified through cluster analysis, San Patricio County, Texas, 1984–85.

Authors are wildlife biologist, U.S. Fish and Wildlife Service, Phoenix, Arizona; and research scientist, Caesar Kleberg Wildlife Research Institute, Texas A&I University, Kingsville. At the time of the research, the senior author was research assistant, Caesar Kleberg Wildlife Research Institute.

The Caesar Kleberg Foundation for Wildlife Conservation funded the study. Appreciation is extended to the Welder Wildlife Refuge for access and housing. This is Welder Wildlife Foundation Contribution 355.

Manuscript accepted 9 May 1989.

study (Lehmann and Ward 1941, Parmalee 1953, Gross 1958, Dillon 1961, Genung and Green 1974, Lehmann 1984, Wood 1985), we determined density, canopy coverage, and percent frequency of occurrence of the following plants on each experimental pasture: erect dayflower (*Commelina erecta* L.), bundleflower (*Desmanthus* sp.), milkpea (*Galactia* spp.), powderpuff (*Mimosa* spp.), American snoutbean [*Rhynchosia americana* (Mill.) Metz.], Texas croton [*Croton texensis* (Klotzch) Muell. Arg.], one-seed croton (*C. monanthogynus* Michx.), western ragweed (*Ambrosia psilostachya* DC.), seacoast sumpweed (*Iva annua* L.), bristlegrasses (*Setaria* spp.), paspalums (*Paspalum* spp.), and panic grasses (*Panicum* spp.). We also measured percent coverage and frequency of occurrence of bare ground and litter. Sampling consisted of 12 randomly located 0.5- × 0.5-m quadrats/line transect, giving 96 points/treated pasture per season. Although sampling took place in each season, we report vegetation data from summer only for economy of presentation. Baker (1988) provided data from other seasons.

Bird densities were estimated seasonally along the 8 line transects/pasture. We recorded the number of birds seen (flushed or perched) and paced the perpendicular distance to observation points during morning (0.5 hour before sunrise to 0900) and evening (2 hours before sunset) walks. Each transect was walked 8 times giving a sampling effort of 25.6 km/treated pasture per season.

We used program TRANSECT (Burnham et al. 1980) solely to obtain an estimate of f(0), the inverse of one-half the effective strip width. Small sample size precluded seasonal stratification of flushing-distance data for bobwhites. For mourning doves and meadowlarks, we stratified by winter-spring and summer-autumn periods in estimating f(0). We then estimated pasture- and species-specific abundance as (total birds seen) (1/total distance walked) (2/f(0)) and converted the estimate to number/40 ha. The Fourier series detection model adequately described ($P>0.29$) flushing frequencies for each species. One-half effective strip widths were 8.5 ± 0.68 m (±se) for bobwhites, 12.9 ± 0.70 m and 12.1 ± 0.70 m for meadowlarks in summer-fall and autumn-winter, respectively; and 13.3 ± 1.45 m and 13.3 ± 1.24 m for doves in summer-fall and autumn-winter, respectively.

Although grazing and soil treatments were replicated in space, the sample size was small and potential interactions between grazing treatment and soil type could not be tested. Therefore, we stress descriptive statistics herein. In particular, we present means of seaonal samples and identify salient trends in seasonal response.

We used subsamples from within treated pastures to analyze responses of selected plant taxa and bird densities (point estimates for each replication of a transect) under a 2 × 2 factorial design. Because of a high frequency of zeros (non-normal distribution), data on density and coverage were rank-transformed for analysis (Conover and Iman 1981) and retransformed for presentation. Frequency values were analyzed with the Chi-square statistic. Inferences arising form the above analyses pertain only to the study site (Hurlbert 1984).

Results and Discussion

Habitat Responses

Mean seasonal frequencies of Type 2 profiles (Fig. 1) were similar on the HS, HC, and MC pastures at 85-89% (Table 1). These frequencies were at least 23% lower ($P<0.01$) on the MS pasture than on the other pastures. We interpret these results to indicate that grazing intensities studied had little effect on structure of ground cover on clay soils. On sandy soils, reduced grazing pressure was associated with an increase in cover available at heights >2 dm.

Within seasons, grazing intensity and soil type also influenced ($P<0.05$) the availability and dispersion of bare ground. Moderate grazing was associated with a 32% decline in the dispersion (frequency) of bare ground on both sandy loams and clays (Table 1). However, coverage by bare ground was similar on the HS and MS pastures, whereas it was >3 times higher on the HC pasture than on the MC pasture. We interpret these results to indicate that higher grazing intensities will increase the dispersion, but not necessarily the availability, of bare ground, depending on soil type. Mean coverage and frequency of litter showed no large responses on any of the pastures (Table 1).

Bare ground is an important component of habitat for ground-foraging, seed-eating birds such as bobwhites (Rosene 1969, Guthery 1986) and mourning doves (Rosene 1939). None of the pastures studied supplied optimum average amounts of bare ground for bobwhites, which range between 30 and 60% (Guthery 1986:115).

Four taxa showed no differences ($P>0.10$) in density, coverage, or frequency of occurrence among experimental pastures. These species or genera were erect dayflower, bundleflower, milkpea, and powderpuff. Dayflower, bundleflower, and powderpuff were common throughout the study area; their lack of response may have been due to broad adaptability. Milkpea was seldom encountered (0–3%) in sample plots. The lack of response simply reflected scarcity of this species.

Four species responded to soil type independent of grazing pressure and pasture interactions ($P<0.05$) (Table 2). Texas croton and American snoutbean had higher density or coverage on pastures with sandy loams than on those with clays, whereas western ragweed and seacoast sumpweed densities were higher on pastures with clays than on those with sandy loams. These results were expected based on known ecological requirements of the species (Jones 1982).

Density of one-seed croton was the only variable that showed a

Table 1. Mean seasonal response of habitat features to heavy (2.8 ha/AU) and moderate (5.6 ha/AU) continuous grazing on sandy loam and clay loams, San Patricio County, Texas, 1984–85.

	Sandy loam				Clay			
	Heavy		Moderate		Heavy		Moderate	
Variable	$\bar{x}$	se	$\bar{x}$	se	$\bar{x}$	se	$\bar{x}$	se
Frequency of Type 2 profiles (%)[1]	87	5.3	65	8.3	89	3.6	85	5.8
Bare ground								
Coverage (%)	12	0.2	11	1.6	17	3.3	5.1	0.8
Frequency (%)	79	3.0	52	5.5	84	3.7	57	3.8
Litter								
Coverage (%)	33	11.4	31	11.8	32	12.8	38	18.1
Frequency (%)	86	6.6	69	13.5	89	5.8	80	14.8

[1] See Fig. 1.

Table 2. Effects of experimental pastures on the density (no./m²), canopy coverage (%), and frequency of occurrence (%) of selected wildlife food plants, San Patricio County, Texas, summer 1984.[1]

Species Variable	Pasture[2] HS	MS	HC	MC	MSE[3]	P[4]	Significant effect
American snoutbean							
Density	0.1	0.3	0.0	0.0	36.9	0.0029	Soil
Cover	0.1	0.3	0.0	0.0	36.9	0.0029	Soil
Frequency	7	13	0	0		0.2000	None
Texas croton							
Density	1.1	0.3	tr[5]	tr	51.4	0.0059	Soil
Cover	2.3	1.4	tr	tr	54.1	0.0056	Interaction
Frequency	24	12	2	2		0.0005	Interaction
One-seed croton							
Density	0.3	0.0	tr	0.0	35.4	0.0025	Graze
Cover	0.1	0.0	tr	0.0	35.9	0.0026	Graze
Frequency	6	0	3	0		0.2000	None
Western ragweed							
Density	0.6	0.7	1.2	5.2	50.1	0.0001	Soil
Cover	0.6	0.3	0.6	2.0	62.7	0.0472	Interaction
Frequency	15	9	30	41		0.0005	Interaction
Seacoast sumpweed							
Density	0.0	0.9	3.1	4.4	41.0	0.0001	Soil
Cover	0.0	0.2	1.7	3.3	35.3	0.0001	Soil
Frequency	0	6	23	51		0.0005	Interaction
Bristlegrasses							
Density	0.1	0.1	0.1	0.0	54.9	0.5249	None
Cover	0.3	0.3	0.2	0.0	55.9	0.6233	None
Frequency	8	5	7	0		0.0250	Interaction
Paspalums							
Density	0.5	0.1	tr	0.3	53.0	0.0020	Interaction
Cover	0.9	0.8	0.1	2.0	63.8	0.0227	Interaction
Frequency	18	4	1	12		0.0005	Interaction
Panic grasses							
Density	0.5	0.1	0.0	tr	47.7	0.0171	Interaction
Cover	0.6	0.1	0.0	0.6	51.0	0.0165	Interaction
Frequency	18	4	0	4		0.0005	Interaction

[1] Table includes only those plants that showed responses ($P<0.05$) on experimental pastures. Erect dayflower, bundleflower, milkpea, and powderpuff showed no response ($P>0.10$).

[2] HS = heavily grazed, sandy loam soils; MS = moderately grazed, sandy loam soils, HC = heavily grazed, clay soils; MC = moderately grazed, clay soils.

[3] Mean square error based on 96 plots/pasture.

[4] Based on F-test of rank-transformed data for density and coverage and chi-square test for frequency.

[5] tr = trace (<0.05).

significant response to grazing pressure in the absence of soil and pasture interaction effects (Table 2). This croton was more dense on the heavily grazed than on moderately grazed pastures. Heavy grazing is known to favor this species (Correll and Johnston 1970).

The most common response was a soil × grazing interaction (Table 2). For example, percent cover of western ragweed and cover and density of paspalums and panic grasses seemed to be favored by heavy grazing on sandy loams and moderate grazing on clays. Baker (1988) discussed interaction effects observed during the present study in greater detail.

The high frequency of interactions could have reflected 2 underlying mechanisms. Plant phenology may vary with soil type independent of grazing program. Phenological stages vary in palatability to livestock. Whether these 2 factors operate simultaneously or independently, they could generate interaction responses such as those observed.

Also, the interactions could reflect relative palatability of a given taxon. For example, slightly unpalatable species might be used more heavily in communities consisting largely of highly unpalatable species than in communities consisting largely of highly palatable species.

Bird Responses

The response of bobwhites to soil type and grazing pressure was variable and ambiguous. Density indices ranged from 0/40 ha on the HS, HC, and MC pastures in autumn and winter to 25.9/40 ha on the MS pasture in autumn. Mean seasonal densities were similar on the MS, HC, and MC pastures (Fig. 2). We interpret these results to indicate that, at the time of the study, the study area provided marginal habitat conditions for bobwhites, and the grazing pressures applied since 1982 had either uniformly depressing or neutral effects on quail. This lack of response to grazing intensity is in contrast to other studies, in which increased grazing pressure associated with short duration grazing seemed to favor quail populations or their key habitat features (Bareiss 1985, Wilkins 1987, Schulz and Guthery 1988). Quail on our study area have responded positively to grazing treatments that increased the availability of bare ground and forbs and reduced the availability of grasses (Hammerquist-Wilson and Crawford 1981). Further, sandier soils generally are more favorable for bobwhites than clayey soils (Lehmann 1984).

Abundance of meadowlarks varied seasonally due to the migratory habits of this species. Averaged over experimental pastures, density (x ± se, no./40 ha) increased from spring (16.7 ± 8.86) to fall (47.1 ± 14.86) to winter (78.7 ± 39.11) and then declined in summer (5.1 ± 1.85). Based on mean seasonal abundance, which largely reflected fall and winter populations, meadowlarks used habitat supported by clay soils more heavily than habitat supported by sandy loam soils (Fig. 2). These soil effects were significant in summer ($P<0.0056$) and winter ($P<0.0005$). Mean seasonal

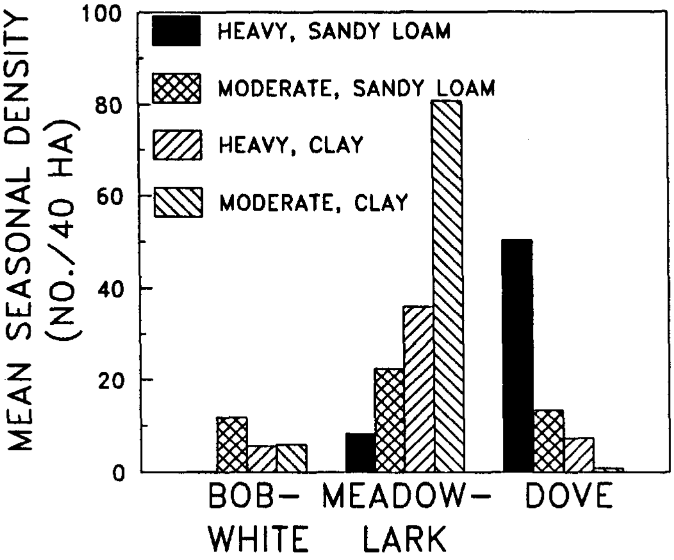

Fig. 2. Mean seasonal densities of 3 bird species on experimental pastures differing in soil type and grazing pressure, San Patricio County, Texas, 1984–85.

abundance was higher in moderately grazed than in heavily grazed pastures in both soil types, but effects were significant ($P<0.0063$) only during summer. No interaction effects were observed ($P>0.05$).

Mourning dove use of experimental pastures also reflected migratory behavior. Mean density on experimental pastures increased from summer (4.8 ± 1.71) to fall (30.9 ± 20.56), remained stable through winter (33.9 ± 24.26), and declined into spring (2.1 ± 0.8). Seasonal density averaged higher on sandy loams than on clays, and higher under heavy grazing than under moderate grazing on both soil types (Fig. 2). Soil effects were significant in autumn ($P<0.0008$) and winter ($P<0.0279$) and grazing effects were significant in winter ($P<0.0073$). We attribute these responses to increased dispersion of bare ground in response to heavy grazing (Table 1), higher densities of croton, a favored food (George 1988), on sandy loams than on clays, and an apparent increase in one-seed croton due to heavy grazing (Table 2). No interaction effects were observed ($P>0.05$).

Conclusion

We believe the most significant implication of our results is the potentially high frequency of interaction effects between grazing pressure and soil type. Because habitat management largely means management of plant taxa and communities, wildlife managers need to understand how important taxa and communities respond to grazing pressure. With such knowledge, they can make grazing management decisions consistent with goals of wildlife management. Our findings imply that the proper decision may vary according to soil type, and by extension, may be influenced by other factors that affect site productivity, such as annual precipitation and length of growing season. Whereas attention to interaction effects complicates management, it also makes possible sensitive and sophisticated management decisions. We recommend further research into the interactive effects of grazing pressure and environmental variables on wildlife habitat and populations.

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Distribution of nitrogen fractions in grazed and ungrazed fescue grassland Ah horizons

JOHAN F. DORMAAR, SYLVER SMOLIAK, AND WALTER D. WILLMS

Abstract

Grazing affects the plant ecology and adds excreta, thereby influencing soil N relationships. Consequently, total N, mineralizable N, exchangeable N, hydrolyzable N, and urease activity were assessed at the Agriculture Canada Research Substation, Stavely, Alberta, in the Ah horizons on rough fescue (*Festuca scabrella* Torr.) grasslands stocked at either light (0.8 ha/AUM) or very heavy (0.2 ha/AUM) fixed rates for 38 years and in exclosures located within each field for an equal period of time. Even though total N expressed as t/ha per Ah horizon remained the same, changes in various N fractions were nevertheless evident. Grazing resulted in more NH$_4^+$-N and NO$_3^-$-N in both fields at the time of sampling and each was greater at the higher stocking rate. Although soil N was less mineralizable, it was more acid-hydrolyzable at the higher stocking rate. Urease activity also increased. The effect on soil N characteristics of increased excreta loads is complex and still not well understood.

Key Words: mineralizable nitrogen, hydrolyzable nitrogen, exchangeable nitrogen, urease activity, stocking rate

A number of previous studies on the grazing experiment sampled for the present study have been published. Johnston et al. (1971) established that very heavy grazing of fescue (*Festuca scabrella* Torr.) grassland range compared with light grazing changed the color of the Ah horizon from black to dark brown and the pH from 5.7 to 6.2, reduced the percent organic matter and percent total P, but increased NaHCO$_3$-soluble P and soil temperature. Total N remained the same, but C/N ratios changed from 11.5 to 9.8. Soil moisture decreased with increased grazing intensity as water intake rate was reduced and, presumably, evaporation increased with the removal of litter. The potential for soil erosion by water is high when about 15% of the soil surface is bare (Johnston 1962). The soil of the very heavily grazed field was being transformed to a soil characteristic of a drier microclimate. Other than total nitrogen (N) which did not show any definite trends (Johnston et al. 1971; Dormaar et al. 1977), no other forms of N have been studied in this long-term grazing experiment. Urease activity in soil from an ungrazed field was less than that in soil of the very heavily grazed field (Dormaar et al. 1984).

The most important forms of available N are NH$_4^+$, NO$_3^-$, and certain simple organic compounds, principally those containing free amide or amino groups. The level of inorganic N in the soil, consisting of both NO$_3^-$ and NH$_4^+$ ions, is governed in natural ecosystems by the balance between supply from mineralization of organic N, rain-borne N, and fixation and losses through immobilization, leaching, volatilization, and uptake by the vegetation (Stevenson 1986). The levels are normally low because of their rapid utilization by the range vegetation. With active grazing, an additional cycle is introduced and consists of N passing through the animal body, after which most of it is usually returned to the soil through excreta.

Following studies of old-field successions from abandonment of cultivated soils to the climax, Rice (1984) established that the amount of NH$_4^+$-N increased from a minimum quantity in the first successional stages to a maximum in the climax and vice versa for NO$_3^-$-N. Further, Dormaar (1988) observed that the quality of the soil organic matter and, possibly, of root exudates may affect the formation of NH$_4^+$-N and NO$_3^-$-N. Grazing changes the vegetation composition and the chemical characteristics of soil (Johnston et al. 1971) but its effect on the mineral N status is not clear. Nitrogen is a key element in the grassland ecosystem, because of its capacity to limit primary and secondary production. A study was made to determine the effects of grazing on the composition and quantity of nitrogen in the Ah horizon of the rough fescue grasslands and to assess the consequences of the effects.

Materials and Methods

The study site was at the Agriculture Canada Research Substation, Stavely, Alberta, situated in the Porcupine Hills, an area managed primarily for grazing by cattle. The vegetation is typical of the Fescue Grassland Association (Coupland and Brayshaw 1953). The soils are members of the Orthic Black Subgroup of the Chernozemic Order (Udic Haploboroll), developed on till overlying sandstone, and have a clay-loam to loam texture. The climate is dry subhumid and annual precipitation averages about 500 mm. Details of the overall grazing trial since 1949 have been given by Johnston et al. (1971) and Willms et al. (1985).

On 15 Oct. 1986, 2 fields grazed by cows with calves since 1949 and adjacent exclosures were selected for sampling. The fields were grazed each year from about 15 May to 15 Nov. The lightly stocked field (field L) was at a rate of 0.8 ha per animal unit month (AUM) and the very heavily stocked field (field VH) at the rate of 0.2 ha/AUM. The grazing season of the latter field, because of deterioration of cover, varied from about 2.5 to 5 months since 1962. Cattle removed about 25 and 80% of available forage in fields L and VH, respectively.

Soil pits were dug and soil profiles were described at each site. In addition, the Ah horizon was sampled in 4 subplots in fields L and VH which were paired with 4 subplots in the exclosures within the same fields, giving a total of 16 samples. The paired plots had similar slope and aspect thereby reducing variability due to site. Only the Ah horizon was sampled because over 70% of the root system can be found here (Coupland and Brayshaw 1953). Even though organic matter and nitrogen levels fluctuate with the seasons (Dormaar et al. 1977, Dormaar et al. 1984), the sampling was made in autumn because the effects of excreta and trampling would be at their peak. The sampling period was similar to that reported by Johnston et al. (1971) as part of a study examining grazing effects on soils.

The samples were hand-sieved through a 2-mm sieve the day they were collected. A portion of each sieved sample was stored in sealed, double polyethylene bags at 4° C; the remainder was dried and ground to pass a 0.5-mm sieve. At the time of sieving, roots and other debris were removed from the soil and discarded. Moisture content of the soil was determined by drying a small portion overnight at 105° C. The mineralizable N analyses were carried out

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Manuscript accepted 23 March 1989.

on the moist soil. All other analyses were carried out on the air-dried soils.

Urease activity, which is important as a decomposing agent for urea, was determined at pH 9.0 by incubating 5 g with tris(hydroxymethyl)-aminomethane buffer (0.05 M), urea solution, and toluene at 37° C for 2 hours, and measuring the ammonium released after steam distillation (Tabatabai and Bremner 1972). Total N was determined by the method outlined by the Association of Official Agricultural Chemists (1950) and hydrolyzable N, amino acid-N, amino sugar-N and NH_3-N by methods described by Stevenson (1982). The relative ability of the soils to mineralize the N from the organic matter was determined as outlined by MacKay and Carefoot (1981); exchangeable NO_3^--N and NH_4^+-N by KCl extraction and steam distillation were as outlined by Keeney and Nelson (1982). All analytical results were expressed on the basis of oven-dried weight of soil.

The data were analyzed as if there were 4 treatments with 4 replications using a one-way analysis of variance, with the assumption that the sampling error represented the experimental error. Single degree of freedom contrasts (Steel and Torrie 1980) were used to test for differences between selected means.

Although replication and application of current statistical analyses to newly established, replicated field plot experiments is common and undeniably desirable and useful, valid information and data can still be gained from early established, unreplicated field experiments including long-term grazing trials, by virtue of their antiquity (Ridley and Hedlin 1968, Dormaar and Pittman 1980).

Results

Soil profiles were up to 69 cm thick (Table 1), and gravel to cobble size quartzitic stones were present throughout the profile together with sandstone ghosts in the lower Bm_2 and Ck horizons.

Table 1. Pedon description of the Orthic Black Chernozemic (Udic Haploboroll) soil at the Agriculture Canada Research Substation, Stavely, Alberta.

Horizon	Thickness (cm)	
Ah	14 to 20	Black (10YR 2/1, moist) clay loam; moderate fine granular; soft, very friable; abundant fine to medium random roots; tongued boundary; mildly acidic.
Bm_1	8 to 21	Dark yellowish brown (10YR 3/4, moist) clay loam; weak, fine subangular blocky; slightly hard; fewer, fine to medium vertical roots; diffuse boundary; neutral.
Bm_2	12 to 20	Dark yellowish brown (10YR 4/4, moist) loam to clay loam; moderate coarse, prismatic to subangular blocky; firm; few very fine, vertical roots; abrupt, wavy boundary; neutral.
Ck	8	Yellowish brown (10YR 5/4, moist) with very pale brown (10YR 8/3, moist) clay loam; angular blocky; friable; strongly effervescent; few roots; mildly alkaline.

With progressive transformation of the soil due to increased grazing pressure, the color of the Ah horizon in field VH changed from black (10YR 2/1, dry) to dark brown (10YR 3/3, dry) indicating a loss of organic matter. The average water content of the Ah horizons of the soils in the exclosures, field L, and field VH, at the time of sampling, was 64, 59, and 52% (w/w), respectively. Between 15 Sept. and 14 Oct. 1986, 92 mm of precipitation occurred in the form of rain and wet snow.

The N characteristics of the samples from the 2 exclosures were similar in each comparison ($P>0.40$) even though, geographically, one exclosure was in an upslope and the other was in a midslope position. Therefore, their data were combined for comparisons with the grazed fields (Table 2).

Total N, exchangeable N, hydrolyzable N, and urease activity in soils increased with grazing intensity, while mineralizable N and amino sugar decreased (Table 2). Soils of the exclosure were similar, with respect to total N and amino sugar, to the soil of field L.

Discussion

Willms et al. (1985) noted that prior to the initiation of the grazing study in 1949, the area was moderately stocked for summer grazing with cattle from 1884 to 1908, with horses from 1908 to 1920, and with cattle again from 1920 to 1943. The latter period, however, included heavy use during the 1930's drought. Finally, the area was used lightly for winter pasture from 1944 to 1949. In 1949, when this study was started, exclosures were established. Even though the range condition in the exclosure of field L had reached near stability 14 years later in a level upslope position and the range condition in the exclosure of field VH was still improving in 1981 due to its steep midslope position (Willms et al. 1985), the soil profile descriptions of the 2 exclosures were now quite similar. In addition, the soil characteristics measured were in the same steady state. The changes in color and depth of the Ah horizons, as noted by Johnston et al. (1971), and the changes in the various N parameters measured (Table 2), thus represent either an intensification or an amelioration of the characteristics existing in 1949 by the grazing scheme imposed.

Soil samples were not taken at the start of the present grazing study in 1949. The first samples analyzed were in 1967 (Johnston et al. 1971); however, the exclosures were not sampled and bulk densities were not determined at that time. Total N at that time was 0.59 and 0.57% for fields L and VH, respectively. These values were the averages of 10 samples randomly selected from grids superimposed on these fields. Of these samples, those closest to and in equal positions to the sites sampled in 1986, averaged 0.78 and 0.79% N for field L and VH, respectively (Table 3). Even though both fields appeared to gain in N, the corresponding C/N values for fields L and VH were generally not out of line (Table 3).

Since the increase in percent N cannot be explained and may be attributed to a sampling discrepancy between 1967 and 1986, it is more meaningful to compare the N of the exclosures with that of field VH as found at the time of sampling in 1986. For this comparison, N mass in the Ah horizon is a more realistic parameter because it accounts for the depth of the Ah horizon and the concentration of N which has, presumably, reached equilibrium with the grazing regime imposed on it.

Concentration of N per se in the Ah horizon cannot explain the effects of grazing soil quality since erosion of the Ah horizon and its bulk density had also been affected. However, on the basis of the N concentrations, depth of Ah horizons and the bulk densities, the Ah horizons in the exclosure and under the VH field contained 12.96 and 13.07 t/ha of N, respectively (Table 3). Although grazing animals ingest a large amount of N in feed, about 75% is excreted (Peterson et al. 1956). The N was, therefore, concentrated in a more dense Ah horizon of the VH field. Similarly, the mass of N in t/ha for field L was 12.94 (Table 3). Hence, rather than using concentrations, the focus has been on more meaningful biochemical parameters to examine the effect of increased grazing pressures on the quality of the soil, i.e., the redistribution of the N within the system.

Table 2. Some nitrogen characteristics of the Ah horizons of a Black Chernozemic soil, sampled 15 Oct. 1986, from 2 fields stocked at either light or very heavy rates and from their exclosures (n=4).

	Exclosures (E)	Stocking rate[1]		Contrasts		
		L	VH	E vs. L	E vs. VH	L vs. VH
Total N (%)	0.93	0.94	1.10	0.55	<0.01	<0.01
Mineralizable N (μg/g of soil)[2]	73.9	66.2	49.8	<0.01	<0.01	<0.01
Exchangeable N (μg/g)						
NH_4^+-N	9.2	12.9	18.3	<0.01	<0.01	<0.01
NO_3^--N	4.56	6.72	10.90	<0.01	<0.01	<0.01
Hydrolyzable N (% of total N)						
Total	74.9	82.5	85.0	<0.01	<0.01	0.06
Amino acid	25.2	27.5	30.2	0.04	<0.01	0.03
Amino sugar	8.0	7.2	6.0	0.34	0.02	0.18
Ammonium	23.5	32.8	36.2	<0.01	<0.01	0.01
Urease activity[3]	252	316	410	<0.01	<0.01	<0.01

[1] Light (L) - stocked at 0.8 ha/AUM; Very Heavy (VH) - stocked at 0.2 ha/AUM.
[2] Change of (NH_4^+ + NO_3^-)-N from 2 successive incubations at 1 and 2 wk periods.
[3] NH_4^+-N released, μg/g of dry soil per 2 hours.

Table 3. C/N ratios and total N per Ah horizon of a Black Chernozemic soil, sampled 15 Oct. 1986, from 2 fields stocked at either light or very heavy rates and from their exclosures (n=4).

	Exclosures	Stocking Rate[1]			
		L		VH	
	1986[2]	1967	1986	1967	1986
Organic C (%)	10.4	9.0	10.4	8.6	8.1
Total N (%)	0.93	0.78	0.94	0.79	1.10
C/N	11.2	11.5	11.1	10.9	7.4
Depth Ah (cm)	17		16		12
Bulk density (Mg/m^3)	0.82		0.86		0.99
Total N in Ah (t/ha)	12.96		12.94		13.07

[1] Light (L) - stocked at 0.8 ha/AUM; Very Heavy (VH) - stocked at 0.2 ha/AUM.
[2] Percent C and N and bulk density were not determined in the exclosures in the 1967 study (Johnson et al. 1971).

The increased grazing pressure resulting from the high stocking rate has altered the N properties of the range soil. Part of this can be related to the increased excreta load. For example, the excreta-related parameters, such as available N (MacDiarmid and Watkin 1972), increased in the grazed areas. Although the mineralizable N, i.e., the potential availability of N, of the whole soil was lower in the grazed than in the ungrazed soils (Table 2), dung N per se has been found to be a very efficient nutrient for plant growth because of its slow-release availability (MacDiarmid and Watkin 1972). Urease activity similarly increased in the very heavily grazed range.

Since there is less mulch and less standing biomass under the very heavily grazed regime, the soil warms up quicker in the spring (Johnson 1962, Johnston et al. 1971) and will be drier (Johnston et al. 1971, Dormaar et al. 1989). There is more NH_4^+-N than NO_3^--N in rough fescue grassland than in grassland associations of semiarid areas. Nevertheless, in this experiment, concentrations of both forms of nitrogen increased with intensity of grazing. Bauer et al. (1987) noted that the difference between ungrazed and grazed levels of soil N could be caused by greater denitrification losses in ungrazed grasslands because of cooler and more moist conditions early in the season. Naturally, with more standing crop, more N will be taken up as well.

A decrease in mineralization rate was to be expected for several reasons. It has been shown that the Black Chernozemic soil under increased grazing pressures changes to a soil characteristic of a drier microclimate (Johnston et al. 1971). Neal (J.L. Neal, Jr., unpublished data) found that soil microbial mass decreases from the dry, subhumid to the semiarid climate of southern Alberta and from field L to field VH. Finally, over 90% of N in most surface soils is organically combined (Stevenson 1986). However, 3 other factors will have to be considered in this context as well. With heavy grazing, the quality of the soil organic matter has changed, since, in spite of increased total N content, this N was not as potentially available. Herbage removal resulted in considerable reduction in weight of roots (Johnston 1961) and thus in root exudates. There is also evidence (Neal 1969) that roots of increasing and invading plants on overgrazed grasslands produce substances that inhibit nitrification. This could be a mechanism whereby these plants conserve the low amounts of nitrogen available in grassland soils. The NH_4^+-N uptake characteristics of these increasers and invaders are, however, virtually unknown. Finally, the chemistry of the pathways of decomposition of the excreta under the influence of the changing microclimate and the root exudates of the increasers and invaders has not been studied in much detail.

Although Sowden et al. (1977) showed that between 86 and 89% of the total N in soils from widely differing climatic zones was hydrolyzable by hot 6M HCl, the range for this study was 75 to 85%. For a sequence of native range to recently revegetated native range on an Orthic Brown Chernozemic (Aridic Ustochrept) soil, this range was 75 to 81% (Dormaar and Smoliak 1985). As grazing pressure increased, the fraction of the hydrolyzable N presented as amino acid-N and NH_3-N gradually increased, while the proportion as amino sugar-N essentially remained the same. Some of the NH_3-N will be derived from indigenous fixed NH_4^+-N and part comes from partial destruction of amino sugars (Stevenson 1982). Nevertheless, the composition of a large percentage of the N in the soil is still unknown. Schnitzer and Hindle (1981) felt that the unidentified N was not proteinaceous, because relatively more 'unknown' N occurred in the inorganic than in the organic fraction of the soil.

Models of N cycling and N budgets have tried to account for soil NH_4^+-N and NO_3^--N, soil organic matter, and N content of above- and below-ground biomass together with the actual plant, microorganisms, and soil interactions (Parton and Risser 1977). However, more detailed analyses of the Ah horizon subjected to various grazing pressures, in terms of the organic and inorganic composition of excreta and root exudates of decreasers, increasers, and invaders, will be necessary to expand these models in order to account for the accompanying plant ecological and microclimatological transformation.

Even though concentrations of total and exchangeable N increased, the decrease in mineralizable and thus potentially available N decreased with grazing intensity. This change is real regardless of the time of sampling. Nevertheless, in a study of this nature, time of sampling may be crucial. Time and extent of availability are essential parameters for optimal plant growth. However, different plants have different N requirements, both in terms of timing and of NO_3^- or NH_4^+ requirements. Rough fescue is largely eliminated by very heavy grazing, while the new grasses and forbs will have different needs that fit the new ecological niche created by overgrazing and increased excreta load.

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SRM Election Results

The Elections Committee, along with several other Colorado Section members, counted the ballots for new officers at the Society for Range Management headquarters. Elected officers are:

Second Vice President—**John L. "Jack" Artz**

Directors (1989–1991)—**Murray L. Anderson** and **Will H. Blackburn**

Directors Anderson and Blackburn will replace retiring Directors Samuel and Sanders in February 1990.

The amendment to the Bylaws regarding Emeritus Membership was approved.

Ballots and tally sheets are retained in the Denver office for one year for review. Approximately 31% of the membership voted.

Soil moisture patterns below mounds of harvester ants

JOHN W. LAUNDRÉ

Abstract

Harvester ants are a major component of western rangeland. Little is known about ants' role in soil water dynamics. Annual patterns of soil moisture under mounds of the harvester ant (*Pogonomyrmex owyheei*, Cole) were studied in southeastern Idaho. Soil moisture at 20-cm intervals to a depth of 100 cm was estimated monthly with a neutron probe. Between 60 and 100 cm, higher levels of moisture were found below mounds than in control areas. The amount of water added to the soil during spring recharge was greater in control areas at 20 cm but greater under ant mounds at depths below 60 cm. Under ant mounds, approximately 1.3 cm more water was added to the soil between 60 and 100 cm.

Key Words: *Pogonomyrmex owyheei*, Idaho, infiltration, recharge

Harvester ants (*Pogonomyrmex owyheei*, Cole) are common mound builders in Idaho. Mound densities can be in excess of 16 mounds per hectare (Sharp and Barr 1960) and can be a dominant visual component of the range ecosystem (Porter and Jorgensen 1988). Mound-building ants have a long-recognized, active role in soil processes. They contribute significantly to mixing of soils and concentrating of soil minerals (Mandel and Sorenson 1982, Levan and Stone 1983). Ant burrows also increase soil porosity which is thought to enhance water infiltration (Mandel and Sorenson 1982). Rogers and Lavigne (1974) found higher levels of soil moisture below mounds of harvester ants (*P. occidentalis*) in Colorado. However, their samples were only from late summer. Little is known about annual soil moisture patterns under ant mounds, especially during spring recharge.

In northwestern semiarid areas, the majority of water infiltration into the soil occurs during the spring snow melt. If harvester ant burrows do affect water infiltration, they could enhance recharge and contribute to soil water reserves. To clarify the role of harvester ants in soil water movements, I documented the pattern of soil moisture below ant mounds and compared these soil water patterns to patterns in adjacent nonmound areas.

Methods

The study area was on the Idaho National Engineering Laboratory (INEL) site. The INEL is a National Environmental Research Park (NERP) operated by the U.S. Department of Energy and is located 65 km north of Pocatello, Idaho. The site receives an average of 20.6 cm precipitation per year. Vegetation is a mixture of sagebrush (*Artemisia* sp.) and grass. Detailed descriptions of vegetation on the site appear elsewhere (Harniss and West 1973, Anderson and Holte 1981).

Soil moisture the first year of the study was determined gravimetrically. Samples were taken with a veihmeyer tube at 20 and 60 cm depths below ground level under ant hill mounds and at the edge of the anthill clearing. Different anthills were chosen each month for sampling. To reduce the variability from sampling different anthills each month, soil moisture under 5 randomly selected hills was monitored with a neutron probe (Campbell Nuclear Pacific Corp, Pacheco, Calif.) for the remaining 2 years of the study. Aluminum access tubes were placed to a depth of 100 cm directly in the middle of the selected ant mounds (treatment tubes). Control tubes were placed toward the edge of mound clearings an average of 4.1 ± 0.24 m from the mounds. Moisture readings were taken at 20-cm intervals from 20 cm to 100 cm below the soil surface in mound and nonmound areas. Readings were taken once monthly. Estimates from each sample depth were used as representative of moisture levels for the soil profile 10 cm above to 10 cm below the sample depths. All moisture estimates are given in percent by volume.

Samples for soil texture analyses were taken at 30-cm depths in mound and control areas. Soil texture was determined gravimetrically by the hydrometer method described in Day (1965). Bulk density of the soil was calculated from core samples (Blake 1965) taken at 30 and 60 cm depths.

All statistical comparisons were paired *t*-test designs and the $P = 0.05$ level of significance, one-tailed, was used throughout. All percent data were arcsine transformed for statistical tests. All means are given ± standard errors.

Results

Soil texture of the study area averaged 43.1 ± 4.1% ($n = 16$) sand, 44.9 ± 3.4% ($n = 16$) silt, and 11.9 ± 1.2% ($n = 16$) clay and was classified as a loam. Bulk density did not differ significantly between mound and control areas for either 30 or 60 cm and averaged 1.3 ± 0.02 g/cm^3 ($n = 30$).

Maximum snow depths for each of the 3 years were 50 cm in 1985, 33 cm in 1986, and 5 cm in 1987. Maximum water contents of the snows equaled 9.4 cm in 1985, 7.1 cm in 1986, and <1.0 cm in 1987.

Figure 1 presents the monthly averages of soil moisture for the different sample depths. At 20 and 40 cm, patterns of moisture were similar between mound and control areas during the summer fall and winter of 1986 and 1987. At 60, 80, and 100 cm, mean water levels under ant mounds were higher in control areas during these times. As moisture patterns seemed similar, these 3 sample intervals were combined into 1 interval extending from 50–110 cm. In a manner similar to Rogers and Lavigne (1974), the mean soil moisture values for 60, 80, and 100 cm were used as 3 estimates of soil moisture for that interval and compared between burrow and control areas (Table 1). The mean soil moisture for the soil profile between 50–110 cm was significantly higher under ant burrows in both summers of the study.

Once infiltration began in the spring, 3 different patterns of recharge became evident. At the 20 cm level, peak recharge levels in non-mound areas were significantly higher than mound areas for all 3 years (1985: $t = 2.56$, $P = 0.03$; 1986: $t = 4.44$, $P = 0.01$; 1987: $t = 3.16$, $P = 0.02$). At the 40 cm level, peak recharge did not differ between the 2 areas (Fig. 1). At 60, 80, and 100 cm depths, mean soil moisture levels were higher under ant mounds than in control areas in 1986 (Fig. 1). Again, mean soil moisture for the 3 sample depths were used as 3 estimates of the soil moisture for the soil profile between 50–110 cm (Table 1). Soil moisture at peak recharge for the sample interval was significantly higher under ant

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Research was funded by the U.S. Department of Energy, Idaho Operations Office, Idaho Falls. Thanks are given to B.L. Keller, O.D. Markham, T.D. Reynolds, P.E. Blom, W.H. Clark, J.B. Johnson, R.D. Northrup, T.R. Eichholz, and S.J. Pew for their assistance.

Manuscript accepted 27 April 1989.

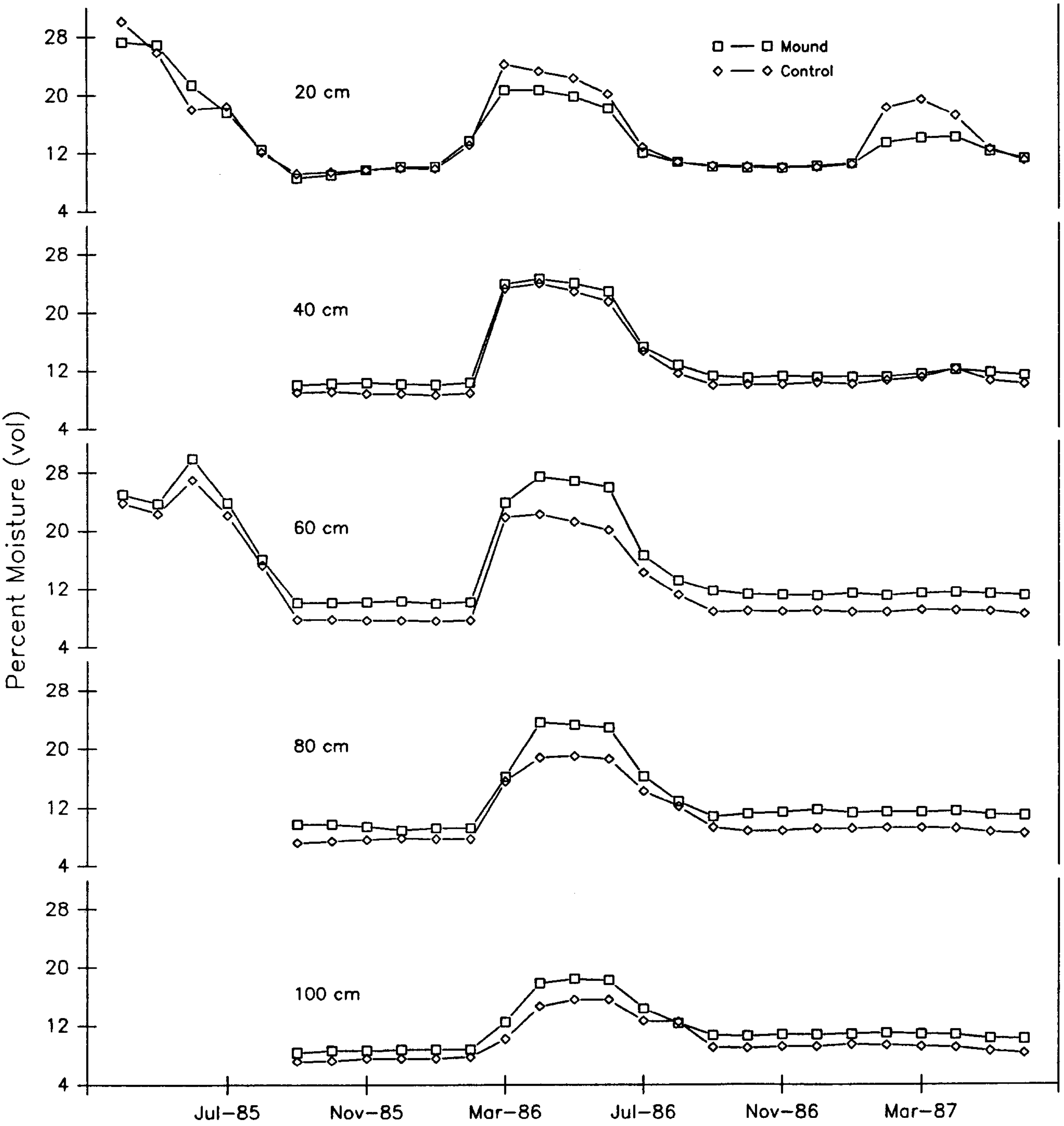

Fig. 1. Monthly soil moisture levels at the 5 sample depths under ant mounds and in control areas. The first 6 estimates for the 20 and 60 cm depths were determined gravimetrically. All the other estimates are based on neutron probe data.

mounds. At the sample depths of 60, 80, and 100 cm, no change in soil moisture was seen in 1987 because there was insufficient snow pack in 1987 for recharge beyond 40 cm. Average soil moisture in the spring of 1985 was higher under ant burrows at 60 cm but the difference was not significant.

Lavigne (1969) found a high number of storage chambers at and below 60 cm in burrows of the harvester ant *P. occidentalis*. The food stores and other organic material in those chambers would be detected by the neutron probe and could result in elevated estimates of soil moisture. If such stores exist for *P. owyheei*, they may account for the difference in average soil moisture between mound and control areas at and below 60 cm at the driest time of the year. This error in estimating soil moisture could bias comparisons of % moisture at peak recharge. To eliminate such bias, I determined the difference in soil moisture between the time of lowest soil moisture (late fall) to the time of peak recharge (early April) for 1986 and 1987. As before, mean differences in soil moisture for 60, 80, and 100 cm sample depths were used as 3 estimates of the soil profile between 50–110 cm. Analysis of the difference in moisture levels did not change the pattern seen (Table 1).

The difference in percent moisture represents the amount water added to the soil from the spring recharge. For 1986 and 1987,

Table 1. Average soil moisture levels, percent by volume, below mound and nonmound (control) areas for 60, 80, and 100 cm depths at end of withdrawal season in 1985 and at peak recharge in 1986. The third column is the average difference in soil moisture between the end of withdrawal season and peak recharge for the 60, 80 and 100 cm depths. All means are ± standard errors.

	Withdrawal		Recharge		Difference	
	Mound	Control	Mound	Control	Mound	Control
60 cm	10.1 ± 1.0	7.8 ± 0.9	27.4 ± 1.6	22.2 ± 2.6	17.3 ± 1.1	14.4 ± 1.7
80 cm	9.7 ± 1.0	7.4 ± 1.5	23.7 ± 3.0	19.1 ± 5.0	14.0 ± 2.4	11.7 ± 3.6
100 cm	8.7 ± 1.8	7.3 ± 1.8	18.3 ± 4.5	15.5 ± 5.0	9.5 ± 2.8	7.8 ± 3.4
Mean	9.5 ± 0.42	7.5 ± 0.15	23.1 ± 2.6	18.9 ± 1.9	13.6 ± 2.3	10.7 ± 1.8
t	6.66		5.82		6.24	
P	0.01		0.01		0.01	

there was 3.0% and 4.8% more water added in the control area at 20 cm than under the ant mounds. Between 50–110 cm in 1986, there was an average of 2.2 + 0.4% (n = 3) more water added under the mounds. This percentage represents 1.3 cm more water added to the soil profile between the 50 and 110 cm depths under ant mounds as compared to control areas.

Discussion

During the summer and fall months of 1986 and 1987, soil moisture estimates 50–110 cm under ant mounds were higher than controls. Based on the work of Lavigne (1969), this difference can likely be attributed to organic material ants store in the high number of tunnels they build in this zone rather than actual differences in soil moisture. Because of this possible bias, comparisons between mound and non-mound areas were based on the difference in soil moisture between pre-recharge low and peak recharge high levels of soil moisture.

Data from the change in percent moisture between low and peak levels indicated that mounds of harvester ants altered water infiltration patterns during spring recharge. MacKay (1981) found that a majority of the burrow complex of *P. montanus* occurred in the top 30 cm of soil. Blom (pers. comm.) has found a similar structure for harvester ants in Idaho. Such burrowing reduces bulk density, changes soil texture (Rogers and Lavigne 1974), and subsequently field capacity. These changes would reduce the amount of water retained under mounds at these depths, allow more water to drain quickly through the upper strata, and result in the lower moisture levels noted at 20 cm in 1985 and 1986. The difference in moisture levels at the 20 cm depth in spring 1987 was likely the result of the low snow pack. In the mound areas, the little snow melt available was absorbed by organic matter in the ant mounds, reducing infiltration to the 20 cm depth as compared to nonmound areas where the snow melt went directly into the soil.

At 40 cm in 1986, sufficient water infiltrated in mound and nonmound areas to attain field capacity, approximately 25% (Foth 1978), for the soil type in the study area. Thus, no difference was seen between mound and nonmound areas at this depth. In 1985, the wettest year of the study, there was sufficient water to inundate the profile to field capacity to 60 cm in mound and mound areas. Unfortunately, no samples were taken deeper than 60 cm during this preliminary year of the study. With less snow pack in 1986, the effect of mounds became evident. At 60 cm, field capacity was attained under mounds but not in control areas and, in general, more water infiltrated to the 50–110 cm depth increment. The increased amount of water under mounds found in this study concurs with the findings of Rogers and Lavigne (1974) who found higher levels of soil moisture below mounds for *P. occidentalis* in northeastern Colorado.

The significance to the ants of the differences in water distribution between mound and control areas is unclear. Possibly the additional water could maintain higher levels of humidity in the burrows during the summer. However during the withdrawal season, the extra water under mounds is removed from the soil and moisture conditions are returned to pre-recharge levels as quickly as control areas.

Wight and Nichols (1966) and Rogers and Lavigne (1974) found increased plant productivity around the perimeter of mound clearings. They attributed this increased growth to water that infiltrates into the soil within the clearing. Presumably plants growing on the edge of mound clearings are extending their root systems into the clearing and depleting the water. Whether the additional water under the mounds would contribute significantly to this productivity is unknown. It was estimated that approximately 1.3 cm of extra water was added to the deep profile under the mound. However, this estimate applies only to the cylinder of soil below the mound, the approximate sampling sphere of the neutron probe. It is unknown how much, if any, water is added beyond that soil volume. If substantial amounts are added, especially in years of moderate precipitation, the extra water reserve may impact biomass production of these peripheral plants. Future work should center on determining the realm of influence ant burrows have on enhancing soil moisture and if such increases significantly affect biomass production.

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Ecology of curlleaf mahogany in western and central Nevada: community and population structure

B.W. SCHULTZ, P.T. TUELLER, AND R.J. TAUSCH

Abstract

Curlleaf mahogany is an important browse species for mule deer in the mountain brush zone of the Intermountain West. Past research on increasing browse availability of curlleaf mahogany has been inconclusive. This appeared to be directly related to limited understanding of community and population structure and dynamics. To obtain information on the community and population structure of curlleaf mahogany we sampled 25, 30 × 30-m macroplots in western and central Nevada. Data on mahogany density, maturity class structure, size, ages, and population growth rates were obtained. Understory cover and composition and percent rock, bare ground, and litter were also recorded. Mahogany density in central Nevada was one-half that in western Nevada, but mahogany cover and total cover were significantly ($P \leq 0.05$) greater. Maturity class distribution in central Nevada was heavily skewed towards large mature mahogany, suggesting an older population dominated by fewer large individuals. This dominance resulted in significantly ($P \leq 0.05$) lower population and relative growth rates and the necessity of canopy gaps for the survival of young mahogany. Range improvement of mature mahogany stands dominated by large individuals will require the removal of the mature and over mature individuals so that young forage producing plants are released from intraspecific competition.

Key Words: curlleaf mahogany, *Cercocarpus ledifolius*, population structure, community structure, size-age-density relationships, overstory-understory relationships

Curlleaf mahogany *(Cercocarpus ledifolius)* is a little studied, evergreen xerophyte (Daubenmire 1959). The species is often found in the mountain brush zone (Scheldt and Tisdale 1970) of the Intermountain West. Although it is an important browse species for mule deer *(Odocoileus hemionus),* curlleaf mahogany is not highly desired by domestic livestock (Smith and Hubbard 1954, Sampson and Jespersen 1963). Excessive browsing and an erect growth form often lead to stands that provide little available browse (Mitchell 1951).

Treatments to increase browse availability have been costly, and largely unsuccessful (Phillips 1970, Thompson 1970, Plummer 1974, Ormiston 1978, Austin and Urness 1980). This is due, at least in part, to a lack of information on stand and population structure and the resulting influences of intraspecific competition. Competition eventually occurs as the individuals present in a population increase in number and size. Indicators of competition are reproduction that is poor or absent (Long and Turner 1975, Oliver 1981), closure of the crown canopy (Assman 1970), and the reduction of growth rates in individual plants relative to their potential (Long and Smith 1984). The objective of this study was to measure stands and individuals of curlleaf mahogany to obtain demographic data useful in quantifying stand structure and population dynamics.

Study Site Descriptions

Curlleaf mahogany communities were studied in 25 macroplots on 3 mountain ranges in western and central Nevada. Nine western Nevada macroplots were located on Peavine Mountain and 4 in the Carson Range. Twelve central Nevada macroplots were located in the Shoshone Range. Sampling occurred during May through August of 1985.

Elevation of mahogany on Peavine Mountain varies from 1,520 to 2,485 m. Annual precipitation averages 36–41 cm and occurs mostly as snow. The average frost-free period is 50–80 days. Curleaf mahogany stands are largely restricted to the Ticino gravelly fine sandy loam (SCS 1983). Effective rooting depth is 51–103 cm. Scattered mahogany occur near 1,890 m on west, east, and north aspects, but dominant stands are present only above 1,980 m. Mahogany stands on south facing slopes are found above 2,260 m. Stands vary in size from several to hundreds of hectares. Smaller stands are most common along rocky ridges, and as islands within low sagebrush *(Artemisia arbuscula)* communities. Large stands occur on hillsides and are commonly surrounded by mountain big sagebrush *(Artemisia tridentata vaseyana).*

Sampling in the Carson Range occurred between 1,550 and 1,890 m. The mixed conifer zone generally occurs above 1,900 to 2,000 m, with intermixed or isolated mahogany stands as high as 2,590 m, but only on southerly aspects or rocky sites. Conifer species completely replace mahogany on north facing slopes above 2,200 m. Sampled communities were in the 36 to 51-cm precipitation zone with most of it occurring as snow during the winter months. Average frost free period is 50 to 80 days. Soils supporting mountain mahogany stands are Duckhill stony loam, Apmat gravelly sandy loam, and the Fraval-Hirschdale-Jumbo association (SCS 1983). Effective rooting depth varies from 20 to over 154 cm.

Mahogany in the Shoshone Range occurs as low as 2,150 m on north aspects, but, sizeable stands are rarely present below 2,380 m. Southern aspects have few mahogany stands below 2,600 m. All other aspects have abundant mahogany stands between 2,450 and 3,050 m. Limber pine *(Pinus flexilus)* is a common associate above 2,900 m. Annual precipitation averages 41 to 51 cm. Unlike western Nevada, heaviest precipitation occurs during the early part of the growing season, March through June (Houghton et al. 1975), and summer rainfall is also more abundant. Frost free period is 30 to 50 days. Stands tend to be restricted to the Foxmount soil series; specifically Foxmount gravelly loam (Carol Jett, personal communication). These are well drained, moderately permeable soils with an effective rooting depth of 51 to 103 cm and an 18 to 38 cm mollic epipedon.

Methods

Field Sampling

An initial field reconnaissance near Reno, Nevada indicated that mahogany stands are comprised of individuals that can be categorized in 6 maturity classes. These maturity classes are: reproduction, juvenile, immature, young-mature, and overmature-decadent (Table 1).

Sampling occurred in 30 × 30-m macroplots, each having at least one young-mature individual (Table 1) and placed as close as possible to a cardinal aspect. Ecotones with adjacent plant communities were avoided. Upper, middle, and lower portions of the

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Table 1. Mountain mahogany maturity classes developed from a reconnaissance of mahogany stands near Reno, NV.

1. Reproduction	young plants; 2 to 7 mm basal diameter; smooth bark; plants may be up to 30 cm in height.
2. Juvenile	young plants greater than 7 mm basal diameter; smooth bark; plants to 60 cm tall.
3. Immature	young plants greater than 1.25 cm basal diameter; smooth bark; plants to 1.5 m tall.
4. Young-mature	cracked bark; 1.5-3.0 m tall; crown broadened; may be multistemmed from base; not suppressed by adjacent larger mahogany plants.
5. Mature	cracked bark; wide full crown; few dead branches; may have several stems from base; may be suppressed by adjacent larger mahogany plants; greater than 3 m tall.
6. Overmature	cracked bark; may be multistemmed; numerous dead branches; may be greater than 3 m tall; frequently suppressed by adjacent larger mahogany plants.

mahogany belt were sampled when the elevation range exceeded 500 m.

Mahogany density (live and dead) and maturity class distribution were recorded in each macroplot (trees/900 m²). All mahogany, except the smallest individuals (reproduction maturity class), were measured to obtain crown diameters (longest and the one perpendicular to it) and height. Crown height and crown diameter measurements were taken on individuals in the reproduction class (Table 1) cut for growth ring analysis. Cover of plants in the reproduction class was estimated in the microplots used for understory sampling.

Crown measurements were used to calculate mahogany percent cover and mahogany crown volume (m³) (Ludwig et al. 1975, Tausch 1980). All measurements were of the green leaf portion of the canopy, and were made to the nearest decimeter. Mahogany seedling density was also obtained in each microplot. Seedlings had 4 to 8 leaves and were usually less than an inch tall.

A subsample of up to 4 individuals from each maturity class present in each macroplot was cut for aging and to determine relative growth rates using growth ring widths (Davis et al. 1972, Brotherson et al. 1980). Cross sections were taken from the largest living stem and as close to the ground as possible.

Three randomly located 30-m belt transects were used to sample understory cover within each macroplot. Species were ocularly estimated in 15, 1 × 2-m (shrub) and 30, 20 × 50-cm (grass and forb) microplots. Crown cover (%) was estimated for shrub and forb species and basal area (%) for grasses. Density of plants in the reproduction class was also recorded in each 1 × 2-m microplot. Corners of the smaller frame were used as points to determine percent litter, bare ground, and rock (120 points).

Data Analysis

Crown diameter, crown height, crown area (m²), and crown volume (m³) were computed for each tree measured. Total crown area (m²) and total crown cover (%) values were calculated for each maturity class and macroplot. Average values were determined for each study area. Relative mahogany cover (mahogany cover divided by total mahogany cover) was calculated for each mahogany and study area.

Mahogany density was averaged for each study area. Density of dead mahogany was also summarized. Seedling counts from each microplot were averaged to determine a mean value (density/m²) for each macroplot and study area.

Understory species cover (%) was summarized by plot and for the entire macroplot and averaged for each study area. Percent litter, bare ground, and rock were determined by the same process.

Growth ring counts and measurements were made along 2 sanded radii on each cross section. Growth rings were identified by a single row of larger vessels in the spring wood. Modifications of a technique using acetic acid and zinc oxide (Parker et al. 1976) were used to enhance the contrast between early and late wood in each annual ring. Time and funding constraints did not allow us to determine if false rings were present. A reference chronology was not available for cross dating.

Yearly growth increments were measured to the nearest 0.01 mm for the 10 years before harvest using a Craighead-Douglas dendrochronograph and a binocular microscope. Age and ring width data for each radii were averaged for each cross section. Ring-width data were used to calculate the stem area increment (cm²/10 years) of each cross section and were summarized by maturity class, macroplot, and study area.

Past population growth rates were estimated from the relationship between the natural logarithms of cumulative stand density and the ages of the surviving stand members (Harper 1977). Because it was impossible to determine the age of every mahogany in each macroplot, a modified version of these growth curves was used. Mean maturity class age was substituted for the ages of the individual survivors. The resulting curve for each location displayed the relationship between cumulative density (ln) and the approximate ages of the survivors by maturity class. Mature and overmature mahogany were combined in each study area because of their similar mean age.

Differences in mean understory cover, mean mahagony cover, mean mahogany crown diameter and crown height, mahogany crown volume, and mean ring widths between study areas were tested for significance ($P \leq 0.05$) with the students t-test (Steel and Torrie 1980). The Kolmogorov-Smirnov test (Steel and Torrie 1980) was used to compare study areas for their relative distribution of mahogany density among the maturity classes.

Results and Discussion

Cover

Largest mahogany plants were generally found on north and east aspects, and smallest plants on south and west aspects. Stand size ranged from less than one to over hundreds of hectares. Smallest stands occurred along rocky ridge lines, and largest stands on sloping mountain sides and in bowls below the mountain crest.

Average total vegetation cover was highest on the Shoshone Range (Table 2) with half of the macroplots reaching 100% vegetation cover. Macroplots in western Nevada had substantially less total cover than macroplots in central Nevada. Mahogany cover (%) in the Shoshone Range averaged over 20% greater than in western Nevada. Differences in mahogany cover between Peavine Mountain and the Carson Range were small. However, relative mahogany cover was virtually identical in each population.

Mature and/or young-mature mahogany accounted for most of the mahogany cover in each study area. Their cover contribution was substantially greater than their relative proportion (%) of the population density (Figs. 1 and 2). Overmature mahogany provided little cover (Fig. 1). Immature and younger mahogany also provided very little cover, even at high densities (Figs. 1 and 2).

Conifer species had higher cover values in the Shoshone Range than in western Nevada, but their actual contribution was small. Pinyon pine *(Pinus monophylla)* was the most frequent tree, but limber pine, when present, provided substantially more cover. Pinyon seedlings were common in all but the highest elevation macroplots.

Average understory cover was almost identical for each study

Table 2. Mean vegetation and soil surface characteristics for 3 mahogany communities in Nevada.

Study area	Cover[1] Shrub	Grass	Forb	Under-story	Curlleaf mahogany	Total vegetative	Relative mahogany	Litter	Rock	Bareground
	%									
Peavine Mountain	8a[1]	1a	5a	14a	56a	70a	80a	67a	23a	10a
Carson Range	7ab	7b	1b	15a	54a	68a	78a	61a	35a	4a
Shoshone Range	11b	2a	2b	15a	79b	98b	78a	76b	14b	10a

[1] Means in the same column followed by the same letter do not differ significantly at the .05 level.

area, but varied widely among the macroplots (2 to 37%). The percent contribution of shrub, grass, and forb species also varied between study areas. Shrub cover was highest in the Shoshone Range and grass cover highest in the Carson Range. Forb cover was highest on the Peavine Mountain (Table 2).

Litter cover (%) was abundant in all areas, but had substantially higher values in the Shoshone Range (Table 2), where litter depth was also greater. Surface rock was abundant in western Nevada, particularly in the Carson Range. Bare ground (%) was low in each study area.

Mahogany Density

Peavine Mountain had the highest mahogany density and the Shoshone Range the lowest (Fig. 3). Mahogany density in individual macroplots varied from 25 to 267 mahogany/macroplot (278 to 2,968 mahogany/ha). Mahogany density in this study was substantially greater than that observed in Utah by Davis (1976) but less than in Montana (Duncan 1975). Few mahogany seedlings were present in macroplots on Peavine Mountain and none were observed in the Carson Range. Abundant seedlings (2.0/m^2) were present in all macroplots in the Shoshone Range.

Maturity Class Distribution

Maturity class distribution on Peavine Mountain was significantly different ($P \leq 0.05$) than maturity class distribution on the Carson and Shoshone Ranges (Fig. 2) based on the Kolmogorov-

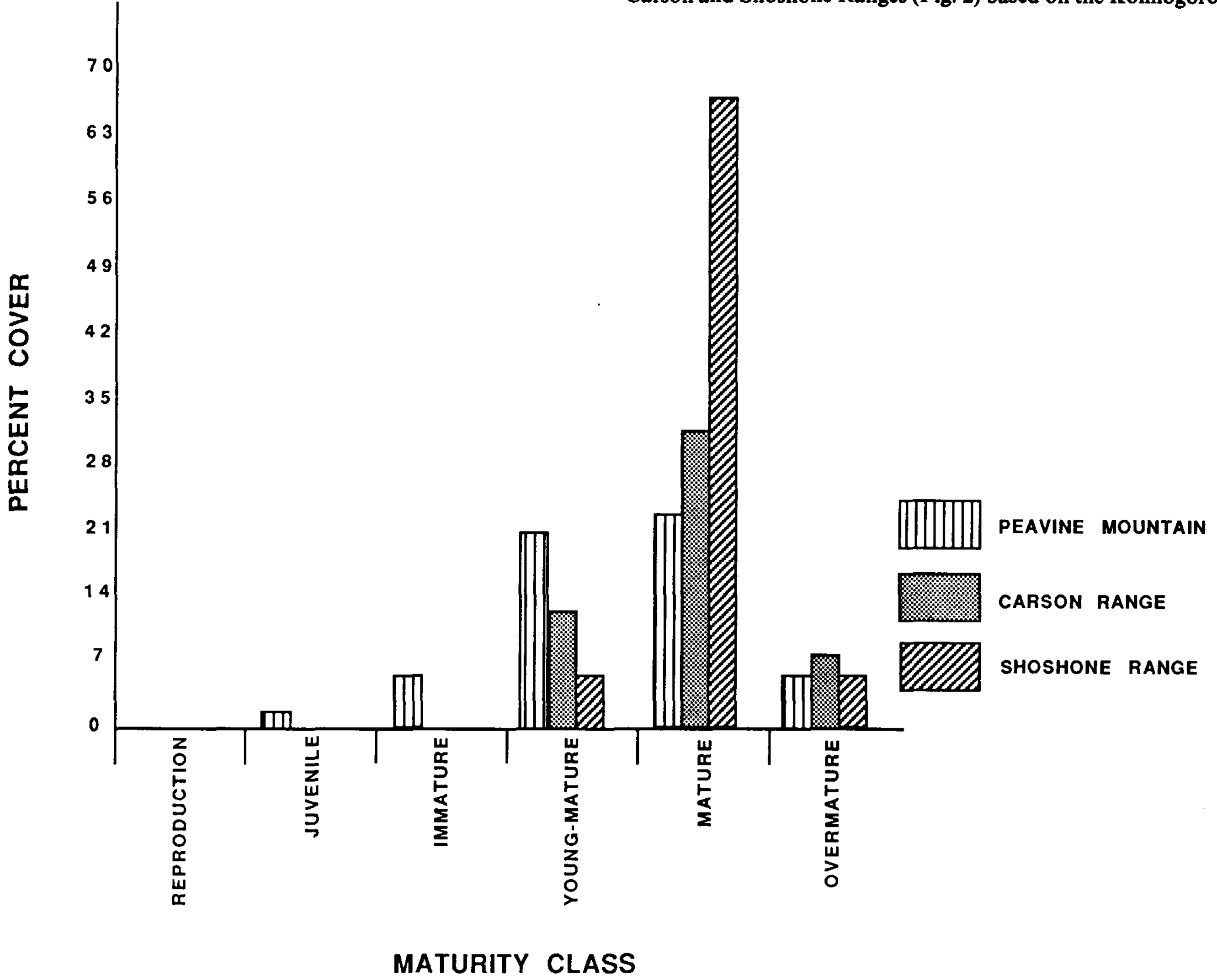

Fig. 1. Average curlleaf mahogany cover for each maturity class at 3 sites in Nevada. Maturity class designations are defined in Table 1.

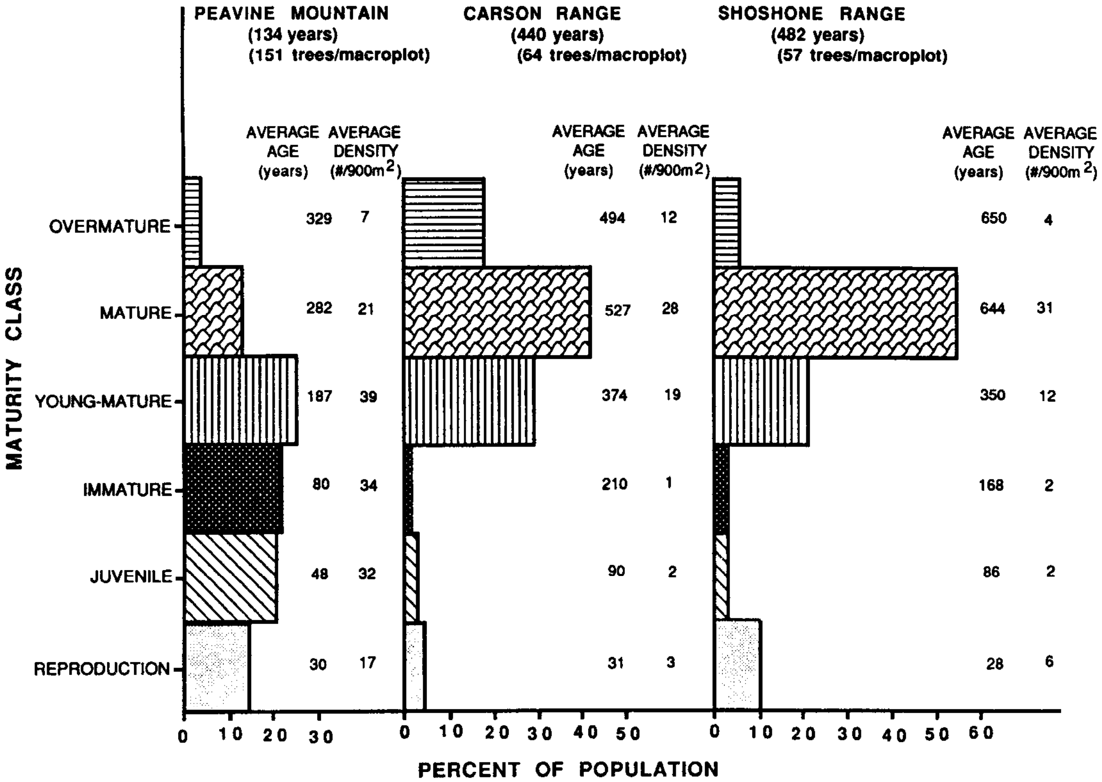

Fig. 2. Average curlleaf mahogany age, density, and relative contribution to total density for each maturity class at 3 sites in Nevada. Maturity class designations are defined in Table 1.

Smirnov tests. Maturity class distribution did not differ significantly ($P \leq 0.05$) between mahogany populations in the Carson and Shoshone Ranges.

On Peavine Mountain no one maturity class dominated the population structure (Fig. 2). Reproduction, juvenile, immature, and young-mature mahogany had significantly ($P \leq 0.05$) higher densities on Peavine Mountain than the other 2 locations. The relative density of the juvenile and immature maturity classes were

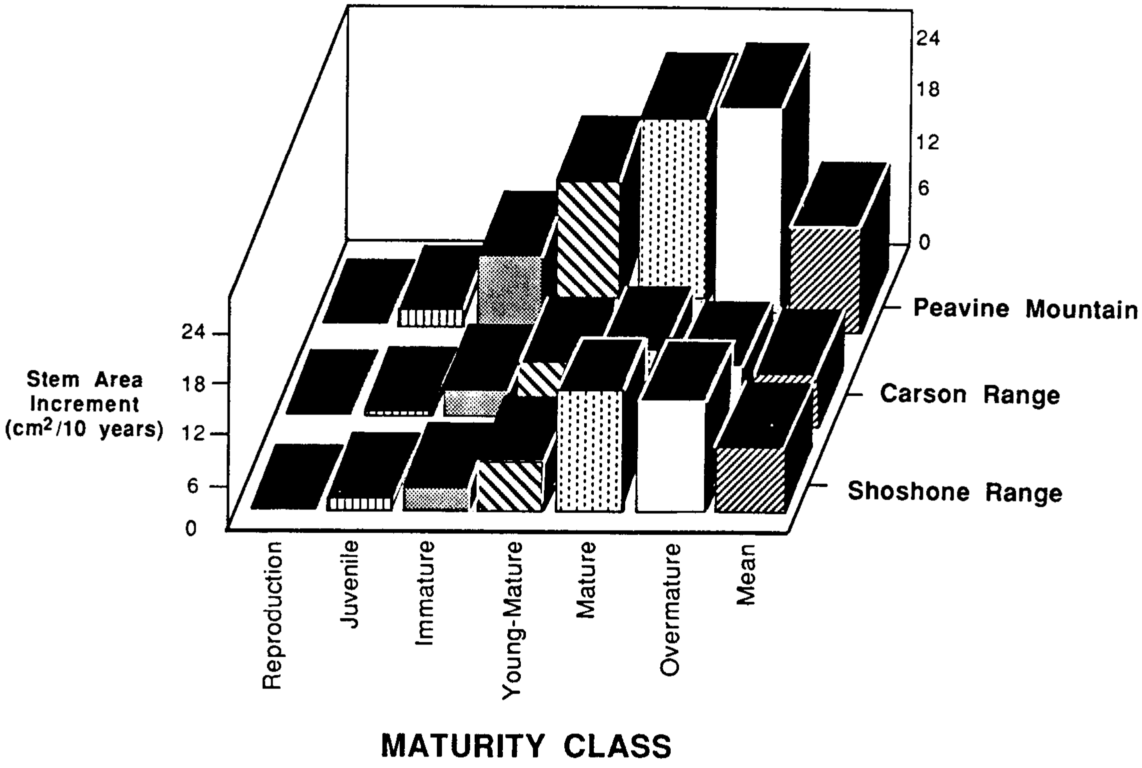

Fig. 3. Average curlleaf mahogany stem area increment values in each maturity class at 3 sites in Nevada. Maturity class designations are defined Table 1.

Table 3. Mean mahogany height and crown diameter in each maturity class for 3 mahogany populations in Nevada.

Maturity class	Height			Crown Diameter		
	Peavine Mountain	Carson Range	Shoshone Range	Peavine Mountain	Carson Range	Shoshone Range
	dm			dm		
Reproduction	2.6a[1]	3.2a	1.6b	5.8a	4.5ab	2.5b
Juvenile	6.3a	6.1a	5.2a	11.1a	10.8ab	8.6b
Immature	11.3a	14.7a	10.7a	19.0a	16.6b	15.6ab
Young-mature	21.1a	29.9ab	31.6b	37.1a	42.9a	37.4a
Mature	25.2a	35.9a	45.6b	53.5a	55.9a	73.1b
Overmature	22.4a	27.7a	39.5b	39.1a	35.0ab	54.0b
Mean	16.4a	31.4b	37.8b	28.8a	43.6b	57.4b

[1] Means within the same row and dimensional parameter followed by the same letter do not vary significantly at the 0.05 level.

also higher on Peavine Mountain (Fig. 2). The general lack of crown closure on Peavine Mountain (Table 2) has permitted a steady increase in density since establishment of the oldest individuals (Fig. 3). This includes high survival of juvenile and immature mahogany during the past 100 years.

Reproduction mahogany were sparse, and their survival and recruitment into juvenile class appears to have been low on both the Carson and Shoshone Ranges (Figs. 2 and 3). Of the 16 macroplots sampled in the Carson and Shoshone Ranges 15 had fewer juvenile than reproduction mahogany, and 13 had fewer immature than reproduction plants. Juvenile mahogany, once established, appear to be recruited into the immature class with little mortality.

Young-mature and older mahogany accounted for over 85% of the population on the Carson and Shoshone Ranges. Mature mahogany accounted for 43% and 55% of the Carson and Shoshone populations, respectively. Significantly ($P \leq .05$) higher densities of overmature mahogany occurred in the Carson Range. This site was the only study area in which overmature mahogany accounted for a substantial portion of the population (19%).

Greater numbers of young-mature compared to immature mahogany occurred in each study area (Fig. 2). Densities of immature mahogany were lower than those in the reproduction class on the Carson and Shoshone Rangers where mahogany were more dominate. Recruitment of young-mature mahogany into the mature class was also low on these 2 ranges, but not on Peavine Mountain. Many macroplots had larger numbers (Fig. 2) of large mature mahogany over topping fewer and smaller (Tables 3 and 4) young-mature individuals. Frequently these young-mature plants lacked a vigorous canopy and were straggly in appearance.

Recruitment of immature mahogany into the young-mature class apears to be a critical point in the survival of plants as part of the overstory on sites dominated by large individuals. This is also reflected in the long time span that young-mature plants remain in the maturity class. Plants now in the young-mature class may represent a period of plentiful establishment occurring about 350 to 400 years ago possibly following some disturbance.

Mahogany Size

Largest mahogany were found in the Shoshone Range and the smallest on Peavine Mountain (Tables 3 and 4). Small differences in average mahogany height, average crown diameter, and average crown volume occurred between study areas for reproduction, juvenile, and immature classes, respectively. The young-mature, mature, and overmature classes usually had large differences in average height, average crown diameter, and average crown volume between study areas.

Mature mahogany on all sites had average crown volumes substantially larger than the other maturity classes (Table 4). Differences in average crown volume contribution between mature mahogany and each of the other maturity classes were greatest on the Shoshone Range. There the population structure was strongly skewed towards mature individuals. On Peavine Mountain the mahogany distribution was not skewed towards any one particular maturity class (Fig. 2).

Total mahogany crown volume was substantially greater in the Shoshone Range than in western Nevada (Table 4). Except for Peavine Mountain, mature individuals accounted for well over half of the crown volume. In the Carson and Shoshone Ranges mature mahogany contributed 65 and 90%, of the total crown volume, respectively, but only 45 and 55% of each population. Overmature mahogany accounted for little crown volume in each study area, and were often similar in size to young-mature plants.

Mahogany encountered in this study were substantially larger than those observed by Duncan (1975) and ranged from smaller to substantially larger than mahogany sampled in Utah (Davis 1976). Dealy (1975) and Davis (1976) found the largest mahogany on dry rocky sites. Our sampling found the largest individuals concentrated on gentle, non-rocky slopes with north and east aspects.

Table 4. Total and average mahogany crown volume (m^3) in each maturity class for 3 mahogany populations in Nevada.

Maturity class	Total crown volume			Average mahogany crown volume		
	Peavine Mountain	Carson Range	Shoshone Range	Peavine Mountain	Carson Range	Shoshone Range
	m^3/macroplot			m^3/plant		
Reproduction	0.5a[1]	0.1a	t[2]ab	ta	ta	tb
Juvenile	5.2a	0.3[3]	0.1b	0.2a	0.2[3]	0.1b
Immature	32.8a	0.8b	0.9b	1.0a	0.8a	0.7a
Young-mature	296.0a	252.3b	101.0c	7.5a	13.3b	8.6ab
Mature	309.9a	821.3a	2063.0b	14.6a	29.9b	66.1c
Overmature	79.5a	193.6a	134.0a	11.2a	14.5a	34.4b
Mean	723.4a	1248.4b	2299.8b	5.8a	19.7a	39.5b

[1] Mean values in the same maturity class and within the same crown volume parameter followed by the same letter are not significantly different at the 0.05 level.
[2] Value is less than .1.
[3] Too few samples in this study area to calculate t-statistic.

These were sites that appeared to have greater effective moisture and better growing conditions than the other sites.

Because smaller plants are out-competed by larger ones (Bella 1971, Grace 1985, Weiner 1984), their mortality is higher than that of the larger plants (Westoby 1981). The resulting population structure becomes dominated by a few large individuals, as was the situation in the Carson and Shoshone Ranges (Fig. 2 and Tables 3 and 4). On Peavine Mountain mahogany density has increased substantially during the past 200 years (Fig. 3). Most of the individuals present have not lived long enough to reach the mature class.

Mahogany Ages

Differences in mean mahogany age (Fig. 2) were only significant ($P \leq 0.05$) between Peavine Mountain and the Carson and Shoshone Ranges. Mahogany age ranged from 7 to 1,350 years. Maximum ages are substantially older than those determined in previous studies (Dealy 1975, Duncan 1975, Davis 1976, Brotherson et al. 1980). Part of this difference in mahogany age may be due to our technique of enhancing annual ring contrast. We were able to see faint or narrow rings that would have otherwise gone uncounted. Because cross-dating was not possible, some error may be present from false or missing rings.

Ranges in age between the youngest and the oldest mahogany in the same macroplot were as much as 1,000 or more years. It was not uncommon for individuals within the young-mature, mature, and overmature classes, respectively, to have age differences of several hundred years.

Reproduction mahogany in each study area did not have significantly different ($P \leq 0.05$) ages (Fig. 2) and were classified as reproduction because of their size. It is now apparent that many were not always reproduction, but sometimes suppressed juveniles. Only after the cross sections were aged was it known that mahogany 10 cm tall can be 30 or more years of age. Schildt and Tisdale (1970) observed a similar situation in Idaho.

Juvenile and older mahogany classes on the Shoshone and Carson Ranges were substantially older than the same maturity classes on Peavine Mountain (Fig. 2). The average age of each maturity class on Peavine Mountain was always older than the preceding maturity class (Fig. 2). In contrast, overmature mahogany in the Carson and Shoshone Ranges were often younger than mature individuals and frequently about the same age as young-mature plants. This indicates many plants in the overmature classes are often severely suppressed individuals that would have otherwise been in the young-mature class.

Relative Plant Growth Rates

Average ring width for the past 10 years was significantly greater on Peavine Mountain than in the other study areas (Table 5). Each maturity class on Peavine Mountain also had significantly ($P \leq 0.05$) greater average ring widths. Both reflect the younger, more open condition of the stands on Peavine Mountain resulting from less dominance by larger, older individuals. These conditions permitted faster growth to occur. A similar pattern exists for average stem area increment (Fig. 3).

Table 5. Mean ring width of curlleaf mahogany for the past 10 years in each maturity class for 3 mahogany populations in Nevada.

Maturity Class	Mean 10 year ring width Peavine Mountain	 Carson Range	 Shoshone Range
	----------------	mm --	---------
Reproduction	0.18b[1]	0.09a	0.09a
Juvenile	0.31a	0.09[2]	0.12b
Immature	0.36b	0.18a	0.14a
Young-mature	0.40b	0.16a	0.14a
Mature	0.36b	0.15a	0.17a
Overmature	0.30b	0.14a	0.15a
Mean	0.32b	0.14a	0.14a

[1] Mean values in the same maturity class followed by the same letter are not significantly different at the 0.05 level.

[2] Too few samples in this study area to calculate t-statistic.

Overstory cover in the Carson Range was patchy. Lower relative growth rates on the Carson Range reflected the effect of intraspecific competition in the dense thickets where cover approached 100%.

Reduced growth rates in individual mahogany were common in the Shoshone Range because of the general crown closure (Fig. 4 and Table 5). Average mahogany cover was almost 80% (Table 2) with many macroplots approaching 100%. Relative growth rates in the Shoshone Range were substantially less than those on Peavine Mountain, reflecting the higher average cover. Mahogany populations on most of the sites sampled on the Shoshone Range have probably reached full site occupancy as defined by Long and Smith (1984).

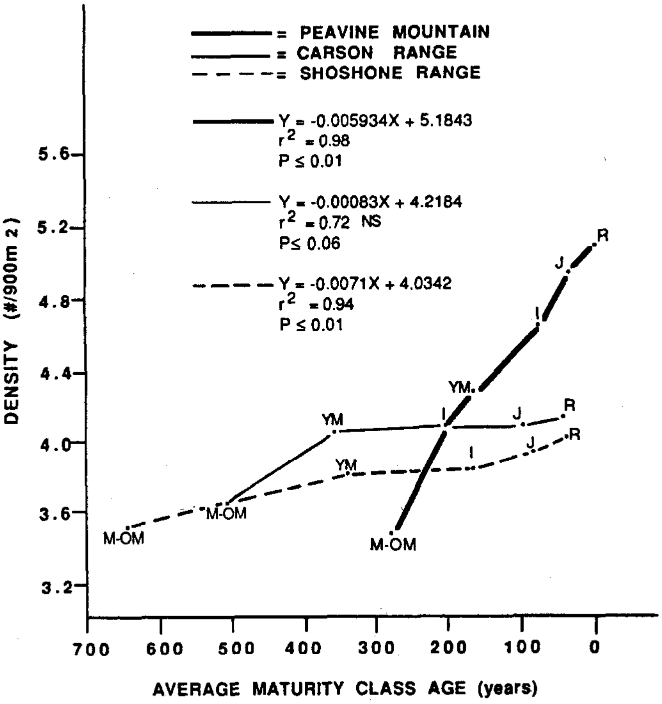

Fig. 4. Approximate population growth rate curves for curlleaf mahogany at 3 sites in Nevada. Maturity class designations of reproduction (R), juvenile (J), immature (I), young-mature (YM), and mature-overmature (M-OM) are defined in Table 1.

Population Growth Rates

The slope of a regression line fitted through each population's growth curve (Fig. 4) can be used to provide an estimate of each study area's population growth rate (Harper 1977). The growth rate of the Peavine Mountain population (0.59) was 7 to 8 times greater than that of the Carson Range population (0.08) and the Shoshone Range population (0.07). Regardless of initial density, each population's growth curve appears to have remained relatively constant during the past 300 years.

Recruitment of new individuals into the Shoshone Range and Carson populations has occurred slowly following the establishment of the current mature-overmature mahogany canopy. The estimated time it would take these two populations to double, assuming no mortality, is 1,028 years in the Shoshone Range, and

900 years in the Carson Range. In contrast, mahogany density on Peavine Mountain has shown a steady increase since the oldest plants were established, and has a doubling time of only 122 years. However, the increases in mahogany populations on Peavine Mountain may have passed their peak. Only 6 plants younger than 20 years were aged, the youngest being 13 years old.

Conclusions

Self-tolerance, the ability of a species to grow and survive under the stress of intraspecific competition (Zeide 1985), is apparent in curlleaf mahogany communities. Reproduction, juvenile, and immature mahogany have characteristics of tolerant species which can grow for decades under a dense overstory. These small mahogany plants appear to live for 100 or more years as part of the understory (Fig. 2). Self-tolerant species also respond with immediate and rapid growth when the overstory is removed.

Indirect evidence of self-tolerance is present when differences in age (Fig. 2), size (Tables 3 and 4), relative growth rates (Table 5 and Fig. 4) and mahogany cover by maturity class (Fig. 1) are compared. Macroplots on Peavine Mountain had substantially lower mahogany cover values. The immature, juvenile, and reproduction mahogany present, which generally were younger, were slightly larger and faster growing than similar plants in the Shoshone and Carson Ranges. This occurred despite deeper soils and greater annual precipitation in the Carson and Shoshone Ranges.

Curlleaf mahogany is probably an intolerant plant when present with other tree species. Conifers, curlleaf mahogany's most common associate, are often considered intolerant species, but they exhibit growth forms of a species more tolerant than curlleaf mahogany. Relative growth rates are greater, their shape more tapered, and they reach greater heights. Consequently, conifer species invading mahogany sites eventually over top them. Because mature mahogany are shade intolerant their competitive ability is lost, and they become senescent.

In communities dominated by curlleaf mahogany the individuals present do not have to compete with a more tolerant species. Individual plants grow as large as site-specific environmental and genetic constraints allow. However, a small population of self-tolerant reproduction plants provide a continuous supply of young mahogany waiting to replace older individuals that die. Numerous researchers (Denslow 1980, Hartshorn 1980, and Shugart 1984) have noted the importance of canopy gaps in forest succession.

Scheldt and Tisdale (1970) felt that excessive utilization on reproduction mahogany was the cause for poor stand recruitment. Davis (1976) believed that succession was dependent upon habitat factors relating to soil moisture storage and soil development. Dealy (1975) observed rapid and elongated root growth in mahogany seedlings, a characteristic that should improve establishment potential in xeric environments. Our results indicated that abundant mahogany reproduction only occurred where canopy closure did not exist (Peavine Mountain). Deer use on mahogany on Peavine Mountain was as heavy as on the Carson and Shoshone Ranges but the additional stress of intraspecific competition was not present. Young mahogany, particularly if abundant, appear to be able to overcome the stress of herbivory, but not the additive effects of herbivory and intraspecific competition.

Suppressed plants not released from competition eventually die, and are probably replaced by a new wave of reproduction individuals. In essence, two mahogany populations occupy the same stand: one composed of dominant mature plants in the overstory, and the other of suppressed individuals in the understory. Suppressed mahogany slowly recycle awaiting the opportunity for recruitment into the overstory when gaps become available.

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Seedbed ecology of winterfat: effects of mother-plant transpiration, wind stress, and nutrition on seedling vigor

D. TERRANCE BOOTH

Abstract

The upward movement of absorbed salts within a plant is influenced by the transpiration stream. This study tested the hypothesis that transpiration by winterfat mother plants affects seedling vigor. Mature plants, growing in a greenhouse, were exposed to forced air and measurements were made on water loss from the plants, concentrations of Ca^{++}, Mg^{++}, Na^{+}, and K^{+} in the diaspores, and on offspring growth parameters. The diaspores produced by the plants were germinated and grown under 2 identical temperature regimes, except that 1 regime included 1 hour of dark-period freezing stress. The forced-air treatment had no detectable effect on mother plants, including no significant ($P \leq 0.05$) effect on water loss or on cation concentrations in the diaspore. However, it did significantly decrease offspring vigor. Analysis of the total test-plant population revealed significant, linear relationships between water loss and: diaspore yield, Ca^{++} and K^{+} concentrations in the diaspore, seedling dry weight, and seedling hypocotyl length. Linear relationships between seedling variables and covariables provided evidence that Ca^{++}, K^{+} and Na^{+} influence seedling weight, moisture, and hypocotyl length. It is concluded that mother-plant transpiration, windstress, and nutrition affect offspring vigor.

Keywords: calcium, magnesium, potassium, sodium, freezing, growth model, environmental stress, seed production

"...one must become at the same time a comparative morphologist, a comparative physiologist, and an ecologist." G. Ledyard Stebbins (1974) on seedling ecology.

Germination characteristics of winterfat [*Eurotia lanata*[1] (Pursh) Moq.; *Ceratoides lanata* (Pursh) J.T. Howell], vary among genetic populations (Workman and West 1967), among locations (Wilson 1931, Asay 1959, Moyer and Lang 1976), and from year to year at a given location (Springfield 1968, 1972, Dettori et al. 1984). Nongenetic variation has been attributed to general environmental conditions (Springfield 1972), but specific cause-and-effect relationships are not well understood.

The influence of the mother-plant environment on seed germination and/or subsequent seedling growth has been noted for such species as winter wheat [*Triticum aestivum* variety Knox, (Riddell and Gries 1958)], plantain [*Plantago aristata,* (Stearns 1960)], and for *Ononis sicula* [a legume native to the Negev desert (Evenari et al. 1966]. In reviewing maternal effects on seed germination, Gutterman (1980) commented on the environmental stimuli of day length, temperature, and position. He cited evidence that these stimuli affect the plant hormonal system, and subsequently the level of hormones in seeds. Poovaiah (1985) has reviewed the functions of Ca^{++} in plant cells, including the role of that ion in cellular response to external and internal (hormones) stimuli. This, and other evidence (Booth 1989), indicate that Ca^{++}, and perhaps other cations, influence seed germination.

The upward movement of absorbed salts, especially Ca^{++}, within a plant is influenced by, among other things, the transpiration stream (Biddulph et al. 1961, Mengel and Kirkby 1982, Devlin and Witham 1983). This study was conducted to test the hypothesis that transpiration by winterfat mother plants affects seedling growth by influencing cation concentrations in the diaspores. Diaspores are the seed-containing units of a plant which function in seed dispersal and in promoting the establishment and survival of the seedlings (Booth 1987). The study also provided the opportunity to separate effects on the offspring of mother-plant transpiration and mother-plant wind stress.

Methods

Plant Material

Forty seed-producing winterfat plants were collected at Cheyenne, transplanted into 7.4 liter pots, and grown in the greenhouse where daytime temperatures were 40–45° C. Aluminum foil caps were fitted over the top of the pots and around the base of the plants to reduce soil evaporation. In separate tests the foil caps reduced soil evaporation by 63% in unshaded pots, and by 74% in unshaded pots exposed to forced air treatments. The tests used a simulated shrub stem with soil at field capacity.

Beginning 8 July 1985, 20 of the 40 plants were randomly selected to be exposed once a week for 15 weeks to 8 hours of forced air (3.3 m/s). Treatment starting date was selected to avoid, as much as possible, treatment interference with seed set, and yet to be in effect throughout the period of diaspore growth and maturation. During the treatment period all pots were weighed weekly. Pots with treated plants were also weighed immediately before and after exposure to forced air. After each weighing, lost moisture was

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Acknowledgment: Dr. Gary V. Richardson, statistician for USDA-ARS, Northern Plains Area, assisted with statistical analysis and manuscript review. The author wishes to thank Dr. Susan E. Meyer, USDA-Forest Service, Shrub Sciences Laboratory, for helpful discussion.

Manuscript accepted 23 March 1989.

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[1] Proposals for conservation of this long-used generic name have been invited (Brummitt 1978).

replaced with Hoaglands solution so that nutrients would not be a limiting factor in plant growth or cation accumulation in diaspores. At diaspore maturity (Nov. 1985), diaspore yield (weight of all diaspores harvested), total aboveground plant weight, and leaf weight were obtained for each plant. Diaspores were separated from seed stalks, allowed to afterripen at room temperature for about 2 months, and stored under refrigeration (Springfield 1974) until used in 1986. Diaspores were used in seedling growth tests and were analyzed for Ca^{++}, Mg^{++}, Na^{+}, and K^{+}. There is some bias in this study because low producing plants did not provide enough material for analysis.

Seedling Growth

Diaspores harvested from treated and untreated plants were used to compare seedling growth under 2 temperature regimes. Each diaspore sample (100 diaspores representing 1 plant) was weighed, mounted on Cobb-Jones germination plates (Jones and Cobb 1963), then imbibed for 2 days at 0 ± 2° C (Booth and Schuman 1983). Germination plates and reservoirs were isolated by sample. Diaspores were cultured for 10 days in germinators at: (a) 15° C with light for 12 hours and at 5° C without light for 12 hours or (b) as in (a), but with a mid-dark cycle temperature drop to -5° C for 1 hour. Light readings at germination plate positions averaged 63 and 74 $\mu E/s/m^2$ for the freezing and nonfreezing runs, respectively. Samples were rotated daily to minimize variation due to location in the germinator. Samples with 60 or fewer diaspores were randomly assigned to 1 of the 2 temperature regimes rather than splitting the available diaspores between the 2 regimes. Data were collected for each mother plant on seedling hypocotyl lengths, and on seedling dry and fresh weights. Seedling samples were oven dried at 60° C for 24 hours.

Cation Analysis

Dried samples were ground, weighed, then ashed at 550° C (Jackson 1958). The ash was dissolved in 6 *N* HCL, evaporated to near dryness, rinsed into 25-ml volumetric flasks, and brought to volume with deionized water. Calcium, K^{+}, Mg^{++}, and Na^{+} were determined on the ash digest by atomic absorption spectrophotometry.

Statistical Analysis

Analysis of variance and analysis of covariance were used to test whether cation concentration was related to water loss and to analyze the relationship between seedling variables and cation concentration in diaspores (Table 1). Analysis of variance, using data from plants represented in both freezing and nonfreezing regimes (paired analysis), compared seedling growth variables (Table 1) with respect to the forced-air treatment of mother plants and to germination temperature regimes. Covariate analysis for seedlings used all data available from each temperature regime. The F-ratio probability value is reported as the Observed Significance Level (OSL). The term "significant" is applied throughout this paper to findings with an OSL ≤ 0.05. However, that level is recognized as an arbitrary point on a continuous scale.

Steel and Torrie (1980) describe analysis of covariance as, using the concepts of both analysis of variance and of regression with 2 or more measured variables, where any measured independent variable is not at predetermined level (i.e., water loss). Covariate analysis has been used here to control error and increase precision of tests, to adjust treatment means of dependent variables for differences in values of corresponding independent variables, and to detect relationships between dependent and independent variables that are approximately linear. It has been particularly useful for separating effects of the forced-air treatments from water loss effects and for detecting relationships with water loss that exist across treatments and would otherwise be obscured by plant to plant variability.

A significant regression line implies that x is of value in explaining the variability in y. The amount of variation in y that is explained by x is estimated by the coefficient of determination (r^2). This coefficient is usually not reported in an analysis of covariance because the model contains factors from noncontinuous variables. For example, forced air was not a continuous variable since plants were either treated or not treated. However, in cases where treatment effects are not significant, and where the treatment sums of squares (SS_{treat}) contribute an insignificant amount to the total sums of squares (SS_{total}), a valid r^2 can be calculated for a significant regression term. This paper will report some r^2 values together with the associated ratio of treatment to total sums of squares.

Results and Discussion

Effect of Forced-air Treatment on Mother-plant Variables

Exposing mother plants to forced air did not cause significant changes in mother-plant water loss, total plant weight, leaf weight, yield of diaspores, average weight of diaspores, or cation concentrations in diaspores (Table 2). This was true even when the covariates were included in the analysis. This indicates that the measured variables were not affected by factors associated with the treatments, such as watering with Hoaglands solution. Lack of treatment differences is believed to be due to a stoma-closing response to wind by treated plants and to the variability in water loss. Water loss ranged from 3,300 to 11,200 g for the forced-air treated plants and from 5,100 to 11,800 go for the untreated plants.

Since the forced-air treatment did not induce water-loss differences between treated and untreated plants, regression analysis of variables with covariables for all plants (ie., across both treatments) was used for testing the hypothesis that transpiration by the mother plants affected cation concentrations in the diaspores. The

Table 1. Winterfat variables and covariables used for evaluating the effects of air movement and transpiration on the cation concentration in diaspores and on offspring vigor.

Mother-plant variables	Mother-plant covariables for cation concentration	Seedling variables	Seedling covariables
Forced air by:	Water loss	Forced air on mother plant, and temperature regime,	Concentration in the diaspore of:
Water loss	Total plant weight	by:	Ca^{++}
Total plant weight	Leaf weight	Seedling dry weight	Mg^{++}
Leaf weight	Diaspore yield	Seedling moisture	Na^{+}
Diaspore yield		Hypocotyl length	K^{+}
Diaspore weight		S.D. hypocotyl length	Water loss
Concentration in diaspore of:			All combinations of above.
Ca^{++}			
Mg^{++}			
Na^{+}			
K^{+}			

Table 2. Means for mother-plant variables as affected by forced-air treatment.

Variable	Untreated	Forced air treated	OSL[1]
Water-loss (g)	6954	6777	.821
Total plant wt (g)	12.8	12.8	.969
Leaf weight (g)	4.28	3.69	.951
Diaspores (g/plant)	2.49	2.54	.951
Diaspores (mg/diaspore)	4.8	4.4	.851
Cation concentration in diaspores (ug/g)			
Calcium	6686	7493	.374
Magnesium	2296	2425	.473
Potassium	22543	21406	.139
Sodium	596	646	.473

[1] Observed Significance Level

effectiveness of regression analysis as a statistical test is enhanced by the range of water loss found to exist in the total test-plant population.

Relationships between Mother-plant Variables and Covariables

Covariate analysis across treatments revealed significant linear relationships between water loss and concentrations of Ca^{++} and of K^{+} in diaspores (Table 3). Calcium in diaspores increased by 0.544 ug/g, and K^{+} increased by 0.352 ug/g of water used by the plant. The concentrations of Mg^{++} and of Na^{+} in the diaspores were not significantly related to water loss. Water loss was also significantly related to diaspore yield and to leaf weight (Table 3). Both increased by 0.4 mg/g of water lost.

Table 3. Statistics describing significant relationships between winterfat mother-plant variables and covariables.

Variable	Covariable	OSL[1]	r^2	SS_{treat}/SS_{total} [2]
			------%	------
Water loss	Ca^{++}	0.003	21.5	2.7
	K^{+}	0.027	12.5	5.4
	diaspore yield	0.012	16.5	0.1
	leaf weight	0.008	18.4	1.6
Total plant weight	Mg^{++}	0.010	17.2	1.4

[1] Observed Significance Level

[2] Values indicate the degree of influence on r^2 by noncontinuous factors of the covariance model.

Diaspore yield is related to the amount of carbon assimilated by the seeds and to the number of diaspores produced. The relationship between water loss and yield is significant because transpiration and yield are both related to photosynthesis. Since green diaspore bracts contain stomata (personal observation), these bracts, and other axillary bracts and leaves associated with developing diaspores, add to the photosynthetic capacity of the plant, to water loss, and to the significant relationship between water loss and yield. Also, phloem sap is probably 75 to 95% water (Salisbury and Ross 1969, Biddulph 1969, Hall and Baker 1972) and diffusion of water through diaspore epidermis may have contributed to water loss. Potassium enhances translocation of assimilates and is the most abundant cation in the phloem (Mengel and Kirkby 1982). The concomitant linear relationships of yield and K^{+} with water loss is indicative of the link between transpiration, photosynthesis/translocation, and yield.

Total plant weight, leaf weight, and diaspore yield were used in covariate analysis of cation concentrations in diaspores. Usually the greater the plant or leaf weight the lower the diaspore cation concentration, indicating a dilution effect from plant material. This relationship was significant between total plant weight and Mg^{++} (Table 3). Magnesium decreased by 39 ug/g of plant material. The relationship between Mg^{++} and leaf weight was not significant (OSL = 0.094) and there were no significant relationships between diaspore weight and the concentration of any cation.

Effect of Forced-air Treatment on Seedling Variables

Offspring were significantly affected by the forced-air treatment of mother plants. Analyzed over both temperature regimes (using only paired data), the forced-air treatment resulted in a significant decrease in the dry weight and in the moisture content of seedlings. The OSLs for these variables were not improved by covariate analysis (Table 4). Also, the forced air probably (OSL = 0.109) decreased hypocotyl length (Table 4). The probability that the observed hypoctyl decrease was real is strengthed by the lack of treatment differences (OSL = 0.329) for the standard deviations of hypocotyl length (Table 3).

Table 4. Winterfat seedling characteristics as affected by forced-air treatment of mother plants.

Variable	Untreated	Forced air treated	OSL[1]
Seedling dry weight (g)	0.1472	0.1172	0.004
Seedling moisture (g)	1.4882	1.1066	0.002
Hypocotyl length (mm)	41	37	0.109
SD hypocotyl length (mm)	12.846	12.194	0.329

[1] Observed Significance Level

Covariate analysis made no improvement in the OSL of treatment means with respect to hypocotyl length under the freezing regime; under the nonfreezing regime, treatment means adjusted for Na^{+} resulted in an OSL of 0.047. Further improvement was realized by using the best combination: Ca^{++}+K^{+}+Na^{+}+water loss (OSL = 0.017). This indicates the importance of these factors to seedling growth. Since the forced-air treatment was not severe enough to produce real differences in water loss or in concentrations of cations in diaspores, the detrimental effects of forced-air on the offspring must be ascribed to factors not measured.

The most likely reason for reduced vigor of offspring from treated mother plants is lower seed mass (as opposed to diaspore mass). This could result from interrupted photosynthesis if stomata closed during forced-air treatments. Although no difference was detected between treatments in the mean weight per diaspore (Table 2), it is likely that seed coverings, which are relatively inexpensive for the plant to produce, hid differences in seed mass. Lack of experimental material precluded measurement of seed mass.

The threshold for wind-induced stoma closure is probably not uniform among winterfat ecotypes. Plants collected from Sterling, Colo. (1,220 m), Cheyenne, Wyo. (1,890 m), and Sheep Mountain near Laramie, Wyo. (2,440 m), averaged 18,700, 14,800 and 11,400 g of water loss, respectively, under a forced-air treatment similar to that described for this study (Booth, unpublished data). Perhaps adaptation to higher, windier habitats was accomplished by changes in the balance between photosynthetic potential and water conservation. We may speculate that a breeze which closes stomata and interrupts transpiration and photosynthesis in the Sheep Mountain or Cheyenne ecotypes might have no effect on stomata in plants from Sterling.

Analysis of covariance for seedlings, which used all the data available from each temperature regime, will be discussed for the freezing and nonfreezing regimes with respect to each variable. The linear models showing significant relationships with growth parameters differ by temperature regime (Table 5). This difference might be indicative of real phenomenon, but could also be the

Table 5. Effects of a 1-hour diurnal freeze on linear models[1] of winterfat-seedling variables with covariables.

Variable	Model without freeze	OSL[2]	Model with freeze	OSL
Dry weight	K^+Na^+water loss	0.010	Ca^{++}+water loss	0.035
Moisture	$Ca^{++}+Mg^{++}+Na^+$	0.008	Ca^{++}+water loss	0.019
Hypocotyl length	$Ca^{++}+K^++Na^+$ water loss	0.038	Mg^{++}	0.145

[1] These are the best models for each variable as judged by the OSL of the models.
[2] Observed Significance Level

result of nonlinear responses caused by the abrupt temperature changes in the freezing regime. Water loss was found to be an important covariable with all seedling variables. Its significance in these analysis appears best explained by assuming (1) that it is correlated with Ca^{++} concentrations in the diaspore, and (2) that it is an indirect measure of photosynthesis. The latter is a valid assumption under arid conditions since leaf water potential has predominate control over stomatal aperture.

Seedling Weight

Covariate analysis revealed a significant (OSL = 0.039), positive, linear relationship between seedling dry weight under the nonfreezing temperature regime, and water loss by the mother plant. Since carbon fixation by a 10-day-old seedling is relatively small, seedling dry weight is primarily a function of the original seed weight. Therefore it is not surprising, given the significant relationship between water loss and diaspore yield, that water loss was related to seedling dry weight. The linear relationship was improved when the K^++Na^+ concentrations in the diaspore were considered in the model with water loss (OSL = 0.010 – Table 5). Potassium accounts for most of this improvement in the significance level. These findings support the interpretation that the forced-air treatment lowered seed mass by interrupting photosynthesis and the translocation of photosynthate. Under the freezing regime Ca^{++} became important, and Ca^{++} + water loss was the only covariable combination that was significantly (OSL = 0.035) related to seedling dry weight.

Seedling Moisture

Diaspore concentrations of Ca^{++} and of Na^+ were most closely correlated with seedling moisture; the covariable combination $Ca^{++}+Mg^{++}+Na^+$ gave the best linear relationship under the nonfreezing regime (OSL = 0.008). The importance of Ca^{++} to seedling moisture content is explained by the known relationship between Ca^{++} and membrane integrity (Mengel and Kirkby 1982, Poovaiah 1985). The importance of Na^+ in the seedling-moisture model is supported by the findings of Booth (1989) and by the work of others (El-Sheikh and Ulrich 1970, Romo and Haferkamp 1987, Eddleman and Romo 1987), who have shown in other species of Chenopodiaceae that Na^+ has a positive effect on the water regime of the plant. In this model, both Ca^{++} and Na^+ were positively related to seedling moisture, while Mg^{++} was negatively related. Under the freezing regime Ca^{++} +water loss was the best model (OSL = 0.019).

Hypocotyl Length

The best linear relationships among single covariables were with water loss (OSL = 0.059) and with Na (OSL = 0.169); the best combination was, $Ca^{++}+K^++Na^+$+water loss. The OSL of the combination model was 0.038 (Table 5). Under the freezing regime, Mg was the only covariable (single or combination) that showed a linear relationship with hypocotyl length (OSL = .145). The relationship was negative.

Standard Deviations of Hypocotyl Length

Sodium was significantly related to standard deviations of hypocotyl lengths (OSL = 0.024), and the best combination, Na^++water loss was a slightly better model with OSL = 0.022. This indicates that the concentration of Na^+ in the diaspore and water loss from the mother plants account for a significant amount of the variation in hypocotyl length. It adds to the evidence of this study, and others (Hilton 1941, Booth 1989), that Na^+ concentrations in the seed influence seedling moisture and hypocotyl length. Under the freezing regime only water loss was significant (OSL = 0.053).

Conclusions and Recommendations

Increased transpiration, as indicated by water loss, increased diaspore concentrations of Ca^{++} and K^+ but not of Na^+ and Mg^{++}. Evidence cited by Mengel and Kirkby (1982) support the conclusion of a direct relationship between transpiration and the Ca^{++} concentration in the diaspores. The relationship between K^+ concentration in the diaspores and transpiration may be indirect, such as the fact that both transpiration and K^+ concentration are related to photosynthesis and to translocation of photosynthate. It may be argued that the significant relationships of Ca^{++} and K^+ concentrations with transpiration are due to the fact that these cations were added in proportion to water loss. However, Na^+ and Mg^{++} were also added in proportion to water loss. Therefore, it is concluded that the volume of water transpired by winterfat mother plants significantly affected seedling vigor by influencing, among other things, the diaspore concentration of Ca^{++}.

Wind stress on winterfat mother plants which occurred after seed set decreased offspring vigor. This occurred at a relatively mild, but steady, wind speed and is assumed to be due to an interruption of photosynthesis when stomata closed. The negative effects of wind stress were seen in reduced seedling dry weights, moisture, and hypocotyl lengths.

Analysis of the relationships between seedling variables and covariables has provided specific evidence of the importance of Ca^{++}, K^+, and Na^+ to winterfat seedling growth. These findings are an indication to seed producers, seed collectors, and to students of seedling growth, of the importance of mother plant nutrition with respect to these cations. Producers may wish to pay particular attention to soil Na^+, since this cation accounted for most of the variability in seedling hypocotyl length. The study also raised questions about the role of Mg^{++}, particularly during seedling freezing stress.

The maintenance of plant transpiration emerged as the single most important factor in seed production. Not only is transpiration a factor in moving Ca^{++}, and possibly K^+, into the diaspore, but also interruptions to transpiration, as in stoma-closing responses to wind, will usually decrease yields (Waggoner 1969, page 356). For this reason seed producers and collectors may wish to avoid winterfat ecotypes that readily close their stoma, or, if wind tolerant ecotypes are needed, that seed be produced or collected in protected places.

A predictive model of early seedling growth will have at least 3 major components: genetic effects, maternal effects, and effects of the seed environment during dormancy and early growth. If we apply to winterfat Gutterman's (1980) list of environmental stimuli that may cause maternal effects (day length, temperature, and seed position), then to the list can be added transpiration, wind stress, and nutrition.

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Herbage production-forest overstory relationships in two Arizona ponderosa pine forests

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Abstract

Utilizing source data for annual herbage production which had been obtained through repeated measurements, though not necessarily taken in each year, in 2 Arizona ponderosa pine *(Pinus ponderosa)* forests from 1959 to 1980, 18 herbage production-forest overstory regression equations were developed and statistically analyzed. In addition to logarithmic and exponential transformations, a hyperbolic transformation met the specific acceptance criteria. Soils were stratified for some herbage components to improve sampling efficiencies. The regression equations presented are considered more useful for long-term planning purposes than for predicting the level of herbage production in a particular year.

Key Words: Pinus ponderosa, herbage production-forest overstory relationships

Quantitative studies describing the growth of herbaceous plants as functions of forest overstories have been conducted in many Arizona ponderosa pine forests (Ffolliott and Clary 1982, Bartlett and Betters 1983). In these studies, linear and nonlinear models generally expressed decreasing herbage production with increasing forest overstory densities (basal area, volume, crown cover) and growth rates. The production of herbaceous vegetation in ponderosa pine forests also has been related to soil parent material (Ffolliott and Clary 1975, Ffolliott and Baker 1977) and soil texture (Clary et al. 1966, Clary 1969), although these latter studies were relatively location-specific. Since the Arizona ponderosa pine forests are managed for both cattle and timber production, knowledge of herbage production-forest overstory relationships is important.

The objective of this study was to evaluate a set of regression equations relating annual herbage production to the overstories of 2 Arizona ponderosa pine forests. As a result of this evaluation, equations meeting specified acceptance criteria were identified to assist land managers in understanding the joint production of herbage and timber in these forests.

Materials and Methods

Study Areas

Source data sets from 2 study areas in Arizona ponderosa pine forests, the Beaver Creek sub-watersheds (Brown et al. 1974) and the Heber sub-watersheds (Ffolliott and Baker 1977), were utilized to develop the herbage production-forest overstory relationships described in this paper.

The ponderosa pine forest overstories on both the Beaver Creek and Heber sub-watersheds represent a simple tree species composition, but a complex spatial structure because of variations in elevation, topography, and soils, and the influence of fire. Ponderosa pine is dominant but intermixed with Douglas-fir *(Pseudotsuga menziesii)* and quaking aspen *(Populus tremuloides)* at higher elevations, and alligator *(Juniperus deppeana),* Utah *(Juniperus osteosperma),* and Rocky Mountain juniper *(Juniperus scopulorum),* and pinyon *(Pinus edulis)* at lower elevations. Gambel oak *(Quercus gambelii)* is found scattered throughout the study areas.

The occurrence of specific herbaceous plants depends largely upon the forest overstory density, climatic patterns, physiographic characteristics, and past land use. Principal grasses and grass-like plant species on the study areas include Arizona fescue *(Festuca arizonica),* blue grama *(Bouteloua gracilis),* mountain muhly *(Muhlenbergia montana),* muttongrass *(Poa fendleriana),* bottlebrush squirreltail *(Sitanion hystrix),* black dropseed *(Sporobolus interruptus),* and sedge (*Carex* spp.). Important forbs and half shrubs are western ragweed *(Ambrosia psilostachya),* fleabane (*Erigeron* spp.), showy goldeneye *(Viguiera multiflora),* globemallow (*Sphaeralcea* spp.), and mullein (*Verbascum* spp.). Shrubs include buckbrush *(Ceanothus fendleri),* mountain mahogany (*Cercocarpus* spp.), cliffrose *(Cowania mexicana),* and New Mexican locust *(Robinia neomexicana).*

Annual temperatures and precipitation on the 2 study areas range between 7 and 9° C and 536 and 635 mm, respectively, values which are similar to those observed generally in Arizona ponderosa pine forests (Schubert 1974). Two major precipitation seasons characterize the study areas. Sixty-five percent of precipitation falls from October through April, with the remainder falling in July through early September.

The soils on the Beaver Creek sub-watersheds, developed on basalt and cinders, are mostly clay loam and loam-sandy loam in texture. They have been described in detail by Williams and Anderson (1967). Soils on the Heber sub-watersheds, developed from undivided materials, unnamed but with mineralogy similar to that of the Coconico sandstone formation, are fine, sandy loam in texture. Elevations of the 2 study areas vary from 1,885 to 2,425

Methods

To develop the herbage production-forest overstory relationships, annual herbage production, measured in kg per ha, and forest overstory density, measured in basal area per ha, specifically in terms of m^2 per ha, were measured, as described below.

Annual herbage production was measured by weight estimates (Pechanec and Pickford 1937) on permanently located 0.90-m^2 circular sampling plots on the Beaver Creek and Heber sub-watersheds. These herbage production values, obtained through repeated measurements, were separated into 4 herbage components for analysis. These herbage components were total herbage, grasses and grass-like plants, forbs and half shrubs, and shrubs.

Herbage production was measured on the Beaver Creek sub-watersheds from 1959 through 1980. Both permanently located clusters of herbage sampling plots and forest inventory plots comprised the sampling basis. Ten clusters of 5 sampling plots each were distributed randomly to measure the herbage production on 7 sub-watersheds, totalling 3,336 ha in area. The forest inventory plots were located in systematic sampling designs with multiple random starts (Shiue 1960) on 5 of the sub-watersheds, totalling 2,089 ha in area, to sample the range of forest overstory conditions. All sampling points were not measured each year. The clusters of herbage sampling plots were measured a minimum of 3 years, while

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Manuscript accepted 24 April 1989.

differing combinations of the forest inventory plots were sampled 1, 2, or 3 years in the study period. The number of sample plots for herbage production measurement and the years of measurement are presented in Table 1.

Table 1. Number of sample plots for herbage production measurements on the Beaver Creek sub-watersheds.

Year	Cluster sampling plots	Forest inventory plots
	n	n
1959	175	
1960	350	
1961	350	
1962	350	
1963	100	
1964		430
1965	150	
1966	100	
1967	50	
1968	100	93
1969	150	
1970	100	515
1971	100	
1972	100	
1973		93
1974		
1975	50	
1976	50	
1977	50	
1978	50	
1979	50	
1980	50	

Measurements of herbage production on Beaver Creek were separated into 3 groups to develop and subsequently evaluate the herbage production-forest overstory relationships. One group of measurements represented soils of all textures sampled. The other 2 groups of measurements, analyzed to determine whether sampling efficiencies could be improved through stratification, represented soils of either clay loam texture or soils of loam-sandy loam texture; these are the 2 soil textures most commonly found in the ponderosa pine forests on the Beaver Creek sub-watersheds. Importantly, a subset of source data for all groups, representing nearly 15% of the source data, was set aside for subsequent validation purposes.

Herbage production on the Heber sub-watersheds was measured annually on 4 small watersheds, totalling 86 ha in area, from 1974 through 1977. On each of the sub-watersheds, 30 clusters of 3 sample plots were established randomly. Approximately 10% of the data were set aside for validation purposes.

Although forest growth rates often are preferred as predictors of herbage production in ponderosa pine forests (Ffolliott and Clary 1974), forest overstory density expressed in basal area per hectare was selected as the independent variable in this study. Basal area is easily determined in the field and is utilized commonly as a basis for forest management planning. The basal area of ponderosa pine trees was estimated by variable-plot sampling techniques (Avery and Burkhart 1983) at the time of initial herbage production measurements and at the end of the study periods on the sub-watersheds. Changes in basal area throughout the study period were minor, averaging less than 3%.

Analysis

Since herbage production generally differs from year to year, average herbage production (by herbage component) in relation to ponderosa pine basal area levels were obtained from the repeated measurements of the sampling plots. Because a preliminary analysis showed that herbage production values were not related to annual precipitation, precipitation was not an independent variable in this study.

Bivariate regression analyses were employed to derive relationships that fitted the data points (Draper and Smith 1966). Dependent variables were total herbage production, and production of grasses and grass-like plants, forbs and half shrubs, and shrubs. The independent variable was ponderosa pine basal area. The following regression models, many of which have been employed previously to define herbage production-forest overstory relationships (Ffolliott and Clary 1982, Bartlett and Betters 1983), were tested:

$$Y = a + b(X) \tag{1}$$
$$\log Y = a + b(X) \tag{2}$$
$$\log Y = a + b(\log X) \tag{3}$$
$$Y = a + b(X^2) \tag{4}$$
$$Y = a + b(X^3) \tag{5}$$
$$Y = a + b(X) + c(X^3) \tag{6}$$
$$\log Y = a + b(X^2) \tag{7}$$
$$\log Y = a + b(X^3) \tag{8}$$
$$\log Y = a + b(X) + c(X^3) \tag{9}$$
$$(X/Y) = a + b(X) \tag{10}$$
$$(X/Y) = a + b(\log X) \tag{11}$$
$$\log (X/Y) = a + b(X) \tag{12}$$
$$\log (X/Y) = a + b(\log X) \tag{13}$$
$$(1/X) = a + b(X) \tag{14}$$
$$(1/Y) = a + b(X) + c(X^2) \tag{15}$$
$$Y = a + b(X) + c(1/X) \tag{16}$$
$$Y = a + b(1/X) \tag{17}$$
$$(1/Y) = a + b(1/X) \tag{18}$$

Descriptive statistics were computed for all of the variables in the regressions and their respective transformations. Since normality of the dependent variables was required for the "F" and "t" tests performed, Kolmogorov-Smirnov "D" values (a = 0.5) were utilized to check the distributions when large kurtosis and skewness were detected for a dependent variable (Sokal and Rohlf 1979).

The herbage production-forest overstory relationships developed were evaluated by coefficients of determination (r^2), standard errors of estimate ($S_{y.x}$), and significance of linear regression coefficients (a = 0.05). Only the relationships with r^2 values greater than 60% were considered for subsequent evaluation. Covariance analyses and, when the dependent variables were not normally distributed, Mann-Whitney "U" tests were conducted to detect significant differences in regression slopes among the models (Sokal and Rohlf 1979).

For each herbage component in a data group, model validation entailed the following steps: observed average annual herbage production for the sampled basal area levels and the related standard error were obtained from the subsets of source data reserved for evalution; observed basal area values were employed as inputs in the appropriate regression equation to estimate herbage production; average predicted herbage production and standard error were obtained from these estimations; and observed and predicted confidence intervals were computed (a = 0.05) and compared (Mankin et al. 1975). At least 70% of an observed confidence interval had to overlap the range of the predicted confidence interval for a regression equation to be accepted. If the dependent variable of a model was not normally distributed, that model was validated by the Mann-Whitney "U" test. All statistical computations were carried out by the program SPSSPC (Norusis 1986).

Results and Discussion

The herbage production-forest overstory relationships presented in this paper were developed from source data collected in cutover, but recently unthinned forests. It is known that herbage production in recently thinned ponderosa pine forests can be greater than that in unthinned forests at similar overstory density levels (Clary and Ffolliott 1966). It is not known, however, if the difference in herbage production-forest overstory relationships between thinned and unthinned forests is short in duration. If the difference is a function of the stocking arrangement and size class distribution of the residual trees (and, therefore, affecting the penetration of light), the difference may be semipermanent in nature. Because herbage production-forest overstory relationships from unthinned ponderosa pine forests can be questionable in estimating the level of herbage production obtained by thinning, herbage production-forest overstory relationships should be redetermined when a forest overstory is reduced by thinning.

For a given ponderosa pine basal area level, the herbage production on a sub-watershed did not differ significantly from year to year. It then was found that, at a given basal area level, the herbage production on the Beaver Creek sub-watersheds generally was different from that on the Heber sub-watersheds. As a result, the herbage production data were grouped to represent, as separate entities, the Beaver Creek sub-watersheds and the Heber sub-watersheds and averaged in terms of basal area for further analysis.

Regression equations for shrub production were statistically meaningless on both study areas and, therefore, were not considered. The relatively high variability in shrub production, both spatially and temporally, suggested that this herbage component was not influenced by forest overstory density. Shrub production, which often is relatively low in Arizona ponderosa pine forests, generally was higher at intermediate values of basal area and lower at the extremes of the basal area range.

Beaver Creek Sub-Watersheds

Of the 18 regression models tested for annual herbage production-forest overstory relationships on soils of igneous parent material, considering all herbage components and soil textures sampled, only the linear (1), semilogarithmic (2), polynomial (6, 7, 9), and hyperbolic (12, 13, 15) models possessed r^2 values to warrant further attention. All of the regression coefficients for these models were highly significant ($a = 0.01$). However, models (1), (6), (7), (12), and (15) subsequently were rejected because the overlap in the observed and predicted confidence intervals did not meet the 70% criterion for acceptance. Model (13) was rejected for total herbage production for the same reason, although it was retained in the relationships for grasses and grass-like plant production and for forb production.

Table 2 presents a summary of the selected regression equations relating herbage production to the overstories of ponderosa pine forests on the Beaver Creek sub-watersheds. The choice of which equation to use in studying the production of a particular herbage component in relation to forest overstories is largely an individual preference, as statistical differences among the equations were inconsequential, for the most part.

It was not surprising that many of the variables in the regression equations shown in Table 2 involved logarithmic or exponential transformations. In previous studies of herbage production-forest overstory relationships in Arizona ponderosa pine forests, either logarithmic or exponential transformations also were common models selected (Bartlett and Betters 1983). However, a hyperbolic transformation, model (13), also met the acceptance criteria. To the knowledge of the authors, a hyperbolic model for herbage production-forest overstory relationships in Arizona's ponderosa pine forests had not been reported previously.

To determine whether sampling efficiencies could be improved through a stratification by soil textures, regression equations describing herbage production-forest overstory relationships on soils of clay loam and loam-sandy loam were compared statistically to those presented in Table 2.

Table 2. Annual herbage production-forest overstory relationships on the Beaver Creek sub-watersheds.

Regression equation	r^2	$s_{y.x}$	F
Total herbage production:			
(2) $\log(Y) = 2.794 - 0.348 \times 10^{-1}(X)$	0.703	0.250	186.3
(9) $\log(Y) = 2.711 - 0.221 \times 10^{-1}(X) - 1.130 \times 10^{-6}(X^3)$	0.765	0.231	127.0
Grass and grass-like plant production:			
(2) $\log(Y) = 2.517 - 0.294 \times 10^{-1}(X)$	0.632	0.244	133.8
(9) $\log(Y) = 2.513 - 0.285 \times 10^{-1}(X) - 9.981 \times 10^{-7}(X^3)$	0.634	0.245	66.1
(13) $\log(X/Y) = -2.681 + 1.596 \log(X)$	0.726	0.278	152.6
Forb production:			
(2) $\log(Y) = 2.262 - 0.397 \times 10^{-1}(X)$	0.647	0.322	141.4
(9) $\log(Y) = 2.273 - 0.416 \times 10^{-1}(X) - 1.638 \times 10^{-6}(X^3)$	0.646	0.324	70.0
(13) $\log(X/Y) = -2.363 + 1.728 \log(X)$	0.623	0.373	96.6

where (Y) = production, kg/ha
(X) = ponderosa pine basal area, m²/ha

For total herbage production, the regression equations for soils of clay loam texture provided higher correlations than the equations in Table 2. Therefore, a greater amount of the variation in total herbage production, as indicated by r^2 values, can be accounted for in the equations for these soils. As a result, the sampling efficiency for total herbage production could be improved through a stratification of soils on clay loam texture and the application of one of the regression equations for total herbage production in Table 3. Correlations of the equations for total herbage production on soils of loam-sandy loam were not different ($a = 0.05$) from those presented in Table 2.

Table 3. Annual herbage production-forest overstory relationships on the Beaver Creek sub-watersheds for soils of clay loam texture.

Regression equation	r^2	$s_{y.x}$	F
Total herbage production:			
(2) $\log(Y) = 2.773 - 0.309 \times 10^{-1}(X)$	0.854	0.143	164.3
(9) $\log(Y) = 2.809 - 0.320 \times 10^{-1}(X) + 5.927 \times 10^{-6}(X^3)$	0.893	0.122	114.9
Forb production:			
(2) $\log(Y) = 2.291 - 0.410 \times 10^{-1}(X)$	0.805	0.216	119.5
(9) $\log(Y) = 2.236 - 0.523 \times 10^{-1}(X) + 1.592 \times 10^{-6}(X^3)$	0.825	0.207	68.1

where (Y) = production, kg/ha
(X) = ponderosa pine basal area, m²/ha

Correlations of all regression equations for the production of grasses and grass-like plants, regardless of the soil texture sampled, were similar to those in Table 2. Therefore, there is no improvement in sampling efficiency through a stratification of soil texture.

In terms of forb production, once again, the regression equations for soils of clay loam texture possessed higher correlations than those presented in Table 2. Model (13) was rejected, because it failed to meet the criteria of acceptance. Therefore, sampling efficiency could be improved through a stratification of soils of clay loam texture and use of one of the regression equations for forb production in Table 3. Correlations of the regression equations for forb production on igneous soils of loam-sandy loam texture were similar to those in Table 2.

Heber Sub-Watersheds

Model (13) was the only model of herbage production-forest overstory relationships on the Heber sub-watersheds with r^2 values in excess of 60% that met the required overlap in the observed and predicted confidence intervals. This model satisfied the criteria of acceptance for all of the herbage components considered.

Table 4. Herbage production-forest overstory relationships on the Heber sub-watersheds.

Regression equation	r^2	$s_{y.x}$	F
Total herbage production:			
(13) $\log (X/Y) = 2.633 - 0.216 \log (X)$	0.841	0.252	554.1
Grass and grass-like plant production:			
(13) $\log (X/Y) = -1.794 + 1.172 \log (X)$	0.774	0.293	373.2
Forb production:			
(13) $\log (X/Y) = -1.601 + 1.254 \log (X)$	0.714	0.363	267.6

where (Y) = production, kg/ha
(X) = ponderosa pine basal area, m^2/ha

Table 4 shows a summary of regression equations selected to relate herbage production to the overstories of ponderosa pine forests on the Heber sub-watersheds.

Management Implications

The simultaneous production of forage for cattle production and wildlife, and timber for the production of primary wood products represents one of the best examples of multiple resource management in Arizona ponderosa pine forests (Bartlett and Betters 1983). However, to manage these forests properly for the joint production of forage and timber, an understanding of herbage production-forest overstory relationships, as described in this paper, is important.

The estimated herbage production values represent averages for given basal area levels obtained from several years of measurement on the study areas. These estimated values, therefore, are more useful for long-term planning purposes than for predicting the level of annual herbage production in a particular year. Annual herbage production could not be predicted from knowledge of precipitation or the other variables considered in this study.

Among the variables tested were annual precipitation amounts, and winter (from October through April) and summer (from May through September) precipitation. These precipitation variables were grouped to represent the current year's precipitation, the previous year's precipitation, and the accumulations of both in relation to the year of herbage production measurement. Other variables considered were topographic positions (specifically, concave swales, lower slope positions, and uplands) and elevation.

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Responses of endophyte-bearing and endophyte-free varieties of *Lolium perenne* L. to fungicide treatment and simulated herbivory

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Abstract

The effects of the presence of fungal endophytes, treatment with a systemic fungicide, and simulated herbivory on growth and biomass allocation were investigated in 2 varieties of perennial ryegrass *(Lolium perenne)*: 'Repell', an endophyte-bearing variety, and 'Pennfine', a low-endophyte variety. In the absence of herbivory or fungicide there were no significant differences in the growth or pattern of biomass allocation between varieties. Treatment with the systemic fungicide benomyl reduced growth of both varieties by approximately 50% and reduced root growth more than shoot growth; fungicide effects were similar in the 2 varieties. Simulated herbivory reduced root growth more in endophyte-bearing Repell plants than in endophyte-free Pennfine plants, and root:shoot ratios of Repell plants were significantly lower than those of Pennfine plants following either moderate or severe herbivory. Statistically significant interactions between fungicide treatment and simulated herbivory were frequent in Repell plants but absent in Pennfine plants, suggesting that the fungicide had both direct phytotoxic effects and indirect effects mediated through the loss of endophytes by the Repell plants. While the proximate cost to seedlings bearing endophyte seemed small, the presence of the endophytes altered the allocation pattern of biomass following herbivory in such a way as to increase the probability of mortality.

Key Words: endophytes, fungicide, ryegrass

Many prairie and pasture grasses are infected by fungal endophytes that ramify throughout leaf and stem tissues (White 1987, Clay 1988). For example, perennial ryegrass (*Lolium perenne* L.) and tall fescue (*Festuca arundinaceae* Schreb.) are infected with the imperfect fungi *Acremonium lolii* and *A. coenophialum* respectively (Latch et al. 1984, White and Cole 1985). These fungi do not produce spores with great dispersal and infection capability; rather the fungi are transmitted from one generation of grasses to another by vegetative growth of hyphae into developing ovules or seeds (Bacon et al. 1977, White and Cole 1986). Thus the persistence of this relationship in natural communities is dependent on the fitness of the host plant.

A number of studies have recently established the toxicity of *Acremonium* in *Festuca* and *Lolium* spp. to a variety of animals (Hoveland et al. 1983, review by Clay 1988). Cattle, sheep, and deer grazing on infected ryegrass or tall fescue have experienced reduced mass gain, tremors, staggers, and even death (Mackintosh et al. 1982, Fletcher 1983). The tendency of some mammals to avoid at least some infected grasses protects both the host grass and the fungus.

Alkaloids produced by fungal endophytes of grasses have also been shown to reduce feeding rates and oviposition and increase mortality in a variety of insects (Clay 1988). Though these chemical defenses are currently effective in reducing insect herbivory, thereby increasing plant yield and fitness, a wide range of studies suggest that insects often become tolerant or resistent to trace compound defenses more rapidly that they evolve *de novo* in plants (Hodkinson and Hughes 1982). This then raises the question of what costs and/or benefits having the fungal endophyte will confer on the host grass once insect herbivores become resistent to the fungal alkaloids.

Little information is currently available on the proximate effects of fungal endophytes on plant growth or biomass allocation (Latch et al. 1985). Two approaches to investigating fungal effects on growth are available: (1) comparisons of endophyte-bearing and endophyte-free varieties of a given species of grass, and (2) comparisons of endophyte-bearing individuals with ones in which the fungus has been killed either by fungicides or by lengthy seed storage (Latch et al. 1985). In this study, we compare those 2 approaches as means of determining how endophyte-bearing and endophyte-free plants will recover from simulated herbivory. Our specific objectives were to: (1) compare the growth of endophyte-bearing and endophyte-free varieties of *Lolium perenne* under controlled conditions, (2) compare the growth of endophyte-bearing *Lolium perenne* plants to plants of the same variety in which the endophytes have been removed by fungicide treatment, and (3) compare the effects of simulated herbivory on an endophyte-bearing variety, an endophyte-free variety, and plants of an endophyte-bearing variety in which the endophytes have been removed by fungicide treatment.

Methods

Cohorts of 2 varieties of *Lolium perenne*: 'Repell', a variety with 100% of its seed infected with *Acremonium lolii,* and 'Pennfine', a variety with less than 25% of its seed infected (Halisky and Funk 1984) were established in flats under an intermittent mister in a greenhouse. Single culms were transplanted to 10-cm pots of 80:20 sand:perlite at 3 wk of age; half the plants of each variety were treated every other day for 2 weeks with a 1.2 g/l solution of benomyl (methyl 1-butylcarbamoyl, 2-benzimidazolecarbamate), systemic fungicide shown to be effective against fungal endophytes of grasses (Clay, Personal communication). This fungicide inhibits mitosis in all fungi except Oomycetes by binding to tubulin and preventing spindle formation (Griffin 1981). All plants were fed weekly with 100 ml of Peters' 20-20-20 complete fertilizer and randomized weekly to minimize bench position effects.

After 4 wk of growth in the greenhouse at ambient light (maximum 800 $\mu E\ m^{-2}\ sec^{-1}$) and temperature (range 10–29° C), each variety-by-fungicide combination was divided into 3 groups: (1) control, (2) moderate simulated herbivory: clipping of each culm to 3 cm height, and (3) severe simulated herbivory: clipping to 1 cm height. Each variety-by-fungicide-by-herbivory combination was replicated 6 times. The clipped portions of each plant were dried at 70° C for 24 hrs and dry mass determined to the nearest 0.1 mg. After 2 wk of post-clipping growth (9 wk total growth) all plants

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We thank Karl Danneberger for supplying seed, James F. White, Jr., Do-Soon Cho, Dan Jacques, and Kathy Harris for constructive comments on the manuscript, and Beth Rosen for greenhouse and lab help.

Manuscript accepted 26 January 1989.

were harvested, divided into root and shoot, and dried and weighed. Leaves from extra fungicided and control plants were cleared, stained, and examined for the presence of fungal endophytes using the trypan blue method of Phillips and Hayman (1970). No endophytes were present in fungicided Repell plants or Pennfine (fungicided or control); all examined nonfungicided Repell plants had endophytes present.

Differences among treatment groups in total plant mass (shoot + root at harvest), total plant yield (mass at harvest + clipped biomass), root mass, shoot mass and yield, and root:shoot ratio were analyzed by analysis of variance and Tukey's Studentized Range Test (S.A.S. 1986) using the 0.05 significance level unless otherwise noted.

Results

In the absence of either herbivory or fungicide, there were no significant differences in the growth or yield of the 2 *Lolium* varieties (Table 1). Growth of both varieties were reduced by fungicide treatment by an average of 49% in total plant mass, 34% in shoot mass, and 66% in root mass (Fig. 1). As a result of the greater effect of the fungicide on roots than shoots, the root:shoot ratio decreased by an average of 82% following the fungicide treatment (Fig. 1). There were no significant differences between varieties in the effect of the fungicide treatment.

Table 1. Comparison of biomass (mg dry mass) and root:shoot ratio of Repell and Pennfine varieties of *Lolium perenne* after 9 weeks of growth. Standard errors of the means are given in parentheses.

Parameter	var. Repell	var. Pennfine
Total Plant Mass	240.4 (29.3)	243.3 (33.2)
Shoot Mass	137.5 (13.1)	124.7 (14.6)
Root Mass	102.9 (18.2)	118.5 (20.5)
Root:Shoot Ratio	0.737 (0.102)	0.936 (0.122)

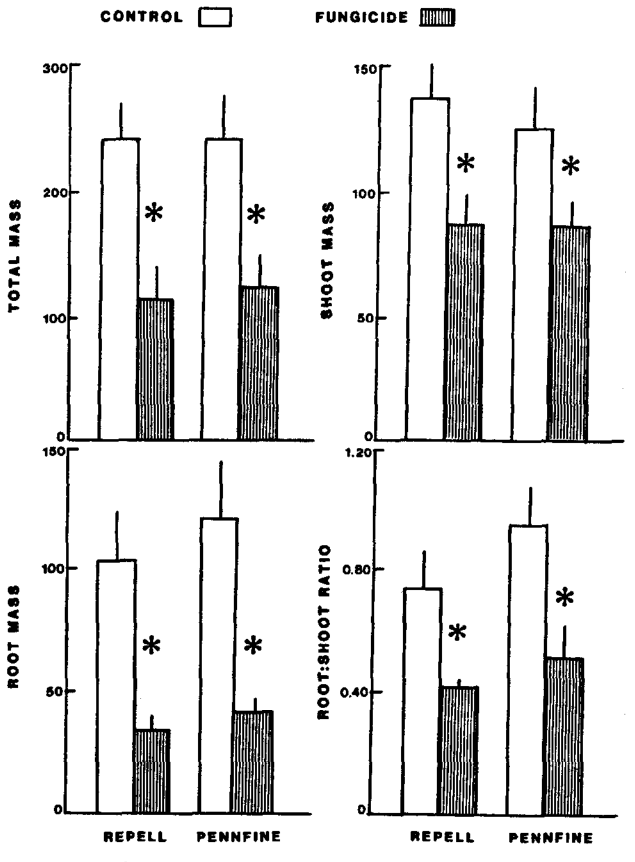

Fig. 1. *Total, shoot, and root mass (mg dry mass) at harvest and root:shoot ratio of Repell and Pennfine plants, with and without fungicide treatment. Means and one standard error are given. Significant differences at* p = *0.05 from analysis of variance are indicated by an asterisk.*

As there were no significant differences in the growth of the 2 varieties in the absence of fungicide treatment, we chose to assess the effect of the presence of endophytes on recovery from simulated herbivory by comparing recovery in non-fungicided Repell and Pennfine plants. Total plant mass, total yield (total mass at harvest + clipped biomass), shoot mass, and shoot yield all decreased with increasing simulated herbivory, but with no differences between varieties (Table 2). Root mass also decreased significantly with increasing simulated herbivory; the root mass of Repell plants was lower than that of Pennfine plants, though the difference was only significant at the 0.074 level (Table 2). Overall, root:shoot ratio decreased by an average of 29.5% and 37.3% following moderate and severe clipping, respectively. However, the root:shoot ratios of Repell plants were significantly lower than those of Pennfine plants at both levels of herbivory (Table 2).

Table 2. Total and shoot growth (mg dry mass) of 2 *Lolium perenne* varieties exposed to moderate and severe simulated herbivory. Within a row, means followed by different lower case letters were different at $p = 0.05$ following analysis of variance and Tukey's Studentized Range test. Standard errors of the means are given in parentheses.

Parameter/-variety	Control	Moderate simulated herbivory	Severe simulated herbivory
	Total Mass at Harvest		
var. Repell	240.4a (29.3)	133.7b (20.4)	82.9c (7.5)
var. Pennfine	243.3a (33.2)	191.5b (32.1)	78.3c (12.6)
Combined	241.8a (21.1)	162.6b (20.1)	80.6c (7.0)
	Total Yield		
var. Repell	240.4a (29.3)	140.2b (21.3)	92.6c (8.5)
var. Pennfine	243.3a (33.2)	196.3b (31.9)	85.7c (13.9)
Combined	241.8a (21.1)	168.2b (20.2)	89.1c (7.9)
	Shoot Mass at Harvest		
var. Repell	137.5a (13.1)	94.6b (15.6)	58.0c (6.2)
var. Pennfine	124.7a (14.6)	107.5b (13.7)	48.1c (6.1)
Combined	131.1a (9.5)	101.1b (13.6)	53.1c (4.4)
	Total Shoot Yield		
var. Repell	137.5a (13.1)	101.1a (16.4)	67.7b (7.1)
var. Pennfine	124.7a (14.6)	112.3a (13.7)	55.5b (7.5)
Combined	131.1a (9.5)	106.7a (10.3)	61.6b (5.2)
	Root Mass at Harvest[1],[2]		
var. Repell	102.9a (18.2)	39.1b (5.2)	24.9c (2.0)
var. Pennfine	118.6a (20.5)	83.9b (21.2)	30.2c (6.7)
	Root:Shoot Ratio[2,3]		
var. Repell	0.737a (0.102)	0.430b (0.036)	0.446b (0.041)
var. Pennfine	0.936a (0.122)	0.750b (0.162)	0.603b (0.057)

[1] difference between varieties significant at $p = 0.074$.
[2] no results for combined varieties are given because of significant or marginally significant differences between varieties.
[3] difference between varieties significant at $p = 0.008$.

Fungicide treatment reduced the recovery from simulated herbivory in both varieties. For Pennfine, this effect was presumably due only to direct toxic effects of the fungicide since we observed no endophytes in this variety. Total plant mass at harvest, total yield, shoot mass, and shoot yield of Pennfine plants were all significantly lower in heavily clipped plants than in moderately clipped or unclipped plants, regardless of fungicide treatment (Fig. 2). The root mass of heavily clipped Pennfine plants was significantly lower than that of unclipped plants in both fungicided and control groups, but the moderately clipped plants root mass did

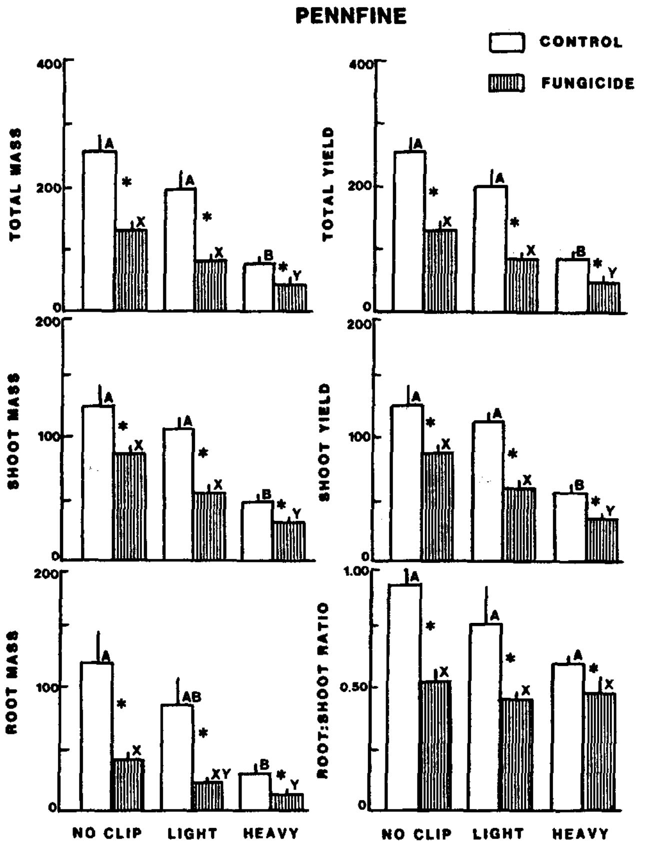

Fig. 2. *Growth of Pennfine plants in relation to fungicide treatment and clipping. Significant differences between fungicided and control plants within a clipping treatment are indicated by an asterisk. Means labelled with the different upper case letters (A,B, for control plants; X,Y for fungicided plants) were significantly different. Standard errors of the means are plotted; all significant differences were at* $p \leq 0.05$.

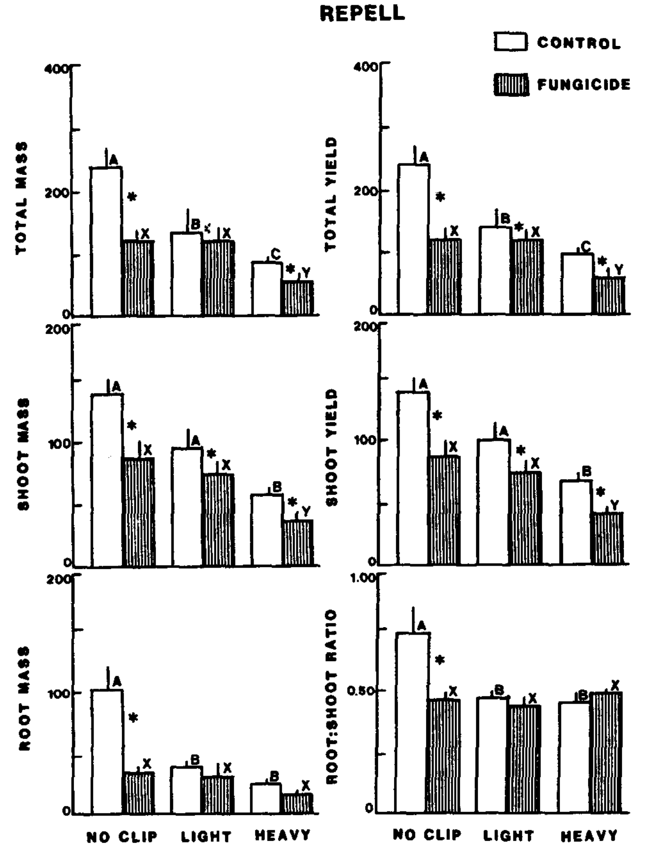

Fig. 3. *Growth of Repell plants in relation to fungicide treatment and clipping. Symbols follow Figure 2.*

not differ significantly from that of the other 2 groups (Fig. 2). The root:shoot ratios of Pennfine plants were lower in fungicided plants than controls, but did not change significantly as a function of simulated herbivory. Simulated herbivory and fungicide treatments did not display a significant interaction for any growth parameters in the Pennfine variety.

In contrast, statistically significant interactions between fungicides and simulated herbivory were frequent in the Repell variety, suggesting that the fungicide had both direct phytotoxic effects and indirect effects mediated through the loss of the endophyte. Total mass at harvest and total yield decreased with increasing clipping intensity in control Repell plants, whereas only the severe clipping affected these parameters in fungicided plants (Fig. 3). Shoot mass and shoot yield also decreased with increasing clipping intensity in both control and fungicided plants, but only the heavily clipped plants were significantly smaller than the unclipped plants (Fig. 3). Both moderate and severe clipping resulted in lower root mass and root:shoot ratio in control plants but not in fungicided plants (Fig. 3). Thus, 2 wk was insufficient for even moderately clipped plants to recover in biomass or yield, and the effects on belowground tissues were greater on the Repell (endophyte-bearing) plants than on the Pennfine (endophyte-free) plants.

Of the 4 fungicide-variety combinations, only the Repell-control combination had fungal endophytes. In that combination, simulated herbivory caused a decrease in relative biomass allocation to roots compared to shoots (Fig. 3). In all 3 endophyte-free treatment combinations, the pattern of biomass allocation (as measured by root:shoot ratio) remained constant over the recovery period no matter what the level of simulated herbivory (Figs. 2 and 3).

Discussion

Some studies of the effect of fungal endophytes on host growth have demonstrated higher growth rates in endophyte-bearing hosts than in endophyte-free plants (Gaynor and Hunt 1983, Clay 1987); in contrast, other studies have found no difference in growth related to the presence of endophytes (Neill 1941, 1952; Siegel et al. 1984). Greater growth in endophyte-bearings hosts has been related to reduced herbivory and to possible production of phytohormones or phytohormone analogues by the fungus (Porter et al. 1985). We have demonstrated that the method used to remove endophytes may induce toxic effects producing differences between endophyte-bearing and endophyte-free plants.

Assessing the cost of the endophyte to the host is a difficult problem because unlike mycorrhizae, which colonize plants after germination, these fungal endophytes are present in the seed even before dispersal. Two methods for removing the endophytes have become available: removal of the endophyte by fungicide application or longterm seed storage and comparative studies of naturally endophyte-bearing and endophyte-free varieties of a species. Our data demonstrate that the fungicide benomyl may be phytotoxic. Benomyl application to a variety of *L. perenne* which lacked endophytes produced a growth decrease of approximately 50% relative to non-fungicided plants, and this growth difference persisted over at least 8 weeks. Others using this method to remove endophytes have resorted to holding the plants for a length period of time after fungiciding before beginning experiments; for example, Latch et al. (1985) held their plants for over 12 months after fungiciding. Though this method seems to help obviate the phytotoxic effects of the benomyl it does constrain studies of the physiology and ecology of endophytes to those with mature, overwintered plants with a perennial life history. At the very least, our results demonstrate that using benomyl to remove endophytes from young grasses has effects beyond the simple removal of the fungus.

One alternative is to store ungerminated seed for a lengthy period of time. As endophyte viability decreases more rapidly than seed viability, longterm storage reduces endophyte infection (Siegel et al. 1985). This process will also reduce seed mass as the seed's carbohydrate reserve is respired. It is clear from a number of studies that seedlings originating from seeds with larger mass are more competitive than those from smaller seeds, at least over the first few weeks of growth (e.g., Black 1958, Stanton 1984). No data are available comparing growth of seedlings rendered free of endophytes by longterm storage with endophyte-bearing seedlings from fresh seed.

A third possibility exists for exploring the costs and benefits of these endophytes: comparative studies of endophyte-bearing and endophyte-free varieties of a given species. We assume this approach has been less popular because it becomes impossible to separate effects due to endophytes from those caused by the genetic differences among cultivated varieties. Clay (1987) reported that aboveground growth of Repell plants was greater than that of plants of Yorktown, another endophyte-free variety of *L. perenne*, though those differences were restricted to aboveground tissues and decreased over time. In contrast, our data suggest that the growth rate and biomass allocation pattern of *Lolium perenne* var Pennfine (a low-endophyte or endophyte-free variety) was indistinguishable from that of the endophyte-bearing var Repell, at least over the initial 8 wk of growth, despite any genetic differences which might exist between cultivars. If such similarities in growth continue throughout the life of the plant, this experimental approach to assessing the effects of endophytes may be superior to the more common ones discussed above.

In the absence of direct enhancement of growth by, for example, phytohormone production (e.g., Porter et al. 1985), an increase in yield and fitness of endophyte-bearing plants will likely result from decreased herbivory. For this to be a longterm advantage to the plant, the losses of carbon and other nutrients to fungal feeding must be small compared to the potential losses to herbivory. In plants which synthesize their own herbivore-inhibiting chemicals, heavily defended plants often produce fewer leaves and are less competitive than plants with lower levels of defensive compounds in the absence of herbivory (Windle and Franz 1979, Coley 1986). When subjected to insect herbivores, however, the growth advantage shifts to the more heavily defended plants. Thus the benefit of synthesizing defensive compounds only outweighs the cost when herbivores are present. Insect herbivores, however, have a tendency to become tolerant or resistent to chemical deterrents, both natural and man-made. Once this occurs with the alkaloids the endophytes produce, the question becomes: what cost will the fungus have to the plant in the absence of any potential benefit?

In 3 of our 4 variety-fungicide treatment combinations, the level of simulated herbivory we applied did not change the relative allocation of photosynthate to root vs shoot; only in endophyte-bearing plants did we observe a decrease in the allocation of biomass to the root system. Though in established grasslands grazing may result in a shift of allocation to leaves and leaf meristems (e.g., Ryle and Powell 1975, Detling et al. 1979), such a change may not be beneficial to a seedling. As seedlings of perennial grasses often allocate a large proportion of their first year carbon gain to developing an effective root system, the combination of a reduction in total plant mass by herbivory and a reduced allocation to roots may decrease the likelihood of that individual successfully overwintering after that first growing season. Whether this endophyte-related change in allocation is due to phytohormone production by the fungus or to utilization of photosynthate before that photosynthate could reach the roots cannot be determined from our experiment. It is clear, however, that the presence of the endophyte does alter the biomass allocation pattern of clipped *Lolium perenne* seedlings and may affect plant fitness even if the total cost in photosynthate to support the fungus is small.

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Control of honey mesquite with herbicides: influence of plant height

P.W. JACOBY, C.H. MEADORS, AND R.J. ANSLEY

Abstract

Stands of honey mesquite *(Prosopis glandulosa* var. *glandulosa)* were treated with aerially applied herbicides at 16 locations in western and northwestern Texas over an 8-year period to determine influence of plant height on herbicide efficacy. Plant height was not found to significantly ($P<0.05$) influence effectiveness of a particular herbicide, but taller plants were found consistently to be more resistant. No basis was found for delaying control of honey mesquite with herbicides until plants reach a particular height.

Key Words: clopyralid, triclopyr, 2,4,5-T, picloram, plant resistance

Honey mesquite *(Prosopis glandulosa* var. *glandulosa)* has maintained essentially the same distribution and density on 22 million ha of Texas rangeland for over 4 decades despite substantial control efforts (Rechenthin et al. 1964). Although mesquite has a proven ability to reproduce in large numbers from seed, such events are mainly episodic, occurring after periods of drought and overgrazing have weakened the competitive ability of native grasses (Fisher et al. 1959, Bovey and Meyer 1981). Reestablishment of mesquite following control by aerial application of herbicides or mechanical top removal may relate more directly to the degree of plant mortality achieved with the treatment than any other factor. Honey mesquite vigorously resprouts from dormant buds at the stem base when apical dominance is broken (Fisher et al. 1946).

The herbicide 2,4,5-T [(2,4,5-trichlorophenoxyl)acetic acid], which was widely used for mesquite control until its production and sale were discontinued in the early 1980's, was highly variable in producing mortality of honey mesquite (Meyer et al. 1972). Much of this variability in control has been attributed to environmental factors; however, growth type and plant height have been suggested as variables which may influence mortality (Fisher et al. 1956, Dahl et al. 1971, Meyer et al. 1972). After considerable observation, Fisher et al. (1956, 1959) concluded that regrowth must reach a height of 1.5 m or more to provide sufficient foliage to intercept and translocate enough herbicide to produce complete plant mortality of honey mesquite. These reports led subsequently to the recommendation in Texas that aerial spraying on mesquite be delayed until plants were at least 1.5 m tall and 4 to 6 years old with dense foliage (Hoffman 1975).

We found little published data to support the concept that honey mesquite can be more effectively reduced or killed as it attains increased age or height. Therefore, our objective in this study was to determine the influence of plant height on degree of mesquite stand mortality in order to test our hypothesis that height of plants has little, if any, influence on degree of mortality following aerial application of herbicides.

Materials and Methods

Herbicides were applied to honey mesquite at 16 locations in western and northwestern Texas from 1797 to 1983. Herbicides included 2,4,5-T, triclopyr {[(3,5,6-trichloro-2-pyridinyl)oxy]acetic acid}, clopyralid (3,6-dichloro-2-pyridinecarboxylic acid) and equal part [acid equivalent (ae)] combinations of each with picloram (4-amino-3,5,6-trichloro-2-pyridinecarboxylic acid). All comparisons for this study were made at the 0.6 kg ha^{-1} rate of application in a total volume of 9 or 18 L ha^{-1} of a diesel oil:water emulsion [1:6 (v:v)]. Treatments were applied by fixed-wing aircraft to two or three 2-4 ha plots in a randomized complete block design. Some herbicide treatments were omitted from specific locations and these missing values were addressed in the analyses.

Evaluations were conducted after 3 growing seasons to allow sufficient time for herbicide activity to be completed and resprouting to occur. Individual plants (200 to 300 per plot) were examined for presence of live stem or leaf tissue and assigned to one of 3 height classes: <1 m = Class I; 1 to 2 m = Class II; and >2 m = Class III.

Data were processed by analysis of variance using percent plant mortality in each height class and plot as a data point. Percentage data were transformed (arcsin $\sqrt{x}$) prior to analysis. Level of significance for mean separation was <0.05 and significantly differing means were separated by Tukey's procedure (Steel and Torrie 1980). Herbicides were compared within and among locations, and mortalities evaluated by height class within and among locations and herbicides. Significant interactions between herbicides, height classes and locations were not found and these sources of variation were incorporated into the general error term for the analyses (Steel and Torrie 1980).

Treatment locations incorporated a broad geographical region typical of rangeland on which honey mesquite poses a major management problem to landowners (Table 1). Although treatments were applied during the recommended 40 to 90 day period following budbreak (Fisher et al. 1959), differences in growth conditions among locations and years of study provide sources of error that are difficult to isolate and partition for statistical analysis without a large number of observations.

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Research was funded in part by: University Lands-Surface Interests, Univ. Texas System, Midland; E. Paul and Helen Buck Waggoner Foundation, Vernon; and Brush Control and Range Improvement Association, Albany. Herbicides were provided by Dow Chemical, USA, and aerial application was furnished by: Hardcastle Ag-Air, Inc., Vernon; Bruton Aerial Spraying, Inc., Garden City, H&W Flying Serv., Midland; and Lynn Culp, Breckenridge. Detailed soil classification and mapping was provided by the Soil Conservation Service, USDA.

This article is published with the approval of the Director, Texas Agricultural Experiment Station as technical article TA-23924.

Manuscript accepted 17 May 1989.

Table 1. Description of experimental locations where aerial applications of herbicides were made to control honey mesquite in western and northwestern Texas. Descriptions include ecological regions in Texas, city nearest to the experimental location, range site, soil classification, and the soil temperature at 30–40 cm depth, air temperature and relative humidity (RH) on the day of treatment, and a general rating of amount of precipitation received from January to the treatment date [normal = (N), above normal = (+), below normal = (-).].

Ecological Region	Location	Treatment Date	Range Site	Soil Classification	Temp Soil	Temp Air	R.H.	Precipitation
					° C	° C	%	
Rolling Plains	Vernon	20 June 1977	clay loam	Typic Paleustolls	30	26–28	79–69	N
	Vernon	6 July 1979	clay loam	Typic Paleustolls	27	23–33	96–62	N
	Vernon	19 June 1981	clay loam	Typic Paleustolls	26	21–26	99–76	+
	Vernon	7 July 1981	clay loam	Typic Paleustolls	27	21–29	94–66	+
	Vernon	25 June 1982	clay loam	Typic Paleustolls	26	19–21	96–86	N
	Vernon	14 July 1982	clay loam	Typic Paleustolls	26	18–27	99–75	N
	Guthrie	7 June 1983	clay loam	Typic Paleustolls	19	10–14	94–84	+
Limestone Prairie	Baird	29 June 1979	clay loam	Typic Paleustolls	27	24–27	74–71	N
	Albany	27 June 1981	clay loam	Typic Paleustolls	27	21–29	74–67	+
Edwards Plateau	Barnhart	27 June 1979	clay loam	Petrocalcic Calciustolls	27	19–22	90–75	N
	Barnhart	26 June 1980	clay loam	Petrocalcic Calciustolls	28	21–30	72–62	-
	Barnhart	15 June 1983	clay loam	Petrocalcic Calciustolls	22	26–29	66–62	-
	Ozona	8 July 1982	clay loam	Petrocalcic Calciustolls	26	23–27	80–76	+
Trans Pecos	Crane	26 May 1977	sandy	Ustalfic Haplargids	28	22–29	84–50	+
South Plains	Post	25 May 1983	deep hardland	Aridic Paleustolls	22	16–22	96–72	-
High Plains	Dumas	7 July 1983	shallow upland	Calciorthidic Paleustols	25	20–33	72–65	-

Results

For most locations, mortality of honey mesquite within a herbicide treatment either remained constant or decreased with increasing plant height (Table 2). Exceptions were found at Albany and Ozona with the combination of 2,4,5-T and picloram, at Dumas with triclopyr, and at Ozona with the combination of clopyralid and picloram. These data, while failing to establish any clear patterns of plant susceptibility by height, illustrate why confusion may exist regarding this relationship. Considering the data for 2,4,5-T alone, there appears to be little basis for suggesting that taller plants are more susceptible than shorter ones.

A more consistent trend was apparent when data were pooled across locations for the individual herbicide treatments (Table 3). Even though mortality of honey mesquite consistently decreased with increasing plant height, rarely were the differences significant. Degree of stand mortality was more consistent for clopyralid or its mixture with picloram than found with the other herbicides. Being more efficacious against honey mesquite than the other herbicides, clopyralid consistently produced high mortality; whereas 2,4,5-T and triclopyr, applied alone or in combination with picloram, produced practically no mortality on occasion. Picloram reduced the variation in mortality achieved by either 2,4,5-T or triclopyr alone by increasing efficacy of those herbicides. However, picloram mixed with clopyralid increased variability over clopyralid alone and was less efficacious against small to medium height plants.

Comparing herbicides across all locations and height classes reiterates the improved efficacy of clopyralid over other herbicides for controlling honey mesquite (Table 3). Relative effectiveness of these herbicides is similar to those reported in other studies (Bovey and Mayeux 1980, Bovey et al. 1981, Jacoby et al. 1981, Jacoby and Meadors 1983).

Table 2. Percentage mortality of honey mesquite at each location according to herbicide and height class. Missing values are designated by dashed lines.

	Herbicides																	
	2,4,5-T			2,4,5-T + picloram			Triclopyr			Triclopyr + picloram			Clopyralid			Clopyralid + picloram		
	(Height Classes)																	
Location and Date	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III
	(%)																	
Vernon 20 June 1977	7	6	1	20	16	6	8	2	5	61	37	37	79	73	73	–	–	–
Vernon 6 July 1979	36	5	27	48	26	16	7	3	2	26	16	9	90	54	41	82	62	53
Vernon 19 June 1981	40	30	23	59	37	21	44	33	21	–	–	–	76	75	60	63	60	56
Vernon 7 July 1981	15	22	25	–	–	–	23	33	33	77	71	67	57	60	38	63	80	64
Vernon 25 June 1982	37	30	26	58	52	45	–	–	–	–	–	–	63	60	49	74	61	40
Vernon 14 July 1972	4	10	7	34	37	34	36	32	26	51	63	55	48	52	48	66	65	44
Guthrie 7 June 1983	10	9	10	24	15	1	24	21	23	20	12	7	–	–	–	38	44	17
Baird 29 June 1979	–	–	–	53	50	43	30	10	22	58	65	57	99	99	70	85	73	64
Albany 27 June 1981	3	1	5	17	27	41	2	8	8	–	–	–	89	71	71	41	50	50
Barnhart 27 June 199	16	4	10	49	45	28	24	19	10	38	22	14	52	77	44	74	70	48
Barnhart 26 June 1980	8	8	8	18	32	8	42	70	36	29	24	7	99	83	37	50	40	45
Barnhart 15 June 1983	59	68	62	36	35	24	35	38	23	27	33	20	86	91	83	82	82	83
Ozona 8 July 1982	10	14	14	49	61	62	–	–	–	–	–	–	62	74	64	73	75	85
Crane 5 May 1977	10	7	4	38	31	24	15	11	7	–	–	–	84	76	61	–	–	–
Post 25 May 1983	19	16	7	20	30	13	30	25	7	29	20	6	–	–	–	58	62	28
Dumas 7July 1983	76	60	54	89	85	90	31	16	87	93	91	85	–	–	–	87	96	91

Table 3. Mean mortality of honey mesquite summarized for all locations by herbicides or equal part mixtures applied at 0.6 kg ha^{-1} and evaluated 3 post-treatment.

Herbicide	Height Class I	Height Class II	Height Class III	Pooled Height $\bar{x}$
	%			(%)
2,4,5-T	25.5 a[1]	24.4 a	21.5 a	23.1 z[2]
2,4,5-T + Picloram	40.4 a	38.3 a	29.9 b	36.2 y
Triclopyr	25.7 a	23.1 a	21.5 a	23.4 z
Triclopyr + Picloram	44.7 a	40.6 a	31.9 b	31.9 y
Clopyralid	76.4 a	74.0 a	58.6 b	69.7 x
Clopyralid + Picloram	67.9 a	66.8 a	56.7 b	63.8 x
Pooled Herbicide ($\bar{x}$)	44.8 a	42.5 a	35.3 b	

[1] Means within a row followed by the same letter (a,b) are not significantly different at the 0.05 level of probability.

[2] Means within a column followed by the same letter (x,y,z) are not significantly different at the 0.05 level of probability.

Pooling mortality data by height class across all locations indicates a stronger difference than shown in previous comparisons (Table 3). Height of honey mesquite plants in this grouping indicates plants become more resistant to herbicides with increasing height, but efficacy was not significantly reduced until plant height exceeded 2 m.

Lack of significant interactions indicates that differences in mortality among herbicides, height classes, or locations were not strongly influenced by one another but rather, each variable responded independently. Therefore, the influence of height would be equally applicable to all herbicides and locations.

Discussion

These data, which are based on observed responses of more than 40 thousand individual honey mesquite plants to aerially applied herbicides, presents a sound basis for rejecting the concept that herbicidal treatments should be delayed until plants reach a particular height. In contrast, these data indicate that honey mesquite may become increasingly resistant to herbicidal control measures as they become taller.

Our data fail to explain why taller plants may be less susceptible to herbicides than shorter plants, leaving the reasons open to speculation. Intuitively, several possibilities can be enumerated. Shorter plants, after absorbing herbicide, have less distance to translocate the material to the basal bud zone. These shorter stems may not absorb or metabolize as much herbicide during translocation as would taller stems. Younger stem tissue, prior to the development of thick bark, may actively absorb herbicide spray and contribute to total herbicide uptake. Taller plants may also develop sufficient foliage to provide a shielding effect on a portion of the canopy, especially on the lower or leeward side of the tree during treatment. Taller plants may be deeper rooted, responding more slowly to soil warming, a factor linked to herbicide susceptibility.

Regardless of the causative factors, implications of this study fail to support the decision for a landowner to delay treatment of honey mesquite with aerially applied herbicides because of plant height. Delaying treatment provides mesquite additional time to grow and become more resistant, to compete with forage plants and reduce production of rangeland, and to interfere with livestock handling.

This study also indicates that risk avoidance can be accomplished by selection of a herbicide which is capable of producing high efficacy with consistency. Current recommendations for retreating mesquite every 5 to 7 years are based on the low efficacy achieved with 2,4,5-T (Whitson and Scifres 1981, Van Tassel and Conner 1986). While this recommendation is still valid for triclopyr, more effective products such as clopyralid create new possibilities through higher degree of stand mortality. It has been noted that forage response associated with mesquite control may be lost 1 to 3 years after treatment unless a high degree of stand mortality is achieved (Dahl et al. 1978, Torell and McDaniel 1986). Achieving high levels of plant mortality would appear to be more advantageous than merely removing top growth, considering current prices for herbicides.

Summary

Height of individual honey mesquite plants was evaluated as influence on the effectiveness of aerially applied herbicides. Plant height was not found to influence the efficacy of any particular herbicide, although taller plants generally showed greater resistance. There does not appear to be any rationale for delaying herbicidal treatment until honey mesquite plants reach a specific height.

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Control of honey mesquite with herbicides: influence of stem number

P.W. JACOBY, R.J. ANSLEY, C.H. MEADORS, AND C.J. CUOMO

Abstract

Following aerial application of herbicides, stands of honey mesquite *(Prosopis glandulosa* var. *glandulosa)* were evaluated to determine the influence of individual plant stem number on herbicide efficacy. A highly significant ($P<0.01$) relationship was found between stem number and plant mortality, with herbicide resistance increasing sharply in plants with greatest numbers of stems. This relationship was consistent among all herbicides and plant heights, which suggests that stem number may be useful in selecting the type of control method employed on specific sites.

Key Words: clopyralid, triclopyr, 2,4,5-T, picloram, brush control, resistance

Honey mesquite *(Prosopis glandulosa* var. *glandulosa)* a dominant shrub on approximately 22 million ha of Texas rangeland, has been targeted for control efforts during the last half century. Aerially applied herbicides have been used extensively to control mesquite because of the ease of application to large areas of rangeland and cost advantages over mechanical alternatives. As with mechanical methods such as chaining, herbicides often kill only the topgrowth, allowing mesquite to resprout as a multi-stemmed plant. The difficulty with controlling multi-stemmed plants in contrast to more naturally occurring few-stemmed plants has been mentioned in other studies (Fisher et al. 1959) but has not received any specific study as a potential factor of plant resistance to herbicidal control.

The objective of this study was to quantify the influence of stem number of individual honey mesquite plants in aerially applied herbicide treatments.

Materials and Methods

Honey mesquite were aerially sprayed with herbicides near Vernon, Texas, in June 1981 and July 1982. Additional sites were treated near Albany in 1981 and near Ozona in 1982. All sites had been subjected to earlier control efforts involving either aerial spraying, chaining, or both. All sites supported mesquite stands containing plants having a range of height and stem number. All sites were characterized as clay loam range sites with Vernon and Albany having Typic Paleustoll soils and Ozona having a Petrocalcic Calciustoll. Topography at all locations was flat to gently rolling.

Herbicides included clopyralid (3,6-dichloro-2-pyridinecarboxylic acid), triclopyr {[(3,5,6-trichloro-2-pyridinyl)oxy]acetic acid}, picloram (4-amino-3,5,6-trichloro-2-pyridinecarboxylic acid), and 2,4,5-T [(2,4,5-trichloro-phenoxy)acetic acid], which were applied by fixed-wing aircraft at 0.6 kg [acid equivalent (ae)] ha^{-1} in 18 L ha^{-1} of a diesel oil and water emulsion [1:6 (v:v)]. At each location, treatments were applied in a randomized complete block design (Steel and Torrie 1980). Each treatment (herbicide) was applied to 2 or 4 individual plots 4 ha in size.

Evaluations were conducted after 3 growing seasons to allow sufficient time for herbicidal action to be completed and resprouting to occur. Within each plot, 200 to 300 individual honey mesquite plants were examined for the presence or absence of live stems or leaves and grouped into one of 3 height classes: < 1m = Class I; 1 to 2m = Class II; and > 2m = Class III. The number of basal support stems were counted for each plant. Stems were considered independent if branching occurred within 15 cm above ground level. Trees were grouped arbitrarily into 3 stem number categories for statistical analysis: 1 to 2 stems = single stemmed; 3 to 5 stems = few-stemmed; and > 6 stems = many-stemmed.

Data were processed by analysis of variance using percent plant mortality for each stem number class by height class and plot within a treatment as a data point. Percentage data were transformed ($\arcsin \sqrt{x}$) prior to analysis. Interactions were evaluated for stem number class × height class, stem number class × herbicide, and height class × herbicide, stem number class × height class × herbicide, and each combination by location; however, no significant ($P<0.05$) interactions were found, including block × treatment interactions. Absence of significant interactions among partitioned sources of variation permitted each source to be examined individually and variation attributed to interactions to be incorporated into the generalized error term. Level of significance for mean separation was $P<0.05$, and significantly different means were separated by Tukey's procedure (Steel and Torrie 1980).

Results

Mesquite mortality varied with the herbicide formulation (Table 1). Over all locations, clopyralid was almost twice as effective as picloram and 3 times as effective as either triclopyr or 2,4,5-T, concurring with previous studies (Bovey and Mayeux 1980, Bovey et al. 1981, Jacoby et al. 1981, Jacoby and Meadors 1983). Plant height did not influence mesquite mortality produced by any specific herbicide or for herbicides as a group, indicating plants of all heights were equally susceptible to a given herbicide.

Mesquite susceptibility to herbicides was strongly influenced by individual tree stem number. Resistance increased proportionally with increasing stem number, averaging 55, 35, and 19% for single-, few-, and many stemmed trees across all herbicides (Table 1). Similar trends were found for each herbicide, despite the difference in efficacy.

Likewise, within each height class by herbicide, resistance increased with increasing stem number, illustrating why interactions among herbicides, height, and stem number were insignificant (Fig. 1).

Although efficacy for any particular herbicide fluctuated among the 6 tests, single-stemmed trees were consistently more susceptible than either few- or many-stemmed mesquite (Table 2). Although

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Research was funded in part by: University Lands—Surface Interests, Univ. Texas System, Midland; E. Paul and Helen Buck Waggoner Foundation, Vernon; and Brush Control and Range Improvement Association, Albany. Herbicides were provided by Dow Chemical, USA, and aerial application was furnished by Hardcastle Ag-Air, Vernon; Lewis Roach Spraying Service, San Angelo; and Lynn Culp Flying Service, Breckenridge. Detailed soil classification and mapping was provided by the Soil Conservation Service, USDA.

This article is published with the approval of the Director, Texas Agricultural Experiment Station as technical article TA-23925.

Manuscript accepted 17 May 1989.

Table 1. Mortality of honey mesquite stands summarized across all locations by herbicide, height, and stem number and across all herbicides for height and stem number.

Herbicide	Mean mortality	Height			Stem number		
		<1m	1-2m	>2m	1–2	3–5	6+
Clopyralid	64 a[1]	64[2]ns.	66	62	85 a[3]	63 b	41 c
Picloram	35 b	33	38	34	53 a	32 ab	20 b
Triclopyr	21 c	17	24	22	37 a	18 b	8 b
2,4,5-T	21 c	20	23	21	38 a	18 b	6 b
All herbicides ($\bar{x}$)	35	34 a	39 a	36 a	55 a	35 b	19 c

[1] Means within the vertical column followed by the same letter are not significantly different at the 0.05 level of probability.
[2] No significant differences were found among means for height classes within a herbicide treatment.
[3] Means within row followed by the same letter are not significantly different at the 0.05 level of probability.

Table 2. Mean mortality o honey mesquite within arbitrary groups based on number of basal support stems after 3 growing seasons following treatment with foliar applied herbicides on western Texas rangeland.

		Herbicide											
		2,4,5-T			Triclopyr			Picloram			Clopyralid		
		(Stem No. Class)											
Location	Date	1–2	3–5	6+	1–2	3–5	6+	1–2	3–5	6+	1–2	3–5	6+
		(%)											
Vernon	6/81	71a[1]	28b	10b	80a	26b	6c	—	—	—	100a	76b	61c
Vernon	7/81	53a	33b	14c	18a	25a	13a	65a	49ab	36b	90a	71b	46c
Vernon	6/82	61a	30b	11c	—	—	—	—	—	—	83a	50b	38b
Vernon	7/82	16a	11ab	3b	37a	18b	7c	41a	15b	4b	73a	58b	22c
Albany	6/81	8a	4a	0a	12a	4a	6a	—	—	—	81a	66b	40c
Ozona	7/82	21a	5b	0b	—	—	—	—	—	—	81a	59b	41c

[1] Means followed by the same letter within a row for a specific herbicide are not significantly different at the 0.5 level of significance according to Duncan's new multiple range test.

this study focused on comparisons among particular herbicides, similar trends in the stem number influence on resistance occurred for equal part mixtures of herbicides (data not shown).

Discussion

While a significant relationship between the stem number and herbicide efficacy was found, precise reasons for this effect were not identified. Other researchers have suggested the presence of independent vascular systems from the basal stem area which serve each stem could promote herbicide resistance (Sosebee et al. 1973). Multi-stemmed plants, by the nature of their growth form, may produce a greater canopy area which could impede herbicide penetration of coverage and also shade the soil more than a single-stemmed tree. Soil temperature has been related to herbicide susceptibility of honey mesquite (Dahl et al. 1971).

Numbers of stems arising from a resprouting stem base may be reflective of the physiological vigor of the plant or the amount of carbohydrate reserves. More importantly, stem numbers may influence carbohydrate source/sink relationships which are directly related to translocation of foliar applied herbicides. If stem carbohydrates are sufficient to provide for initial canopy development, a multi-stem tree might have less demand on root carbohydrates and create a weaker sink than a single-stemmed tree.

Self-pruning by trees as they advance in age suggests that competition for light, nutrients, and water might play a role in herbicide resistance. Under stress, stems might react differently when treated with a herbicide, allowing some tissue to survive.

Any one or all of these possibilities could contribute to differential survival of honey mesquite and each presents research opportunities for understanding plant resistance to herbicides.

Management Implications

From a management perspective, our findings should allow a landowner to anticipate lower degrees of control on many-stemmed growth forms of honey mesquite compared to stands supporting mainly single- to few-stemmed plants. Many-stemmed stands, being highly resistant to foliarly absorbed herbicides, could be treated with another form of brush control such as prescribed fire or rootplowing. If aerial spraying is desired, use of a highly effective herbicide such a clopyralid would offer a higher potential for control of honey mesquite. As more information is collected regarding the causative factors for herbicide resistance by woody plants such as honey mesquite, landowners will be able to better plant and conduct their brush control operations.

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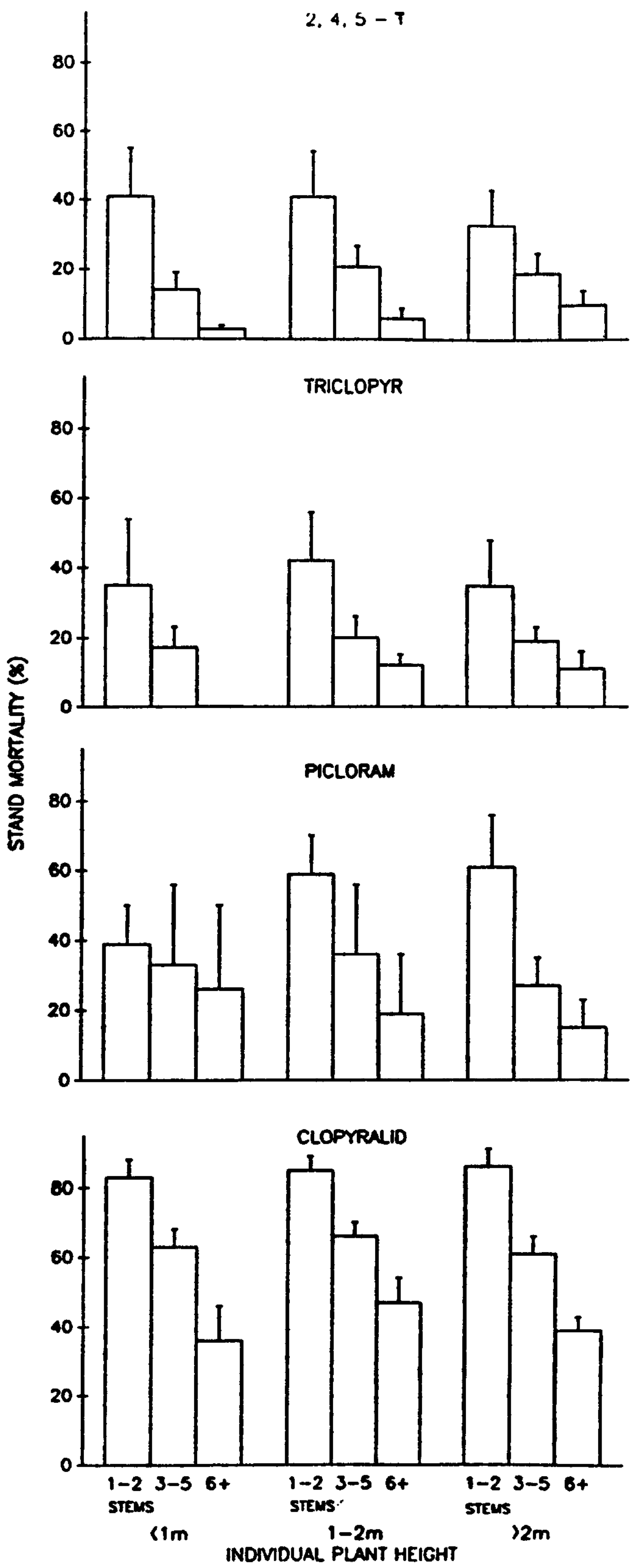

Fig. 1. Mortality of honey mesquite stands following aerial application with 2,4,5-T, triclopyr picloram or clopyralid at 0.6 kg/ha^{-1} in western Texas as influenced by number of stems per plant within 3 height classes. Vertical lines on bars represent the s.e. of $\bar{x}$.

Effects of manual application method on application time, thoroughness, and tebuthiuron outlays

NICHOLAS S. VAN PELT AND NEIL E. WEST

Abstract

Small-plot trials of effective herbicides for manual woody-weed treatments should be validated on large tracts where rapidity, thoroughness, and efficiency of application are integral to operational-scale recommendations. A 7.9 hectare woodland chaining in Utah, with 248 *Juniperus osteosperma* Torr. (Little) and *Pinus monophylla* Torr. & Frem. saplings per ha, was divided into nine 25-m by 350-m strips for timed tebuthiuron (*N*-[5-(1,1-dimethylethyl)-1,3,4-thiadiazol-2-yl]-*N*,*N*'-dimethylurea) manual application trials in fall 1986 and summer 1987. About 1 ha was treated per hour, and 6 to 15% of the trees were missed. Three application methods differed in total and aggregate time outlays, accuracy, and tediousness, but were highly similar in formulated tebuthiuron expenditures of 1.5 to 2.0 kg/ha (0.21 to 0.28 kg/ha tebuthiuron a.i.). Time expenditures were moderately predictable ($r^2 = 0.62$) from treated tree density and mean tree height, whereas percent trees missed was unrelated to density or method. Placing herbicide particles at the stem base and basing dosages on stem height are preferable to dripline applications and crown-volume based dosage estimations.

Key Words: *Juniperus osteosperma*, *Pinus monophylla*, range improvement planning, brush removal, woody weed control

Large areas of western U.S. rangeland support woody vegetation that hinders forage production or livestock management. Thousands of hectares have been manually treated with individual-plant herbicide methods (Johnsen and Dalen 1984). Research on herbicide formulations, dosage rates, and manual placement is usually conducted on small plots, resulting in substantial time devoted to each target plant relative to its size. Treatments on larger, more heterogeneous areas minimize time spent in travel and at each target plant. Plot-based recommendations to brushland managers need validation on large areas, where rapidity, thoroughness, and efficiency of treatments are crucial to treatment and enterprise success. Mediocre control or ambiguous outcomes are often due to application shortfalls, rather than to ineffective herbicide formulations (Johnsen and Dalen 1984, Ueckert and Whisenant 1982). Thoroughness is closely tied to the need for repeated attention ('reweeding') and reinvestment.

Previous studies have used hired labor. Fitness, training, motivation, and supervision must affect outlays, thoroughness, efficiency, and consistency, but these factors are rarely controlled experimentally. In extreme cases, shirking means that practically no control results from some of the man-hours nominally invested (Johnsen and Dalen 1984). When ranchers or others with an economic stake in the results have treated brush or trees on foot or horseback, outcomes are more favorable and less ambiguous (Evans and Young 1986).

Our study objectives were: (1) to develop preliminary estimates of the labor time and herbicide quantities required to treat a representative tract of tree-dotted Intermountain rangeland; (2) to test time and quantity differences among 3 effective application methods; and (3) to assess thoroughness of first-time treatments, as percent trees left untreated. The research goal was to improve tactical planning for tree reduction and forage rejuvenation (Scifres 1987).

Study Area and Methods

A 7.9 ha (19.4 ac) rectangular plot was established on a west-facing bajada of the East Tintic Mountains, 58 km (32 mi) SW of Provo, Utah. The privately owned site, known as the Jordan macroplot, lies on a gentle, almost planar slope at about 1,858 m (6,100 ft) elevation. The soil is Borvant gravelly loam, classified as a fine-loamy, mixed, mesic shallow Aridic Calcic Palexeroll. The mountain front was double-chained in 1964, but tree control was poor. Major plant species present were *Juniperus osteosperma* (Torr.) Little (Utah juniper), *Pinus monophylla* Torr. & Frem. (singleleaf pinyon), *Artemisia tridentata* spp. *tridentata* Nutt. (basin big sagebrush), *Purshia tridentata* (Pursh) DC. (antelope bitterbrush), and *Tetradymia canescens* DC. (spiny horsebrush) (Welsh et al. 1987).

Nine 25-m by 350-m strips, similar to those used in aerial applications, were demarcated, running downhill. Strips were temporarily outlined with mason's line and removable posts. All trees were then tallied by species. The height in decimeters (dm) of every other tree was measured. Tree stem aggregation for the whole plot was quantified using the Pielou index (Goodall and West 1979), based on a stratified-random sample of 210 tree coordinates. Tree, understory vegetation, and soil surface cover were estimated from fifty 40-m line intercepts randomly established and oriented throughout the macroplot (Canfield 1941).

Equally effective treatment methods (rate and placement choices) were derived from results of nearby tebuthiuron (*N*-[5-(1,1-dimethylethyl)-1,3,4-thiadiazol-2-yl]-*N*,*N*'-dimethylurea) research (Van Pelt and West 1989). Method 1 consisted of applying one Graslan^{TM} Brush Bullet (1.8 g clay briquettes; .25 g tebuthiuron a.i.) per 3 dm (1 ft) of total tree height to the stem base. In Method 2, one briquette per 3 dm height was also used, but briquettes were placed at equal intervals at the crown margin or "dripline". Method 3 used the same placement as Method 2, but with one briquette per 100 dm^3 estimated crown volume. Each method was randomly assigned to 3 strips. Timed tebuthiuron application trials were conducted on 10 and 11 Oct. 1986, and repeated on 29 and 30 July 1987. Ambient temperatures were 0 to 2° C (32 to 36° F) in 1986, and 25 to 32° C (78 t 89° F) in 1987. The applicator traversed the length of a strip top to bottom, using one of the methods for all trees encountered therein. Briquettes were dispensed from a tree-planter's belt bag containing 2.0 kg (4.4 lb) of Graslan (1986) or a placebo (1987). Each strip was only treated once with tebuthiuron, and no strip was given a particular minimum, ideal, or maximum total dosage. The applicator maintained a brisk pace, with primarily diagonal and lateral movement between single trees or clumps. Some backtracking occurred, but no "hunting" of trees within or

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Manuscript accepted 9 May 1989.

just off the strip was permitted. All treated trees were marked with spray paint. Time elapsed was recorded after the applicator had traveled midway into the strip and after completion of the strip. After all strips had been treated, missed trees (unmarked) were tallied on both occasions by species and size (seedling or sapling) while the applicator slowly walked uphill through each strip. Thoroughness was expressed as percent of trees missed by method and strip or half-strip.

After the number of treated trees per sector was determined, times elapsed were calculated and expressed as total time for all sectors and strips allocated to each method, and as average time per area by method. An identical procedure was followed for herbicide outlays in 1986. Supplemental data were obtained on time spent treating and traveling between individual trees with Methods 1 and 2 (n=100).

To assess differences between prescribed and actual dosages applied to trees treated with Method 3, 35 trees of all sizes were relocated and the briquettes beneath them were counted. Crown volume of each tree was estimated from crown height and the average of 2 perpendicular crown width measurements (Tausch 1980). The median amount that should have been applied (one briquette per 100 dm^3) to each tree was compared with the actual median amount using the two-sample rank sum test at p = 0.05 (Steel and Torrie 1980). Either or both the 1986 and 1987 treatment occasions and all macroplot strips were used in 5 linear and nonlinear multiple regressions of time spent against tree density and estimated mean tree height (SAS Institute, Inc. 1982).

Results

The 9 strips allocated to herbicide treatments contained a total of 1,960 trees (1,307 juniper, 653 pinyon), with from 161 to 280 trees per 25- by 350-m strip. The macroplot supported 165.4 juniper per ha (67.4/ac) and 82.7 pinyon per ha (33.6/ac), for an overall density of 248.1 trees/ha (101.0/ac). Live tree cover was estimated as 3.3% (Table 1). Trees allocated to Method 1 (stem base/scaled to height) had a mean height of 18.7 dm (CV = 38.4%; n = 315), trees allocated to Method 2 (dripline/scaled to height) averaged 17.5 dm (CV = 41.5%; n = 304); whereas trees for Method 3 (dripline/scaled to crown volume) had a mean height of 17.9 dm (CV = 44.7%, N = 298). These means were not significantly different ($p>0.05$). The height distributions of the populations for each method were similar (Fig. 1). The macroplot dispersion index (1.01) for the species combined was not significantly ($p>0.05$) different from random.

Table 1. Cover estimates obtained from 50 40-meter line intercepts within the entire macroplot.

Estimated cover parameter	Mean (1 SE)
	(%)
Bare ground	25.6 (1.3)
Plant litter	22.2 (1.3)
Grass crowns	12.5 (1.1)
Big sagebrush	13.0 (0.8)
Bitterbrush	16.7 (1.4)
Spiny horsebrush	0.4 (0.1)
Live Utah juniper	2.1 (0.4)
Live singleleaf pinyon	1.2 (0.3)
Other plant species	1.9 (0.3)
Tree debris	3.9 (0.5)

The cover of big sagebrush and antelope bitterbrush plants was uniform (Table 1). Maximum heights of these shrubs were about 1.2 m (x = 0.7 m) and 1.1 m (x = 0.8), respectively. These and other understory species and debris made foot travel somewhat indirect.

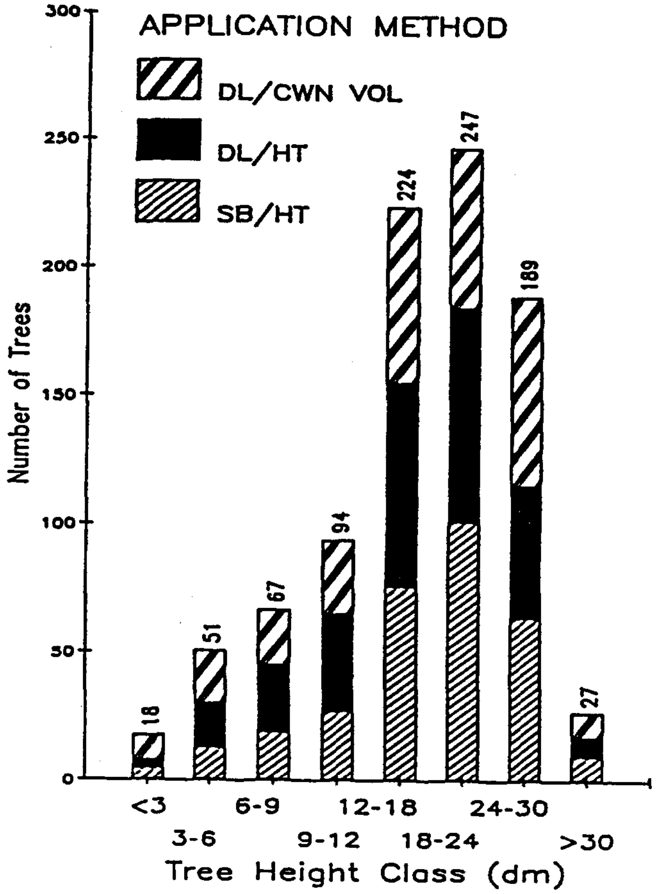

Fig. 1. The estimated height structure of the sapling stand in the Jordan macroplot, showing the contributions of trees assigned to each of the 3 application methods (DL = dripline; HT = height; SB = stem base). Top of bars, Method 3; middle, Method 2; bottom, Method 1.

The times required to work through 9 strips were 8 hours, 7 min in Oct. 1986 and 8 hours, 49 min in July 1987. Numbers of trees treated and times spent per strip and sector were variable (Table 2). The number of trees treated differed little among methods, and the differences within a method between the 2 occasions were slight (Table 3). Differences between methods in time expenditures were small and mostly not significant ($p>0.05$). Similar amounts of herbicide were used in all methods, but appeared to be slightly greater for the methods 2 and 3, which utilized the dripline placement (Table 3). In all methods, from 0.21 to 0.28 kg/ha (0.18 to 0.25 lb/ac) of active ingredient was expended, corresponding to 1.5 to 2.0 kg/ha (1.3 to 1.8 lb/ac) of formulated tebuthiuron. The trees missed were usually seedlings and small saplings with crowns that did not extend above shrubs (Table 2). Those and larger trees missed were mostly at the sides of the strips. No species bias was evident. The methods were indistinguishable in thoroughness, and percent missed was unrelated to density (Table 2).

In the supplemental individual-tree applications, Method 2 was slightly but not significantly ($p>0.05$) more time-consuming than Method 1 (8.2 sec vs. 7.1 sec; CV = 38.7 and 44.0%, respectively). This difference was very similar to that revealed by the main timed trials (Table 3). Using Method 1, about 54% of the applicator's time was spent in treating and painting the trees, whereas about 46% was consumed in inter-tree travel.

Relocating briquettes beneath trees treated with Method 3 showed that applicator-in-motion estimates of tree volume resulted in severe underestimates of the briquettes to apply, particularly for

Table 2. Trees treated and missed, the incidence of missed trees, and time expenditures by application method and strip sector. October 1986 occasion. Means and times rounded to the nearest integer. One SE in parentheses.

Sector and strip	Trees treated	Number missed	Percent missed	Total time used (min)
Method 1				
Strip A				
upper	102	12	10.5	27
lower	65	9	12.1	12
Strip C				
upper	96	6	5.8	23
lower	73	8	9.9	21
Strip G				
upper	118	16	11.9	31
lower	114	20	14.9	24
Total, all sectors	568	71	——	138
Mean, all sectors	95 (8.8)	12(2.2)	11.1(1.2)	23(2.6)
Method 2				
Strip D				
upper	61	7	10.3	21
lower	83	10	10.7	21
Strip F				
upper	75	9	10.7	22
lower	132	15	10.1	29
Strip H				
upper	124	14	10.1	35
lower	119	14	10.3	38
Total, all sectors	594	69	——	166
Mean, all sectors	99(12.1)	11(1.3)	10.4(0.1)	28(3.0)
Method 3				
Strip B				
upper	73	9	10.9	28
lower	69	13	15.8	238
Strip E				
upper	76	9	10.5	20
lower	111	18	13.9	25
Strip I				
upper	125	11	8.0	39
lower	131	13	9.0	48
Total, all sectors	585	73	—	183
Mean, all sectors	98(11.5)	12(1.4)	11.0(1.2)	30(4.4)
Grand total	1747	213	——	487
Grand mean	97(5.9)	12(0.9)	10.9(0.5)	27(2.0)

Table 3. A comparison of time and tebutiuron (a.i.) expenditures among methods and occasions.

Comparison and occasion	Application Method		
	Method 1	Method 2	Method 3
Total time, min			
Oct. 1986	138	166	183
July 1987	156	167	206
Mean time/ha, min			
Oct. 1986	51.8a	61.8ab	69.2b
July 1987	59.3a	61.8b	79.0c
Mean time,tree, sec			
Oct. 1986	14.6a	16.8ab	18.8b
July 1987	16.4a	16.8b	21.2c
Total A.I. Expended, 1986			
KG	0.6a	0.7a	0.7a
Lb	1.4a	1.5a	1.5a

[1] Means in a row having the same letter are not significantly different ($p > 0.05$).

larger trees. The amounts put out in Method 3 were not significantly different ($p > 0.05$) from the amount prescribed by height (Methods 1 and 2). These results agree with the finding of no differences in herbicide quantities (Table 3) among methods despite contrasting tree-dimension "cues".

The correlation between treated-tree density and time spent was significant ($r = 0.56$ to 0.62; $p < 0.05$; n = 18 to 36). A log e transformation of tree density did not improve the equations' predictive value, nor did mean tree height. The resultant multiple regression equations tended to overpredict time outlays in sparse sectors, and both over- and underpredicted times for the most dense sectors. Mean time per tree appeared to decrease with increasing density because less travel time was needed between application motions.

Discussion and Conclusions

The study site was not easy to traverse, and contained many tall saplings. Nonetheless, all strips were readily treated, about 10% of the trees were consistently missed, and overall cool and warm season time outlays only differed by 9%. About 1 hectare could be treated per hour. Tebuthiuron outlays were conservative for all 3 methods and did not vary significantly among them (Table 3). The amounts would have been smaller had the stand not been dominated by trees 1.5–2.7 dm (5 to 9 ft) tall. Most Intermountain and southwestern chainings are occupied by shorter trees (Dalen and Snyder 1987).

Excluding marker setup time, the macroplot could have been treated by 1 person in an arduous day, or by 2 persons in about 5 hours. An equivalent tract with few or no shrubs would have required an hour or 2 less, as would a project that only utilized the least tedious method (stem base/scale to height, Method 1). An adult applicator on foot or horseback can comfortably carry 10 kg (22 lb) of herbicide, enough to last until a lunch break or to the end of the workday in stands this dense. Walking briskly with a 10 kg load requires about 3.5 kcal of output, less than the level (5.0 kcal) necessitating rest periods (Oglesby et al. 1989:247-248).

Applicators should be afforded a simple, effective method and encouraged to work rapidly through strips, not searching for every tree. Even carrying 10 to 15 kg of herbicide, fit persons will not exceed 35% of their maximum aerobic power, and they can maintain that pace for several hours without discomfort (Levine et al. 1982). Because thorough applications are more mentally than physically taxing, psychologically encouraging conditions should be selected: well-demarcated areas for each crew member, minimal obstacles (including debris windrows), clear sight lines, and cool and/or cloudy weather. Spot-painting trees adds to a sense of accomplishment. It also enables followup work, which a supervisor could do (Herbel et al. 1958). Followup is optional, depending on the miss rate, the character of the untreated trees, and the desired future stand condition. Total control (no initial misses, or thorough followup) is rarely economicaly justifiable (Scifres 1987).

Time outlays, thus labor costs, are not tightly predictable from an exact knowledge of tree density and mean tree height. More terrain and stand variables would be needed in a valid multivariate predictor, but the cost of isolating and measuring them may be worthwhile only in research contexts (e.g., Hazard and Pickford 1984). Approximate coefficients for undergrowth and slope may suffice in adjusting cost estimates to a project setting.

Future rangeland researchers could work with labor specialists to devise ways of training and motivating hired seasonal, semiskilled, and/or youthful workers. Productivity and worker commitment must be sustained over periods long enough to achieve real gains in brush reduction. Long-term fatigue and boredom are poorly understood aspects of worker satisfaction, safety, and productivity (Oglesby et al. 1989), which we did not address in this study.

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Statement of Ownership, Management, and Circulation

(Act. of August 12, 1970, Sec. 3685, Title 39, United States Code)

1. *Title of Publication:* Journal of Range Management
2. *Date of Filing:* September 29, 1989
3. *Frequency of Issue:* Bimonthly
4. *Location of Office of Publication:* 1839 York Street., Denver, Colo. 80206
5. *Location of General Business Office:* Same
6. *Name and Address of:*

Publisher: Society for Range Management, 1839 York Street, Denver, Colo. 80206

Editor: Patricia G. Smith, 1839 York Street, Denver, Colo. 80206

Managing Editor: Peter V. Jackson III, 1839 York Street, Denver, Colo. 80206

7. *Owner:* Society for Range Management, 1839 York Street, Denver, Colo. 80206
8. *Known Bondholders, Mortgagees, etc.:* Wyatt Company, 1850 M St. NW, #700, Washington, DC 20036
9. *For Completion by Nonprofit Organizations Authorized to Mail at Special Rates:* The purpose, function, and nonprofit status of this organization and the exempt status for Federal income tax purposes have not changed during preceding 12 months.
10. *Extent and Nature of Circulation*

	Avg. for 12 months	Actual for issue nearest filing date
A. *Total copies printed*	5,613	5,334
B. *Paid Circulation*		
1. Dealers, counter sales	0	0
2. Mail subscriptions	5,027	5,124
C. *Total paid circulation*	5,027	5,124
D. *Free distribution*	6	6
E. *Total distribution*	5,033	5,130
F. *Copies not distributed*	580	204
G. *Total*	5,613	5,334

I certify that the statements made by me above are correct and complete.—*Peter V. Jackson,* Managing Editor.

Creosotebush control and forage production in the Chihuahuan and Sonoran Deserts

HOWARD L. MORTON, FERNANDO A. IBARRA-F, MARTHA H. MARTIN-R, AND JERRY R. COX

Abstract

Creosotebush (*Larrea tridentata* [Sesse & Moc. ex DC.] Cov) and other shrubs have spread into semidesert grasslands of the southwestern United States and northern Mexico; and as creosotebush increases, perennial grasses decrease. This study evaluated 3 rates of tebuthiuron and 4 mechanical treatments in 1981 and 1982 for creosotebush control at 4 locations, 3 in Chihuahua, Mexico, and 1 in Arizona, U.S.A., and compared forage production after treatment with untreated checks. Creosotebush mortalities averaged across locations and years were 75, 87, 93, 3, 33, 68, and 68% for the 0.5, 1.0, and 1.5 kg ai/ha tebuthiuron (*N*-(5-(1,1-dimethylethyl)-1,3,4-thiadiazol-2-yl]-*N,N'*-dimethylurea), land imprinting, 2-way railing, disk plowing, and disk plowing with contour furrowing treatments, respectively. Forage production averaged across locations and years was 529, 524, 606, 303, 344, 290, 330, and 302 kg/ha for the 0.5, 1.0, and 1.5 kg ai/ha tebuthiuron, land imprinting, 2-way railing, disk plowing, disk plowing with furrowing, and untreated check treatments, respectively. Precipitation was below long-term means at all Chihuahuan locations in 1983, and forage production was significantly greater on most treated plots where brush was controlled than on untreated checks. At the Arizona location precipitation was above the long-term mean in 1983 and all plots treated in 1981, except the disk plowing and disk plowing with furrowing which destroyed perennial grasses, produced significantly more grass forage than the untreated checks. Precipitation was above the long-term means at all locations in 1984 and about half of the plots treated with tebuthiuron produced significantly more forage than the untreated checks but not any mechanically treated plots. When treatments reduced shrub density and remnants of native forage grasses were present, forage production increased in both wet and dry years.

Key Words: tebuthiuron, railing, disking, land imprinting, tarbush, whitethorn acacia, mesquite, *Larrea tridentata*

Creosotebush (*Larrea tridentata* [Sesse & Moc. ex DC.] Cov) and associated desert shrub species dominate approximately 19 million ha in the United States (Platt 1959) and approximately 45 million ha in northern Mexico (Leopold 1950). Studies by Buffington and Herbel (1965) indicate that creosotebush continues to spread onto desert grasslands. It is important to control creosotebush and other shrubs because as they increase in density, perennial grass production decreases (Anderson et al. 1957).

Proper grazing management has no effect on creosotebush density and no biological control methods are available. Tebuthiuron has been the most effective selective broadcast treatment for creosotebush control on rangelands in the Southwestern United States (Bovey and Meyer 1978, Scifres et al. 1979, Herbel et al. 1985). Jacoby et al. (1982) reported that 0.5 and 1.0 kg/ha of tebuthiuron reduced the density of creosotebush near Ft. Stockton, Texas, by 86 and 99%, respectively, and grass production 32 months after treatment was 257 kg/ha on an untreated area and 702 and 1,039 kg/ha on plots treated at 0.5, and 1.0 kg/ha, respectively.

Root plowing and disking are among the oldest methods for controlling woody vegetation. However, these operations destroy existing herbaceous vegetation and should be limited to areas where plant removal will be followed by reseeding. Effective mechanical treatments cut off the shrub below the crown. Chaining, railing, roller chopping, land imprinting, and rotary mower reduce cover but do not kill shrubs which sprout from roots and crowns. Thus, native grass growth is enhanced for only 2 to 5 years (Scifres 1980). Previous studies have evaluated either chemical or mechanical methods for their effectiveness in controlling creosotebush and effects on forage production but have not directly compared both chemical and mechanical methods. This study was conducted to evaluate 3 chemical and 4 mechanical treatments for control of creosotebush and other woody species, and compare native grass production on treated and untreated areas at 4 sites in southwestern United States and northern Mexico.

Materials and Methods

The study was conducted at Rancho La Reforma, 60 km east of Hidalgo del Parral, Chihuahua; Rancho Los Pozos, 30 km northeast of Villa de Aldama, Chihuahua; and Rancho El Toro, 100 km east of Villa Ahumada, Chihuahua, all within the Chihuahuan Desert; and the Santa Rita Experimental Range (SRER), 40 km south of Tucson, Arizona, in the Sonoran Desert. Elevation was 1,500 m at La Reforma; about 1,400 m at Los Pozos and El Toro; and 970 m at SRER. Long-term mean annual precipitation at La Reforma, Los Pozos, El Toro, and SRER is 430, 224, 227, and 320 mm, respectively, and occurs primarily from June through September at the Chihuahuan locations, but is bimodal at SRER, with about 60% occurring June through October (Fig. 1) (COTECOCA 1978, Green and Martin 1967). Slope inclination varies from 2 to 16% at La Reforma, and from 0 to 5% at the other 3 sites. Surface soil textures at the 4 sites are sandy loams underlain by a caliche hardpan that ranges from 5 to 100 cm below the soil surface. Physical and chemical properties of the soils are shown in Table 1.

Creosotebush was the dominant shrub species at all locations except La Reforma, where it shared codominance with whitethorn acacia (*Acacia constricta* Benth.), tarbush (*Flourencia cernua* DC.), and shrubby senna (*Cassia wislenizeni* Gray). Mariola (*Parthenium incanum* H.B.K.) and whitethorn acacia were abundant at Los Pozos; javelina brush (*Condalia ericoides* [A. Gray] M.C. Johnston) and honey mesquite (*Prosopis glandulosa* Torr.) at El Toro; and velvet mesquite (*Prosopis velutina* Woot.) and desert zinnia (*Zinnia pumila* Gray) at SRER. The most prevalent

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Appreciation is extended to Elanco Products Company for the herbicide and fencing materials at the Mexican sites; Consejo Nacional de Ciencia y Tecnologia (Mexico) for financial support; Drs. Luis Carlos Fierro, Thomas N. Johnsen, Jr., and Jimmie T. LaBaume for technical assistance; Chris Cochran for assistance in soil classification; personnel of Rancho Experimental La Campana, Chihuahua and Aridland Watershed Management Research Unit, Tucson, for assistance in setting up plots, applying treatments, and collecting data; Eloy Morales, Sergio Mendoza, and Gilberto Valdez for permission to use their land and housing facilities; and the Rocky Mountain Forest and Range Experiment Station for permission to use land on the Santa Rita Experimental Range.

Manuscript accepted 24 April 1989.

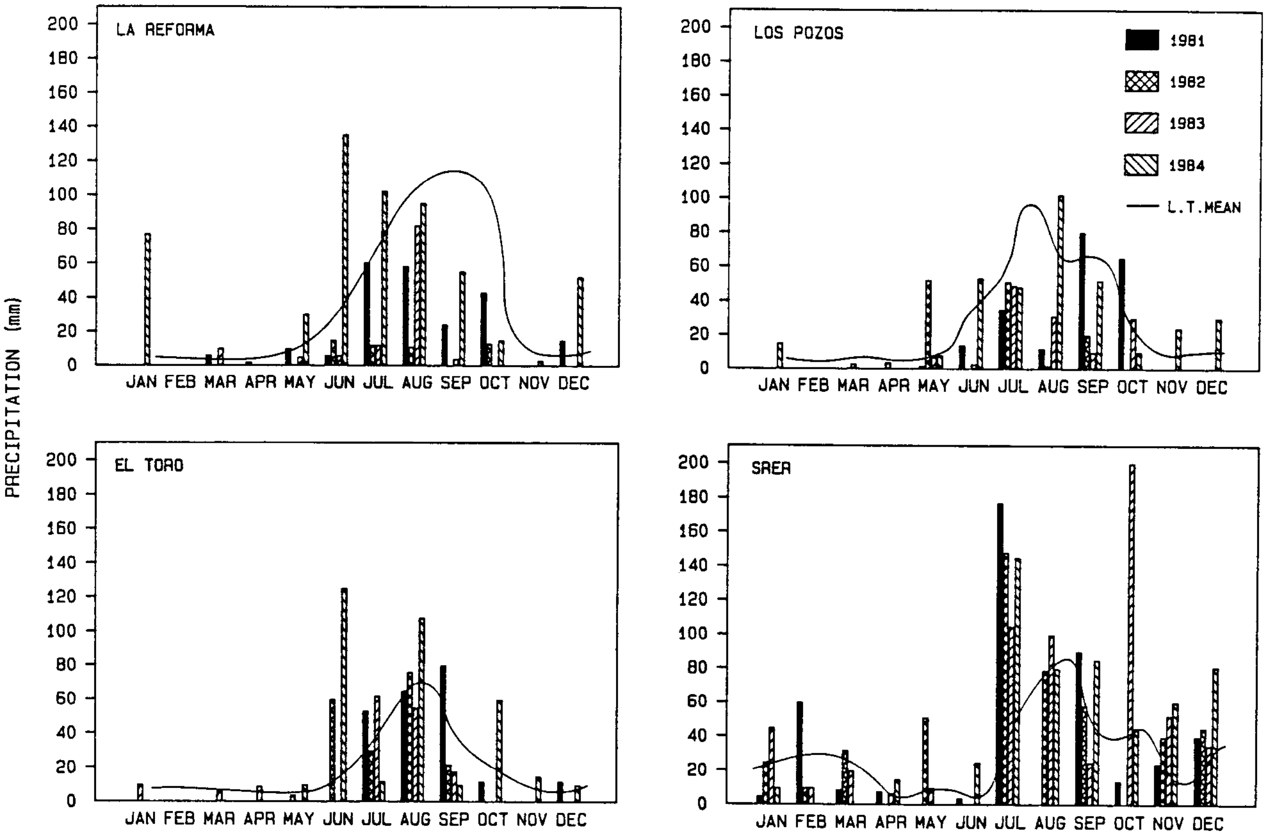

Fig. 1. Monthly precipitation (mm) from 1981 to 1984 and long-term mean (L.T. mean) at Ranchos La Reforma, Los Pozos, and El Toro, Chihuahua, Mexico; and Santa Rita Experimental Range (SRER), Arizona, U.S.A.

native grasses at the 4 locations were fluffgrass (*Erioneuron pulchellum* [H.B.K.] Tateoka) at all locations; black grama (*Bouteloua eriopoda* Torr.) at La Reforma and El Toro; spike pappusgrass (*Enneapogon desvauxii* Beauv.) at La Reforma and Los Pozos; threeawns (*Aristida* spp.) at Los Pozos and SRER; and bushmuhly (*Muhlenbergia poterii* Scribn.) at Los Pozos, El Toro, and SRER.

Study sites (about 30 ha) were fenced to exclude livestock in summer 1981 and divided in half with treatments placed on one side in 1981 and on the other in 1982. Each part was further divided into 24 plots, each 50 by 100m. The experimental design was a randomized block with 3 replications. The following 8 treatments were applied: broadcast applications of 20% pellets of tebuthiuron at (1) 0.5, (2) 1.0, and (3) 1.5 kg ai/ha, (4) land imprinting, (5) 2-way railing, (6) disk plowing, (7) disk plowing with contour furrowing, and (8) untreated check. Tebuthiuron pellets were distributed by hand and the plot was covered 4 times: twice lengthwise on 10 swaths spaced 5 m apart and twice crosswise on 20 swaths, spaced 5 m apart. The clay pellets were 3.2 mm in diameter and approximately 4.8 mm in length.

Mechanical treatments were applied between 15 June and 17 July 1981, and between 26 May and 27 June 1982. Land imprinter

Table 1. Physical and chemical properties of the upper 20 cm of soils at Ranchos La Reforma, Los Pozos, and El Toro in Chihuahua, Mexico and at Santa Rita Experimental Range (SRER) in Arizona, U.S.A.

Location	Percent soil particles					Organic Matter	ph	Electrical Conductivity	Series	Classification[1]
	>2 mm	<2 mm	Sand	Silt	Clay					
	(%)							(ds/m)		
La Reforma	45	55	59	26	15	3.6	6.9	2.9	Kimbrough	loamy, mixed, thermic shallow, Petrocalcic, Calciustoll
Los Pozos	29	71	60	29	11	1.5	7.2	1.3	Jerag	loamy, mixed, thermic shallow, Petrocalcic Ustollic Paleargid
El Toro	23	77	66	24	10	1.1	7.9	1.1	Algerita	loamy, mixed, thermic, coarse, Ustollic Typic Calciorthid
SRER	17	83	58	28	11	0.7	7.9	1.1	Anthony	loamy, thermic, Typic Torrifluvent

[1] Soil classification is from Soil Survey Staff (1975).

Table 2. Percent mortality with 95% confidence intervals (CI) for creosotebush and major associated woody species after 3 tebuthiuron and 4 mechanical treatments applied in 1981 and 1982 at 4 locations in the Chihuahuan and Sonoran Deserts.[1]

Brush species	Treatment year	Tebuthiuron kg ai/ha 0.5	Tebuthiuron kg ai/ha 1.0	Tebuthiuron kg ai/ha 1.5	Land imprinting	Two-way railing	Disk plowing	Disk plowing with furrowing	Untreated check
		(% mortality ± 95% CI)[2]							
		(Rancho La Reforma)							
Creosotebush	1981	73±8	59±7	82±6	----[3]	55±5	81±6	76±10	4±2
	1982	60±5	89±5	97±3	0±2	42±3	44±5	55±6	1±1
Whitethorn	1981	33±6	53±6	89±5	----	11±4	14±4	36±6	0±1
acacia	1982	82±4	88±4	98±2	48±5	18±5	32±5	69±4	0±0
Tarbush	1981	98±3	96±4	99±1	----	38±10	68±9	97±2	4±5
	1982	100±5	100±4	98±6	0±2	88±13	74±10	97±5	4±4
Shrubby	1981	90±6	93±6	98±5	----	64±10	47±10	73±14	0±2
senna	1982	100±10	80±8	81±18	0±3	97±5	76±14	62±11	7±10
		(Rancho Los Pozos)							
Creosotebush	1981	83±4	84±4	90±3	----	34±3	79±4	68±3	0±0
	1982	66±6	90±4	98±2	0±2	62±3	48±3	43±4	6±2
Whitethorn	1981	95±15	89±18	100±9	----	27±14	58±11	20±14	19±14
acacia	1982	95±6	91±6	97±5	42±6	38±10	51±10	50±8	0±1
Mariola	1981	94±6	88±7	100±2	----	66±8	74±9	41±10	9±4
	1982	95±4	92±3	100±0	48±6	81±5	95±3	96±2	0±0
		(Rancho El Toro)							
Creosotebush	1981	78±6	94±4	96±2	----	27±6	82±5	89±4	0±0
	1982	91±4	100±2	98±2	13±4	12±4	87±4	83±5	0±0
Honey	1981	39±10	53±10	77±12	----	21±7	51±10	67±10	0±1
mesquite	1982	74±6	90±10	93±6	0±1	15±6	55±9	68±9	0±2
Javelina	1981	98±7	100±4	95±10	----	0±3	94±16	94±8	9±8
brush	1982	98±4	100±4	100±4	12±7	30±10	71±9	84±8	0±2
		(SRER))							
Creosotebush	1981	58±5	92±5	98±4	0±1	7±2	38±6	47±6	0±1
	1982	70±6	87±6	88±5	0±1	26±6	88±4	87±4	0±1
Velvet	1981	100±4	86±4	85±11	42±11	50±15	78±22	100±6	0±6
mesquite	1982	91±10	94±16	92±11	35±15	85±11	64±13	92±17	0±7
Desert	1981	91±3	100±1	100±1	2±1	33±3	69±3	54±4	0±0
zinnia	1982	100±2	100±1	100±4	80±4	5±2	93±2	87±2	0±2

[1] Treatments evaluated between 26 September and 31 October, 1984.

[2] Mortality calculated from the number of live plants of each species in ten 44-m^2 plots on each of 3 treated plots in 1984 and at the time of treatment. The 95% confidence intervals for binomial distribution were determined for each mean based on the size of sample use to calculate mortality.

[3] Land imprinting treatments were not applied at these locations in 1981.

treatments were applied only at SRER in 1981 and at all sites in 1982. Tebuthiuron was applied in May both years.

Shrub populations were estimated before treatment and in the fall of 1984 on 10 randomly placed 44-m^2 quadrats, excluding a 5-m perimeter. Brush mortality was calculated by species on each plot from densities at the time of treatment and the fall of 1984. Confidence intervals for binomial distribution (95%) were calculated for each mortality value based on the sample size (Steel and Torrie 1960). Confidence intervals were used to show mean differences rather than analyses of variance because of shrub population variability at each location.

The rail consisted of three 2.65-m lengths of railroad steel bolted together to form a triangle and weighted with rocks (approximately 770 kg). The rail was pulled over the plot twice in opposite directions. A standard 3-bottom disk plow on a 3-point hitch weighing 500 kg was used at the Mexican sites, and a pull-type 3-bottom disk plow weighing 1,000 kg was used at the SRER. Both disk plows had 64-cm disks which penetrated soils to 30 cm. A border disk constructed contour furrows at 10-m intervals.

The land imprinter, fabricated from 1.27-cm steel plate, consisted of 2 non-directional geometric forms (V-pitter and pit-digger) welded on separate 1- by 1-m cylinder capsules. Capsules were linked on an axle shaft. Capsules were filled with water, and iron boxes located at the front and rear were filled with rock to improve soil penetration (Dixon and Simanton 1980). Total weight was approximately 4 metric tons (Fig. 2).

Fig. 2. Land imprinter pulled by track tractor. Note iron box filled with rocks mounted on frame and V-pitter geometry of left capsule and pit-digger geometry of right capsule.

Native perennial grass forage production was estimated in the fall of 1983 and 1984 using a weight estimate technique (Pechanec and Pickford 1937). Twenty 30.5 by 61-cm quadrats were randomly placed in each plot excluding a 5-m band on the perimeter to eliminate treatment effects from adjacent plots, and forage weights visually estimated. Plants in 5 quadrats were clipped at the soil surface. Clipped forage was dried at 40° C for 48 hours in a forced-draft oven, and dry weights from unclipped field samples calculated using regression techniques (Campbell and Cassady 1949). We hypothesized that the treatments would increase forage production above that on untreated plots. When F values were significant, the forage on treated plots was compared with the forage on untreated check plots by Dunnett's one-sided procedure (Steel and Torrie 1960).

Brush control programs are expected to increase forage production. To test this assumption we calculated linear correlation coefficients (*r*) and linear regression equations between shrub density and forage production in 1984 on all plots at each of the 4 locations. At Los Pozos and El Toro 43 degrees of freedom were used to evaluate the significance of correlation coefficients because land imprinting treatments were not applied in 1981. At La Reforma 42 degrees of freedom were used because the land imprinting treatments and 1 disking with furrowing treatment were not applied in 1981. At SRER 46 degrees of freedom were used because all treatments were applied in both years.

Results and Discussion

Total precipitation at all Chihuahuan locations was below long-term means in 1981, 1982, and 1983 (Fig. 1). Precipitation was 25 and 59% of long-term means during summer 1982 at La Reforma and Los Pozos, respectively. At El Toro total precipitation was 70% of long-term mean in 1983, but July and August precipitation was near normal (117 mm versus 120 mm). Precipitation was above average at all Chihuahuan locations in 1984. At SRER precipitation was above average in all years.

Creosotebush Mortality

Tebuthiuron usually killed about 60% or more of the creosotebush plants at all rates and locations (Table 2). Across all locations and years creosotebush mortalities averaged 72, 87, and 93% at 0.5, 1.0, and 1.5 kg ai/ha, respectively. Creosotebush mortalities from all tebuthiuron rates averaged across both years at La Reforma, Los Pozos, El Toro, and SRER were 77, 85, 93, and 82%, respectively. Land imprinting killed 13% or less of the creosotebush and was the least effective control method. Average creosotebush mortalities across all locations from 2-way railing treatments in 1981 and 1982 were 31 and 36%, respectively. Highest mortality of creosotebush from 2-way railing was 62% at Los Pozos from the 1982 treatment and least mortality of creosotebush was 7% at SRER in 1981. Disking and disking with furrowing across all locations and years each killed an average of 68% of creosotebush plants. Disking treatments were more consistently effective at El Toro than at the other locations (Table 2). In 1981 mechanical treatments at SRER were applied immediately after 20 mm of rainfall to moist soil, but in 1982 they were applied before summer rains to dry soil. The higher soil moisture content in 1981 prevented desiccation of roots and crowns and contributed to the lower mortality rate of creosotebush in 1981 than in 1982 at the SRER location.

Associated Shrub Mortality

At La Reforma whitethorn acacia was less susceptible to low rates of tebuthiuron in 1981 than was creosotebush, but at Los Pozos whitethorn acacia populations declined by 89% or more on tebuthiuron plots (Table 2). All rates of tebuthiuron killed nearly all of the tarbush, shrubby senna, javelina brush, mariola, and desert zinnia plants. Honey mesquite was less susceptible to tebuthiuron than creosotebush at El Toro; however, at SRER tebuthiuron caused higher mortalities of velvet mesquite than creosotebush (Table 2).

Land imprinting in 1982 killed 48 and 42% of the whitethorn acacia plants at La Reforma and Los Pozos, respectively; but land imprinting was not an effective control measure for tarbush, shrubby senna, and honey mesquite. Both mariola and desert zinnia appeared to be marginally susceptible to land imprinting if treated when the soil was dry.

Two-way railing was less effective in controlling whitethorn

Table 3. Forage production in 1983 and 1984 after 3 tebuthiuron and 4 mechanical treatments were applied in 1981 and 1982 at 4 locations in the Chihuahuan and Sonoran Deserts.

Location	Treatment year	Tebuthiuron kg ai/ha 0.5	1.0	1.5	Land imprinting	Two-way railing	Disk plowing	Disk plowing with furrowing	Untreated check
		kg D.M./ha							
		(Production in 1983)							
La Reforma	1981	182*	248*	258*	—[1]	162	290**	409**	104
	1982	166**	206**	117	89	190**	142**	149**	105
Los Pozos	1981	94**	101**	104**	—	62	65	68	56
	1982	95**	78	77	107**	73	84*	101**	70
El Toro	1981	575	411	402	—	313	311	388	665
	1982	427	371	301	236	106	118	186	334
SRER	1981	393**	308**	270**	280**	404**	137	171	104
	1982	422	297	289	280	411	117	120	380
		(Production in 1984)							
La Reforma	1981	842*	1127**	1414**	—	84	295	253	279
	1982	986*	1263**	1376**	448	603	689	636	390
Los Pozos	1981	488	747*	868*	—	147	80	308	135
	1982	545	351	556*	255	211	230	380	133
El Toro	1981	731	766	680	—	898	899	805	1029
	1982	1028*	583	1119*	486	154	186	376	501
SRER	1981	554	1138*	778	153	509	283	199	213
	1982	938	392	1091	699	1177	709	730	330

*Significantly greater than check ($P \leq 0.05$) according to Dunnett's one-sided procedure.

**Significantly greater than check ($P \leq 0.01$) according to Dunnett's one-sided procedure.

[1] Treatment not applied at these locations in 1981.

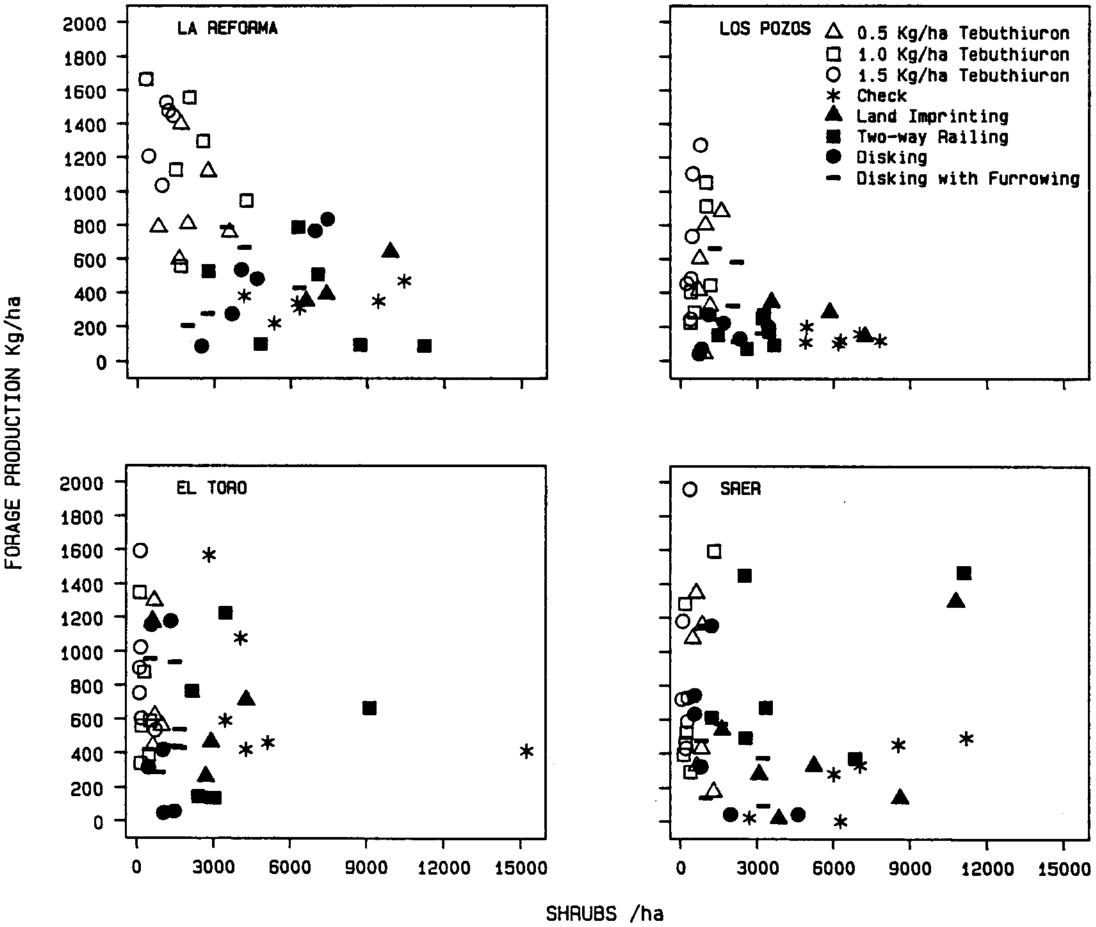

Fig. 3. Forage production in 1984 at different shrub densities on plots receiving 3 chemical and 4 mechanical treatments at 4 locations in 1981 and 1982.

acacia, tarbush, shrubby senna, and mariola in 1981 than in 1982 due to low rainfall in 1982. This low rainfall probably contributed to desiccation of the plants and higher mortality of these species in 1982 than in 1981.

Disking and disking with furrowing gave erratic control of whitethorn acacia, velvet and honey mesquite, and shrubby senna; but they consistently controlled javelina brush, mariola, and desert zinnia when applied to dry soil.

Forage Production

Forage production in 1983 on untreated plots at La Reforma and Los Pozos was between one-third and one-half what it was in 1984 due to low June to September precipitation in 1983. In 1983 forage production on most treated plots at La Reforma and Los Pozos was significantly greater than on untreated check plots, but not at El Toro (Fig. 1 and Table 3). Total precipitation at El Toro was 70% of long-term mean in 1983; July and August precipitation was near normal. This indicates that competition for moisture between shrubs and forage grasses was not a factor at El Toro in 1983. At SRER all plots treated with tebuthiuron in 1981 and some plots mechanically treated in 1981 produced significantly more forage than the untreated check plots.

Forage production in 1984 was significantly greater on one half of the plots treated with tebuthiuron than on untreated check plots but not on any plots treated mechanically (Table 3). Figure 3 shows that because tebuthiuron caused high mortality rates, shrub densities at all locations were reduced to less than 4,000 plants/ha, but the mechanically treated plots often supported shrub densities only slightly lower than untreated check plots.

Linear correlation coefficients between shrub density and forage production were significant ($P \leq 0.01$) for La Reforma and Los Pozos but not for El Toro and SRER (Table 4). The lack of a significant correlation between shrub density and forage production at El Toro and SRER in 1984 is attributed to low shrub density and timeliness of summer rains. All but 3 plots at El Toro had 5,000 or fewer shrubs/ha; consequently, the effect of high shrub density was not measured. Forage production was highest at all locations only where shrub density was less than 3,000 plants/ha (Fig. 3), but forage production was not always high where shrub densities were low. On some of the plots forage plants were not present when the study began. On other plots mechanical or chemical treatments injured or destroyed forage grasses so that they were unable to respond significantly to reduced competition from shrubs. July and August rains in 1984 at both El Toro and SRER apparently were sufficient to fulfill the needs of both grasses and shrubs.

Table 4. Correlation coefficients (r) and linear regression equations for shrub density (X=plants/ha) and forage production (Ŷ=kg D.M./ha) in 1984 on plots treated with 3 tebuthiuron and 4 mechanical treatments at 4 locations in the Chihuahuan and Sonoran Deserts.

Location	Correlation coefficient	Linear regression equation
La Reforma	–0.607**	Ŷ=1128–0.096X
Los Pozos	–0.459**	Ŷ= 511–0.063X
El Toro	–0.158	Ŷ= 729–0.024X
SRER	–0.119	Ŷ= 667–0.010X

**Significant at the 1% level of probability.

Conclusions

We found that mortalities of creosotebush from tebuthiuron at 0.5 and 1.0 kg ai/ha were often 60% or more, and at 1.5 kg ai/ha tebuthiuron always killed 80% or more of the creosotebush plants. Whitethorn acacia and honey mesquite mortalities from the 2 low rates of tebuthiuron were often less than 65% but at 1.5 kg ai/h tebuthiuron usually killed 80% or more of these shrub species. Mortality of tarbush, shrubby senna, mariola, javelina brush, and desert zinnia were at least 80% from all rates of tebuthiuron. Land imprinting and 2-way railing seldom gave shrub mortalities greater than 60%. Disking and disking with furrowing each killed an average of 68% of creosotebush plants and destroyed perennial grasses.

When shrub density was less than 3,000 plants/ha grass forage production was highest at all locations. Low shrub density and high forage production were more consistently achieved with tebuthiuron than with mechanical treatments, because the most effective mechanical treatments destroyed perennial grasses as well as shrubs. We conclude that forage production on semiarid grassland in northern Mexico and southwestern United States with shrub densities greater than 6,000 plants/ha and a remnant of perennial forage grasses will increase after shrub removal. Forage production on semiarid grasslands with shrub densities below 6,000 plants/ha probably will not increase significantly after shrub control.

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Nitrogen accumulation and acetylene reduction activity of native lupines on disturbed mountain sites in Colorado

S.T. KENNY AND R.L. CUANY

Abstract

Lupines are pioneering plants in many disturbed mountain habitats in Colorado. The purpose of this work was to determine if *Lupinus argenteus, L. caudatus,* and *L. alpestris* could be useful revegetation plants in a reclamation program. Paired soil samples from 33 disturbed sites supporting native lupines were used to determine if lupines increased the nitrogen content of the soil. Soil samples collected 10 cm from lupine tap roots averaged 13.8 mg kg^{-1} more exchangeable ammonium and 2.7 mg kg^{-1} more nitrate than soil samples collected 3 m from lupine plants. Field measured acetylene reduction rates of detached lupine nodules averaged 10.0 μmol ethylene g^{-1} nodule dry weight h^{-1} for *L. argenteus* and 17.3 μmol ethylene g^{-1} nodule dry weight h^{-1} for *L. alpestris*. Soil adjacent to lupines had higher levels of inorganic nitrogen than soils 3 m from lupine plants and lupines had the ability for biological nitrogen fixation as shown by the acetylene reduction assay, suggesting that native lupines are potentially useful revegetation plants in a reclamation program.

Key Words: *Lupinus alpestris, Lupinus argenteus, Lupinus caudatus,* dinitrogen fixation, soil nitrogen, nodule activity

Soil disturbances in mountain regions require revegetation to reduce environmental degradation. Disturbed soils often have low soil fertility with nitrogen and phosphorus deficiencies most common (Bauer et al. 1978). Bauer et al. (1978) report several studies which show that annual applications of nitrogen fertilizer result in more efficient utilization of nitrogen. Legumes are plants capable of symbiotic biological dinitrogen fixation associations which convert atmospheric nitrogen into a form of nitrogen used by the plant. Establishing legumes may be beneficial to a revegetation program because of their ability to biologically fix dinitrogen and thereby possibly increase soil nitrogen levels, which could reduce the necessity for annual applications of nitrogen fertilizer.

Crockett and Becker (1976) studied the dinitrogen fixation potential of 5 native North American grassland legumes and found that pioneering legumes had potential dinitrogen fixation rates 8 times greater than the species that occupied primarily climax communities. Johnson and Rumbaugh (1986) reported that *L. argenteus* in Utah and Montana had specific nodule acetylene reduction activities between 8 and 37 μmol ethylene g^{-1} nodule dry weight h^{-1}. They also found that lupines growing on disturbed sites had larger nodule mass and higher specific nodule acetylene reduction activity compared to lupines growing in undisturbed sites.

As part of a study on the use of native lupines for revegetation programs (Kenny 1981), a study was undertaken to determine if native stands of *Lupinus argenteus* Pursh, *L. caudatus* Kellogg, and *L. alpestris* A. Nels. growing in disturbed sites in Colorado are capable of biologically fixing atmospheric nitrogen. The first part of the study measured soil nitrogen content around lupine plants and the second measured in situ acetylene reduction.

Materials and Methods

Soil Nitrogen Content

The Kjeldahl method has been used for estimating soil nitrogen accumulation near nitrogen fixing plants (Palaniappan et al. 1979). Two soil samples were collected from a 10 cm depth 10 cm from lupine tap roots and an additional 2 samples were obtained at a 10 cm depth 3 m from lupine plants. As the samples were taken, root fragments, nodules and dead plant fragments were removed. The paired samples were taken in July 1978 from 33 disturbed sites which had lupines as the dominant vegetation. All samples were air-dried and ground to pass a 2-mm sieve. The paired samples from each location were analyzed for exchangeable ammonium and nitrate by steam-distillation (Bremner 1965a) and for total nitrogen by a semimicro-Kjeldahl method (Bremner 1965b). The replicate soil sample nitrogen values were averaged, the pairs grouped by species and the differences between pairs analyzed by a paired *t*-test.

Acetylene Reduction

The reduction of acetylene to ethylene and subsequent measurement by gas chromatography of the ethylene produced is a sensitive, but indirect, measurement of dinitrogen fixation (Burris 1972). Acetylene reduction measurements enable both estimates of potential dinitrogen fixation and comparisons of potential for dinitrogen fixation among plants to be made. Twelve of the 33 sites in the soil nitrogen content study were sampled in early August 1979 when all sites were in mid-flower. Plants were excavated, and a segement of root with intact nodules was cut from the plant, trimmed to within 1 cm of the nodules, and placed into a 60-ml serum bottle. After the bottle was sealed with a rubber serum stopper, a 1-ml volume of acid-washed acetylene was injected into each bottle. The bottles were buried in the soil to simulate nodule depth and to maintain in situ temperature during incubation. Two bottles representing each plant were prepared. To determine any nonrhizobial dinitrogen fixation, bottles containing soil and root segments without nodules were similarly prepared. None of the bottles with soil or root segments without nodules had measurable ethylene production. Samples were incubated on site for 1 hour. The bottles were transferred to a chest filled with dry ice and kept frozen until returned to the laboratory for analysis. To determine any loss of ethylene during transport to the laboratory, known volumes of ethylene were injected into empty stoppered serum bottles and handled similarly to the bottles with nodules. Later analysis of the ethylene-only bottles demonstrated that no loss of ethylene occurred.

Analysis of ethylene production was by gas chromatography using a flame ionization detector. One-half milliliter volumes were withdrawn from the reaction bottle and injected into the gas chromatograph. The operating parameters included an oven temperature of 100° C, 20 cc min^{-1} N_2 carrier gas flow rate, injection port temperature of 185° C, detector temperature of 220° C, and a 1.8-m × 3.2-mm stainless steel column packed with 80–100 mesh Porapak N. Peak heights were measured and ethylene concentration in each sample was calculated by reference to an ethylene standard. After the acetylene reduction assay, nodules were

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Manuscript accepted 9 March 1989.

Table 1. Comparison between soil nitrogen levels in soil samples collected at a 10 cm depth 10 cm from lupine tap roots and 3 m from lupine plants growing on disturbed mountain sites in Colorado.

Species	Number of sites sampled	Exchangeable Ammonium		Nitrate		Total Nitrogen[1]	
		Soil Sample Distance from Lupine Tap Roots					
		10 cm	3 m	10 cm	3 m	10 cm	3 m
		mg kg^{-1}					
L. argenteus	24	32.7 ± 34.4	19.9 ± 25.1	7.6 ± 5.8	5.3 ± 4.6	1056 ± 1001	1016 ± 1032
Paired t-value		4.70**		6.22**		0.86NS	
L. alpestris	5	38.2 ± 9.1	20.4 ± 9.1	11.3 ± 5.1	7.7 ± 3.1	1060 ± 609	885 ± 491
Paired t-value		9.18**		2.97*		1.60NS	
L. caudatus	4	20.7 ± 10.5	9.7 ± 8.2	6.8 ± 1.4	4.6 ± 2.6	1325 ± 983	1241 ± 859
Paired t-value		4.13*		3.55*		0.96NS	

[1] Mean ± Standard Deviation. * and ** indicate significant difference between pairs for nitrogen level at $P = 0.05$ and $P = 0.01$, respectively. NS indicates no significant difference between pairs for nitrogen level.

removed from the root segments, washed, dried at 60° C, and weighed.

Results and Discussion

The nitrogen analysis results from 33 disturbed habitat soil collection sites are summarized by lupine species in Table 1. The sites with a range in elevation between 2,130 and 3,350 m were located throughout the Rocky Mountain region of Colorado. The sites were road construction disturbances, abandoned mine tailings, open meadows created by past fires, ski slope construction or logging operations, and a sand dune. Most of the soils were loam or sandy loam in texture. Lupines were the dominant vegetation with grasses and sometimes small shrubs growing at the sites. A complete description of each site is listed in Kenny (1981). The sand dune soil was the only one without measurable exchangeable nitrogen. Exchangeable ammonium levels ranged between 0 and 117.5 mg kg^{-1}, nitrate between 0 and 97.4 mg kg^{-1}, and total nitrogen between 69 and 4,808 mg kg^{-1}. The highest nitrogen levels were on a ski slope that had been fertilized. Significant differences ($P \leq 0.05$) in exchangeable nitrogen were detected between the paired samples, with exchangeable ammonium being 13.8 mg kg^{-1} higher and nitrate being 2.7 mg kg^{-1} higher in samples obtained adjacent to lupine roots compared to samples obtained at a 3-m distance. No significant differences were found between the paired samples for total nitrogen. The higher inorganic nitrogen levels around lupines could be due to either their large tap roots, which could extract nitrogen from greater soil depths than plants without tap roots, or the lupines using symbiotically fixed atmospheric nitrogen to meet their nitrogen needs, thereby extracting less inorganic nitrogen from the soil than other plants. For whatever reason, the soil around lupines had more inorganic nitrogen than soil 3 m from lupine plants, suggesting that lupines increase the level of inorganic soil nitrogen.

A site description, the field conditions at the time of sampling, and the mean ethylene production rates for 8 of the 12 sites sampled for acetylene reduction are presented in Table 2. Not all the nodules from a plant were collected, so it is not possible to calculate an acetylene reduction rate on a per plant basis. At the other 4 sites, no measurable ethylene production was recorded. The soil at these 4 sites was dry. Soil moisture for these 4 sites was estimated by feel and appearance to be about 40% of field capacity whereas soil moisture at the other sites was estimated to be 75% or more of field capacity. Dry soil conditions are known to depress dinitrogen fixation (Sprent 1973). The acetylene reduction rates ranged between 0.9 and 42.0 µmol ethylene g^{-1} nodule dry weight h^{-1}. The North Sand Hills site had the highest rate of acetylene reduction and the nodules found were individual small nodules. The nodules collected at the other locations were large interconnected masses of small nodules. Pate (1977) suggested that such perennial nodules probably exhibit low dinitrogen fixation per unit of nodule mass. The difference in size may account for the higher rates of acetylene reduction by the North Sand Hills nodules. Except for the Climax site, the highest rates of acetylene reduction were from those sites which were sampled on a sunny day. Nodules sampled on a cloudy day had low rates of acetylene reduction, which indicates that photosynthetic activity likely influences the rate of acetylene reduction, but carbohydrates stored in the plant or nodules might be available for dinitrogen fixation during times of low photosynthetic activity. Trinick et al. (1976) found that several lupine species have no diurnal rhythm for acety-

Table 2. Field measured acetylene reduction by native lupines growing on disturbed mountain sites in Colorado.

Species and site	Elevation	Site description	Sampling conditions				Ethylene production[1]
				Temperature			
			Time	Air	Soil	Sky	
	(m)		(MDT)	(° C)			µmol g^{-1} nodule dry wt h^{-1}
L. argenteus							
North Sand Hills	2926	Sand dune	1315	26	17	Clear	29.6 ± 7.6
Dumont Lake	2896	Roadside with grasses	0915	18	11	Clear	16.9 ± 9.4
Blue River	3048	Roadside with grasses	1230	18	14	Cloudy	7.4 ± 0.5
Tennessee Pass	3048	Clearing in lodgepole pine re-growth forest	1800	22	14	Cloudy	6.7 ± 2.4
Hoosier Pass	3109	Roadside with grasses	1200	17	10	Cloudy	4.3 ± 2.2
Climax	3353	Molybdenum tailings	0945	22	11	Clear	1.2 ± 0.4
L. alpestris							
Hideaway Park	2682	Roadside with grasses	1530	26	17	Clear	18.0 ± 0.4
Hot Sulfur Springs	2347	Roadside with grasses	1730	21	15	Clear	16.6 ± 5.5

[1] Mean ± Standard Deviation.

lene reduction; only "long periods of dull weather" and extreme shading reduced overall activity in lupine nodules. Since previous weather conditions at our sites were unknown, further study is warranted to determine any diurnal response to acetylene reduction in these lupine species. The one-time measurements reported in Table 2 indicate that additional studies are necessary to estimate the contribution of biologically fixed atmospheric nitrogen to the lupine's nitrogen requirements during the growing season since soil moisture, nodule size, and sunshine were shown to influence acetylene reduction.

Lupines are colonizers of disturbed soils and other eroded areas. *L. alpestris* and *L. argenteus* reduce acetylene and therefore have the potential for biological dinitrogen fixation. The native lupines studied increased mineral nitrogen concentrations in the soil around their roots. It is likely that their improvement of the soil's nitrogen status prepares the way for later succession. This suggests a role for lupines in revegetation and reclamation of disturbances. Plummer et al. (1968) suggested that native lupines were well adapted for game range improvements, but an end use of a reclaimed area might also include grazing by domestic livestock. Lupines contain alkaloids poisonous to livestock (Keeler et al. 1977), but the Colorado study (Kenny 1981) and a study by Davis (1982) showed significant variation between lupine collection sites for alkaloid content. In the Colorado study, lupine accessions ranged in total alkaloid content from less than 1.0 g kg^{-1} dry weight to 23.2 g kg^{-1} dry weight. It should therefore be possible to select low alkaloid germplasm for use in reclamation programs.

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Clipping and long-term grazing effects on biomass and carbohydrate reserves of Indian ricegrass

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Abstract

Long-term heavy grazing had little effect on root and crown biomass of Indian ricegrass (*Oryzopsis hymenoides* [Roem. and Schult.] Ricker), nor did it significantly affect the total nonstructural carbohydrate (TNC) reserve levels or the seasonal cycle of reserves in this grass. Fifty years of protection from livestock use had not resulted in ecotypic differentiation in Indian ricegrass for these variables. Clipping reduced crown biomass more than root biomass and removal of 90% of the aboveground biomass resulted in more than a 50% reduction in crown biomass and reserve carbohydrate pool.

Two commercial strains of Indian ricegrass ('Nezpar' and 'Paloma') were compared with native Chaco Canyon strains in a uniform garden study. The Nezpar strain was superior to Paloma and the Chaco Canyon strains in production of crown biomass and TNC reserves at the more mesic garden site. The native strains from the more arid Chaco Canyon site were superior to both cultivated strains in production of roots. The native Chaco Canyon strains were little affected by clipping and have promising genetic potential for tolerance of drought and heavy grazing.

Key Words: Indian ricegrass, *Oryzopsis hymenoides*, heavy grazing, ecotypic differentiation, belowground biomass, carbohydrate reserves

A plant is considered to be a source-sink system where active photosynthetic tissue produces compounds which are used for maintenance and growth, stored in situ, or translocated to other sites of utilization or storage (Burt 1964, Maggs 1964, Neales and Incoll 1968). Deregibus et al. (1982) stated that a reduction of carbohydrate reserves resulting from defoliation after the peak growth period might be caused by a reduction in the leaf area and assimilate production after active aboveground growth had ceased, when meristematic activity was low, and when there were other demands for assimilates below ground. They pointed out that this was at a time when carbohydrates were normally being produced in excess of demand, hence they could be transported to belowground structures for root growth or maintenance, or be converted to long-chain carbohydrates for future growth demands.

Labile carbohydrate reserves are a major source for carbon for regrowth after defoliation (Graber 1931, Cook 1966, Youngner 1972, White 1973, Trlica 1977, Deregibus et al. 1982). However, some researchers have been critical of the role of reserve carbohydrates for regrowth following defoliation (May and Davidson 1958, Moore and Biddiscomb 1964, Davidson and Milthorpe 1965, Caldwell et al. 1981). Studies that utilized radioactive carbon have given some supportive evidence for the use of storage carbohydrates in regrowth (Pearce et al. 1969, Smith and Marten 1970, Chung and Trlica 1980), but reserves may only be needed for a short time to produce the first few leaves.

Several researchers have found that carbohydrate reserve storage in grass species was not significantly affected by grazing or defoliation treatments if the grazing or defoliation was discontinued in time to allow plants to grow up and replenish reserves before fall quiescence (Sampson and McCarty 1930, McCarty and Price 1942, Hyder and Sneva 1963, Paulsen and Smith 1968, Menke and Trlica 1983). This was partially true in the case of Indian ricegrass (Trlica and Cook 1971).

Effects of grazing or defoliation may not only be seen in terms of total nonstructural carbohydrate (TNC) concentration, but also in terms of weight of the storage organs per se (Weinmann 1952). Therefore, determination of total amount of carbohydrate pools in the storage organs (pool = % TNC × biomass of the plant part analyzed), rather than just the concentration of TNC reserves, may be important in assessing regrowth potential of plants (Buwai and Trlica 1977b, Santos and Trlica 1978). Some researchers have contradicted the traditional view that grass crowns represent the major organ for storage of soluble reserves based on determination of soluble carbohydrate pools in crowns (Caldwell et al. 1981, Richards and Caldwell 1985, Richards et al. 1987). These researchers have found little correlation between crown and stem base TNC concentration or carbohydrate pools with regrowth following defoliation.

Crowns of Indian ricegrass (*Oryzopsis hymenoides* [Roem. and Schult.] Ricker) may provide a better indication of TNC storage reserves and defoliation effects than do roots, if crown mass and reserve levels are large. Coyne and Cook (1971) found that crowns of Indian ricegrass had higher TNC concentrations than did roots. Trlica and Cook (1971) found that crown TNC concentration in Indian ricegrass was usually more affected by defoliation than was root TNC concentration.

The main objective of this study was to determine effects of previous long-term heavy grazing and clipping on root and crown biomass and nonstructural carbohydrates in crowns of Indian ricegrass. Another objective was to compare biomass and TNC variables of native and commercial strains of this species in a uniform garden environment to assess the genetic potential of the strains.

Methods and Materials

Root and Crown Biomass

Chaco Canyon In Situ Study

An experiment was conducted within and adjacent to the Chaco Canyon Culture National Historical Park (Chaco Canyon) in northwestern New Mexico. Plots were located on a hilltop, hillside, and in a swale on both heavily grazed and protected (ungrazed) pastures at about 580 m elevation as described by Orodho et al. (1990) and Trlica and Orodho (1989). The 0.4-ha

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Financial assistance was provided by the Food and Agriculture Organization of the United Nations through Project KEN/80/003, the U.S. Department of Agriculture Competitive Grants Program on Desertification, and Colorado State University Agricultural Experiment Station through Project 100.

The authors would like to thank Drs. Charles Bonham, Robin Cuany, Mark Brick, and Wayne Leininger for their assistance throughout the course of this study and for their critical review of the manuscript. The U.S. Park Service, Bureau of Land Management, and Southwestern Colorado Research Center are recognized for granting permission to use their land for this study. We thank Walter P. Herriman and Tom Vaughan, Superintendents of Chaco Culture National Historical Park, and their staff members for use of their facilities while conducting this study. We also thank Adrian Fisher and Mark Stack for their assistance and use of their facilities for conducting the uniform garden study.

Manuscript accepted 23 March 1989.

plots located outside the National Park on lands managed by the Bureau of Land Management (BLM) were fenced in April 1984 to prevent livestock grazing during 1984 and 1985, when the study was conducted. National Park Service and BLM records indicated that this area had been heavily grazed year long by cattle, sheep, goats, and horses for more than 50 years. The area within the National Park was fenced 50 years ago to prevent livestock use within the Park. Two adjacent plots with similar soils, slope, exposure and vegetation were selected at each of the 3 topographic positions. One of the plots at each site was located within the protected area of the National Park, while the other was located on the adjacent, heavily-grazed area managed by the BLM. Plots were located at least 200 m from the Park boundary fence in both the grazed and protected areas at each of the 3 sites to reduce genetic exchange among the grazed and protected sites.

The long-term average annual precipitation recorded at the headquarters of the National Park was 240 mm. Precipitation at the Chaco Canyon site was 110 and 130% above normal in 1984 and 1985, respectively. Most of the precipitation comes during the summer and fall months. The mean monthly temperature ranges from 5 to 35° C and the monthly mean minimum temperature ranges from -11 to 11° C. Soils at the study area are a sandy loam.

Two shrubs, winterfat (*Eurotia lanata* [Pursh] Nutt.) and fourwing saltbush (*Atriplex canescens* [Pursh.] Nutt.) were dominant in the overstory vegetation at the Chaco Canyon study site. The most common grasses were Indian ricegrass, galleta (*Hilaria jamesii* [Torr.] Genth.), blue grama (*Bouteloua gracilis* [H.B.K.] Lag. ex Steud.), and bottlebrush squirreltail (*Sitanion hystrix* [Nutt.] J.G. Smith). *Eriogonum* spp. and Russian thistle (*Salsola kali* L.) were common forbs in the area. Orodho et al. (1990) found that previous heavy grazing at this research area had resulted in a reduction of fourwing saltbush; however, there had been little effect on grass cover, density or production. Density of Indian ricegrass at the Chaco Canyon study site was only 1.5 plants/m^2, whereas density of plants in the uniform garden study were 6–9 plants/m^2. However, Indian ricegrass plants were much larger and grew in association with a number of other species at the Chaco Canyon study site, so competition within the community could have affected results of the in situ field study (Mueggler 1972).

The experiment was a randomized block design which consisted of 2 former grazing intensities (heavily grazed and ungrazed for 50 years) and 4 defoliation intensities (0, 30, 60, and 90% removal of photosynthetic tissue-estimated). The 3 topographic sites served as replications. Four plants within each plot assigned to each defoliation treatment were randomly selected at each date of sampling. Four additional plants were selected from each defoliation intensity for sampling in 1985 at the quiescence stage. Defoliation was done at anthesis in either early June 1984 or late May 1985 for those plants that would be sampled at quiescence in late November 1985. The 4 selected plants were excavated and only crown material was retained during the 1984 sampling. These plants were collected at the second leaf stage (late April), anthesis (early June), maturity (late July), and quiescence (late November) phenological stages in 1984. The fifth sample period was at quiescence in late November of 1985, when roots as well as crowns were sampled with a 13- × 24-cm coring device. These last samples were collected using the same technique and equipment described in the next section to assess root and crown weights in the Cortez uniform garden study.

Cortez Uniform Garden Study

The Cortez study site used for the uniform garden experiments was located at the Southwestern Colorado Research Center near Yellow Jacket, Colorado, which is about 24 km north of Cortez. The Center is located in the dryland farming region of the southwestern corner of Colorado at about 2,130 m elevation. The Center receives annual precipitation of about 360 mm, half of which falls as snow during the winter months. Precipitation in 1984 and 1985 was 105 and 120% of normal, respectively. There is a frost-free period of 120 days. The monthly mean maximum temperature for this area is normally under 33° C, while the monthly mean minimum temperature is above -12° C. This is quite similar to the temperature regime at Chaco Canyon, but precipitation is much greater at the Cortez site.

The principal soil series at the Cortez study site is representative of major acreages of the agricultural land in the area and is silty clay loam soil. These soils have a high water-holding capacity and store winter moisture upon which success of agriculture in the basin is dependent. Topography of the region consists almost entirely of rolling hills and the dominant vegetation types are grassland and pinyon-juniper woodland.

Two strains of Indian ricegrass were obtained from the Chaco Canyon study site. Transplants were excavated from 3 heavily grazed sites adjacent to exclosures on the hilltop, hillside, and swale locations. The transplants from each of the 3 topographic locations were combined in equal proportions to constitute the grazed strain. Similarly, transplants from sites adjacent to plots within the Chaco Culture National Historical Park were combined in equal portions from similar topographic positions to constitute the ungrazed strain.

Grazed and ungrazed plots were located approximately 400-m apart to reduce pollen and seed transport between the 2 populations. Two other strains tested in the uniform garden experiments, 'Paloma' and 'Nezpar', are commercially released cultivars of Indian ricegrass. Paloma transplants were obtained from agronomic plots at the Cortez study site, while Nezpar transplants were obtained from a seed production field near Dolores, Colorado, approximately 25 km northeast of the Cortez study site.

All transplants were excavated in April of 1984, reduced to approximately the same basal area (135 cm^2), and potted before being transported to the Cortez study site. Each plant was subdivided into 4 equal-sized bunches and immediately planted into a well-prepared seedbed at 30-cm plant and row spacings. Weeding was done periodically by hand. We assumed that little intra-plant competition would occur during the 2 years of study.

The uniform garden experiment was a split-split-plot design having factorial arrangement of treatments with 4 replications. Two nitrogen (N) treatments (0 and 50 kg/ha) composed the main plots, 2 clipping treatments (90% of active photosynthetic material clipped and unclipped) made up the sub-plots, and the 4 strains of Indian ricegrass were the sub-sub-plots. Five transplants of each strain of Indian ricegrass were planted in a row within each treatment. Nitrogen was applied in early June of 1984 and in late May of 1985, while clipping was done at the anthesis stage of phenological development in both years. The nitrogen fertilizer application had no significant ($P>0.05$) effect on any measured parameter; therefore it will not be discussed further in this paper.

Root and crown samples were collected in early August at the end of the growing season immediately following the 1985 aboveground biomass harvest. One of 5 plants was selected at random from each treatment in each replication to be collected. A cylindrical sampling core of 13-cm diameter and 24-cm long, with a sharp cutting edge, was placed directly over the selected plant crown and hammered into the ground. We estimate that this core would sample approximately 60–80% of the individual plant root biomass and 100% of the crown biomass, with little contamination of root biomass by neighboring plants. The roots and crowns within the core sample were obtained by digging around the metal core and excavating it. The crowns were separated from the roots, with obvious decayed materials being discarded, and the live crown tissue was washed with tap water and placed into a glass jar. The crown tissue was covered with 95% ethanol immediately following washing to reduce enzymatic activity, and then sealed tightly.

Crown samples were taken to the laboratory where jars were placed, with their lids open, in a forced-draft oven at 60° C. Ethanol was evaporated and the samples completely dried before they were weighed and then ground in a Wiley mill to pass through a 0.5-mm screen. The ground samples were kept in sealed polyethylene bags prior to laboratory analysis.

Plant roots were separated from crowns immediately after they were obtained from the field. Roots were removed from soil by a floatation method (McKell et al. 1961) using 0.05-mm screens. The root samples were oven-dried at 60° C and weighed.

Carbohydrate Analysis

The prepared crown samples from the Cortez and Chaco Canyon study sites were taken to a laboratory for TNC analysis. TNC was extracted from each 0.5-g plant sample with 0.2 N sulphuric acid (Smith et al. 1964). The extracts were then used to determine TNC concentration on a glucose-equivalent basis by using an iodometric titration developed by Heinze and Murneek (1940), but using modified reagents as suggested by the Association of Official Analytical Chemists (1965). Standard curves were determined for each stock solution. The TNC percentages were multiplied by the weight of the plant organ to determine carbohydrate pool quantity.

Data Analysis

All data on root and crown weights, TNC concentration, and carbohydrate pools were analyzed using analysis of variance procedures (Steel and Torrie 1980). The calculated F-values were tested at the $\alpha = 0.05$ level of probability, and if significant ($P \leq 0.05$) interactions were found, then analysis within levels of a factor were conducted. When significant ($P \leq 0.05$) differences were detected, Duncan's New Multiple Range Test was used to separate significant ($P \leq 0.05$) means.

Results and Discussion

Root and Crown Biomass

Long-term heavy grazing (i.e., greater than 50 years) did not significantly affect root biomass of Indian ricegrass in the top 24 cm of soil at the Chaco Canyon study site (data not shown). There were, however, significant differences in root biomass (Fig. 1) among the 4 strains of Indian ricegrass transplanted into the uniform garden at the Cortez site. No significant differences in root biomass among the grazed and ungrazed strains of Indian ricegrass from the Chaco Canyon study site were found. It should be noted that these 2 strains had greater root biomass than did either of the 2 cultivated strains of Paloma and Nezpar (Fig. 1). Paloma had the lowest root biomass among the 4 strains of Indian ricegrass tested in the transplant garden at the Cortez study site. Greater root biomass for the 2 native strains of Indian ricegrass should be advantageous under droughty conditions.

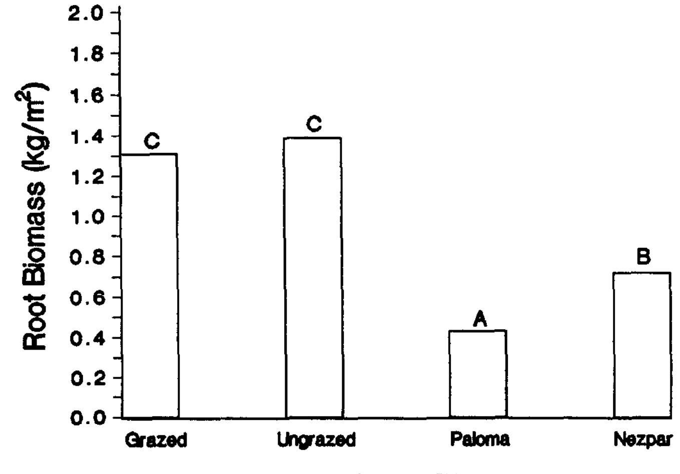

Fig. 1. Root biomass for 4 strains of Indian ricegrass at the Cortez common garden site in August 1985. Values are the average over replications, fertilization, and clipping treatments. Means labeled with similar letters are not significantly different ($P > 0.05$).

Defoliation at 30, 60, or 90% removal of photosynthetic tissue at anthesis in early June had little effect on root biomass of in situ Indian ricegrass at the Chaco Canyon study site. Clipping Indian ricegrass at anthesis in the Cortez uniform garden also had little effect on root biomass and there was no significant clipping-x-strain interaction. The present research supported earlier work reported by Buwai and Trlica (1977a), who found no change in total root weights of blue grama and western wheatgrass (*Agropyron smithii* Rydb.) after defoliation. Results of this research did not support that reported by Deregibus (1983), who found a reduction of root biomass in *Paspalum dilatum* (Poir) as a result of defoliation. Santos and Trlica (1978) also found that the biomass of crowns and roots of blue grama and the root biomass of western wheatgrass were reduced by frequent defoliation. A number of other researchers have also reported reduction or stoppage of root growth following defoliation (Crider 1955, Oswalt et al. 1959, Jameson 1963, Davidson and Milthorpe 1965).

Any defoliation caused significant reductions in crown biomass of Indian ricegrass at the Chaco Canyon study site compared with unclipped plants (control) (Fig. 2). Although there were no differences in crown weights of plants defoliated at 30 and 60%, plants defoliated at 90% had significantly lower crown weights.

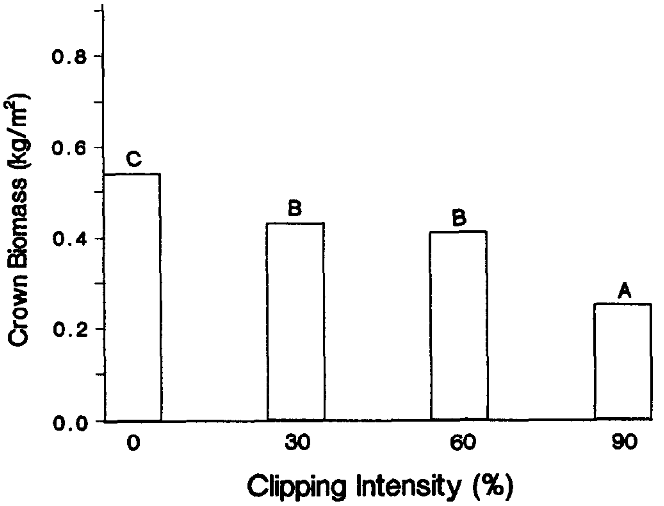

Fig. 2. Crown biomass for in situ Indian ricegrass at the Chaco Canyon study site as affected by defoliation intensity. Values are the average over slope position and previous grazing history. Means for the defoliation intensity labeled with the same letter are not significantly different ($P > 0.05$).

Clipping of Indian ricegrass at anthesis resulted in a significant increase in crown biomass of Nezpar, but did not cause any significant change in crown weights of Paloma or the 2 native strains taken from the Chaco Canyon study site (Fig. 3). This significant clipping-x-strain interaction was caused mainly by the reaction of the Nezpar strain to the single defoliation. These findings were not in agreement with results obtained from the defoliation treatments at the Chaco Canyon study site, where several intensities of defolia-

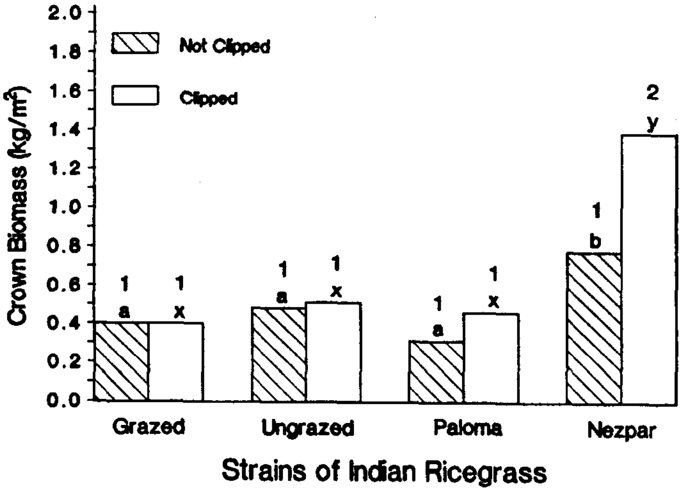

Fig. 3. Crown biomass for 4 strains of Indian ricegrass at the Cortez common garden site as affected by clipping treatment. Values are the average over replications and fertilization treatments. The clipping treatment across the 4 strains labeled with a similar letter is not significantly different ($P>0.05$). The clipping treatment within each strain labeled with a similar number is not significantly different ($P>0.05$).

tion resulted in a decrease in the crown weights of a grazed and ungrazed strain of Indian ricegrass. This may have resulted from possible differences in soil moisture and plant competition (Meuggler 1972) at the 2 study sites. Plants grown at the Cortez uniform garden site had higher soil moisture and relatively less competition from other plants and exhibited more growth, tillering, and increase in crown biomass as compared with in situ plants at the Chaco Canyon study site. The Chaco Canyon study site had low soil moisture after plants were defoliated, which also affected plant growth (Orodho et al. 1990).

Total Nonstructural Carbohydrate Concentrations and Pools

The seasonal TNC concentration trend of depletion during initial growth followed by replenishment of reserves in crowns was shown for both grazed and ungrazed strains of Indian ricegrass at the Chaco Canyon study site (Fig. 4). There were no significant differences in seasonal trends in crown TNC between grazed and ungrazed plants, which indicated that long-term heavy grazing had not significantly affected these trends. There was also no significant interaction for TNC among grazed and ungrazed plants with different phenological stages of development. Similar seasonal trends in carbohydrate reserves have been described for other range species by a number of authors (Sampson and McCarty 1930, Troughton 1957, Hyder and Sneva 1959, Weinmann 1961, Coyne and Cook 1971, Trlica and Cook 1972, Menke and Trlica 1981). However, no previous work was found on seasonal trends in carbohydrate reserve cycles of grasses under different grazing histories.

Results of this study did indicate that there were significant differences in TNC concentrations among in situ Indian ricegrass plants within the different intensities of defoliation at Chaco Canyon. There were no differences in TNC concentrations of plants in the 30% and 60% defoliation intensities (Fig. 5a). Greatest TNC concentrations were found in the crowns of these plants as compared with plants from either the control or 90% defoliation intensity. As expected, plants that had been subjected to 90% defoliation had the lowest TNC concentrations. Cook and Child (1971) noted that Indian ricegrass that had undergone previous defoliations showed good recovery with rest, except for those

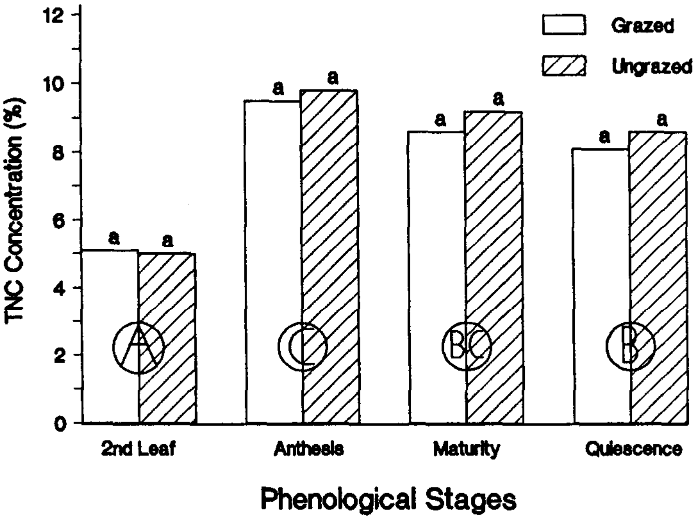

Fig. 4. Total nonstructural carbohydrate (TNC) concentrations in crowns of Indian ricegrass at the Chaco Canyon study site during 1984 as affected by long-term heavy grazing and phenological stage of development. Means for phenological stages labeled with the same capital letter are not significantly different ($P>0.05$). Means for previous grazing treatments within each phenological stage labeled with the same small letter are not significantly different ($P>0.05$).

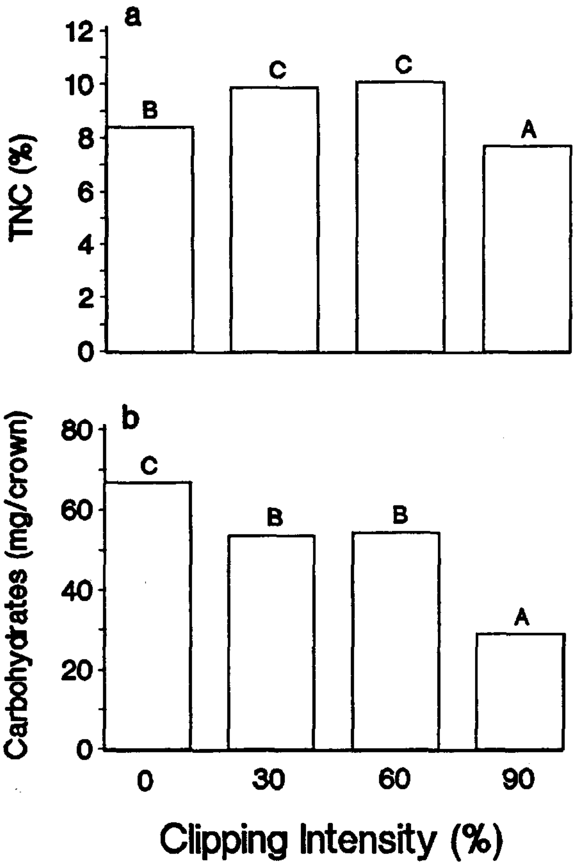

Fig. 5. Total nonstructural carbohydrate (TNC) concentrations (a) and total nonstructural carbohydrate pools (b) in crowns of Indian ricegrass at the Chaco Canyon study site as affected by clipping intensity. Values are the average over slope position and previous grazing history. Means for defoliation intensities labeled with the same letter are not significantly different ($P>0.05$).

clipped at 90%. Trlica and Cook (1971) reported that TNC reserves in both roots and crowns of Indian ricegrass were usually higher among control plants than they were for heavily defoliated plants. They noted that TNC concentrations were significantly lower when defoliation occurred during late spring or near maturity in the summer.

The total carbohydrate pools in crowns of Indian ricegrass at the Chaco Canyon study site following defoliations are illustrated in Fig. 5b. Defoliation at 90% resulted in the lowest total carbohydrate pool in crowns of Indian ricegrass, whereas the greatest carbohydrate pools were found in control plants. There were no significant differences in total carbohydrate pools among plants from the 30 and 60% defoliation treatments.

There appeared to be little correlation between TNC concentration and the total carbohydrate pool in crowns of Indian ricegrass (Fig. 5a & b). The trend observed for total carbohydrate pools in crowns was more correlated with crown weights following defoliation (Fig. 2) than with TNC concentrations (Fig. 5a). Santos and Trlica (1978) found that TNC concentration in blue grama was little affected by clipping, but that total carbohydrate pools were less because of a reduction in mass.

A single clipping in the uniform garden study had no significant effect on TNC concentrations in crowns of grazed and ungrazed strains of Indian ricegrass from the Chaco Canyon study site (Fig. 6a). On the other hand, clipping resulted in a significant increase in TNC concentration in crowns of the Paloma and Nezpar strains. Clipped Nezpar plants had more than twice the TNC concentration as the other 3 strains studied. No differences were found for TNC concentrations between the clipped and unclipped plants for the grazed and ungrazed strains of Indian ricegrass.

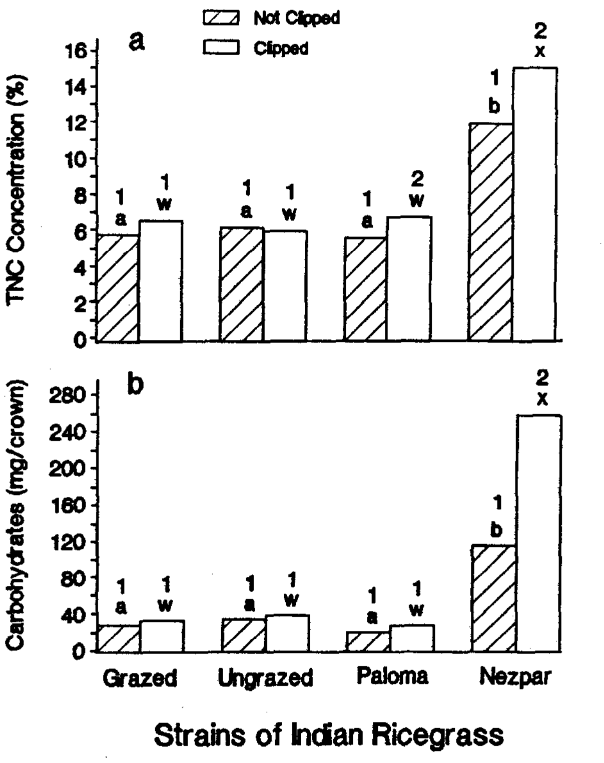

Fig. 6. Total nonstructural carbohydrate (TNC) concentration (a) and total carbohydrate pools (b) in crowns of 4 strains of Indian ricegrass at the Cortez uniform garden study as affected by clipping. Values are the average over replications and fertilization treatments. The clipping treatments across the 4 strains labeled with a similar letter are not significantly different ($P>0.05$). The clipping treatment within each strain labeled with a similar number is not significantly different ($P>0.05$).

Clipping resulted in a significant increase in the total carbohydrate pool in crowns of Nezpar, but had no significant effects on the other strains of Indian ricegrass tested (Fig. 6b). Carbohydrate pools among grazed, ungrazed, and Paloma strains were quite similar. Nezpar had the greatest carbohydrate pool in crowns of both clipped and unclipped plants compared with any of the other 3 strains tested in the uniform garden. The carbohydrate pool averaged about 5 times greater for this strain and the carbohydrate pool more than doubled with clipping. Again, carbohydrate pool size was affected more by crown weight than TNC concentration. There was a lack of correlation between TNC concentration and total carbohydrate pool in Paloma following clipping. Clipping resulted in a significant increase in TNC concentration in crowns of Paloma (Fig. 6a), but did not affect the total carbohydrate pool size of this strain (Fig. 6b).

Summary and Conclusions

Long-term heavy grazing had no significant effect on root and crown biomass of Indian ricegrass at the Chaco Canyon study site, nor did it significantly affect TNC reserves in this grass. This indicated that 50 years of protection from heavy livestock grazing pressure had not resulted in significant selection and differentiation of Indian ricegrass into an ecotype with different root and crown biomass or TNC reserve concentrations. We also found that other morphological and chemical characteristics of this grass had not been affected by long-term protection from livestock grazing (Trlica and Orodho 1989). Either long-term heavy grazing in this area has eliminated or greatly reduced nonresistant genotypes, or Indian ricegrass employs high regrowth capacity rather than defense mechanisms to overcome intense herbivory (Meijden et al. 1988, Olson and Richards 1988).

Crown biomass of Indian ricegrass was affected more by defoliation than was root biomass. Defoliation intensities affected TNC concentration and carbohydrate pools in crowns of Indian ricegrass. A 90% defoliation intensity resulted in more than a 50% reduction in the carbohydrate reserve pool. A seasonal trend of carbohydrate reserve depletion during initial growth and subsequent replenishment of reserves at a later growth stage was evident in Indian ricegrass. This pattern of the TNC cycle and amount of carbohydrate reserves were not affected by long-term heavy grazing.

Significant variations in root and crown biomass and in TNC concentrations existed among the 4 strains of Indian ricegrass and in response to clipping. Nezpar was superior to all other strains of Indian ricegrass tested at the more mesic Cortez uniform garden site with respect to crown biomass and carbohydrate reserves. Clipping resulted in greater crown biomass and TNC concentration of Nezpar, while clipping had little effect on the Chaco Canyon strains. This indicated that Nezpar was a better strain of Indian ricegrass to be recommended in the Cortez area with higher elevation and annual precipitation above 360 mm.

The 2 strains of Indian ricegrass from Chaco Canyon were not different from each other but were superior to Paloma. Their superiority was particuarly evident in their greater root biomass. These 2 strains from Chaco Canyon have promising genetic potential in their tolerance to drought and long-term heavy grazing. It is recommended that these Chaco Canyon strains be further evaluated for these traits and constituted into a single improved cultivar for use in revegetation of more arid regions (precipitation less than 250 mm) and at lower elevations in the western United States.

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Comparative photosynthetic responses of big bluestem to clipping versus grazing

L.L. WALLACE

Abstract

The gas exchange responses of big bluestem *(Andropogon gerardii)* were followed after defoliation by either cattle grazing or clipping and compared with the response of nondefoliated (control) plants. Grazed plants had significantly higher rates of photosynthesis than either clipped or control plants. The photosynthesis/transpiration ratio as well as stomatal sensitivity to humidity indicate that leaves of grazed plants may have developed in a higher light and lower moisture environment than that of their clipped counterparts. Although the experimental design could not preclude any indirect effects of animal activity (saliva, waste products, or trampling) on the grazed plants, the microenvironmental differences caused by grazing may be crucial in determining the responses of grasses to clipping versus grazing.

Key Words: *Andropogon gerardii*, Oklahoma, stomatal sensitivity, photosynthesis/transpiration ratio

A great deal of interest has been expressed in graminoid response to defoliation. Studies have focused on herbage production, plant morphology, and plant growth in response to defoliation, as well as responses to the method of defoliation, clipping versus grazing (Robinson et al. 1937, Vickery 1972, Reardon et al. 1974, Howe et al. 1982, King et al. 1984). The consensus appears to be that clipping or mowing a sward at a given height does not adequately mimic grazing. The primary reasons for this difference are: (a) grazing does not remove uniform amounts of forage from all tillers, hence removal of herbage from all tillers is unrealistically severe (Stroud et al. 1985), and (b) grazing animals have substantial indirect effects such as soil compaction and recycling of nutrients via dung and urine (Bauer et al. 1987; Wallace 1987a, b) that are not mimicked by clipping. Unfortunately, there have been few explicit tests of these mechanisms.

In this study, I attempted to ascertain some of the mechanisms which account for the differences that have been shown between clipping and grazing. By examining the photosynthetic responses of grazed, clipped, and nondefoliated (control) plants, I wished to determine which factors were not most closely correlated with plant response to these forms of defoliation. I expected that changes should be found in plant physiology that may precede changes that have been noted in plant morphology and productivity. Thus, the data presented here represent a preliminary assessment of the differences in the responses of big bluestem *(Andropogon gerardii)* to either clipping or grazing.

Methods

Three 40 × 40-m plots were established adjacent to one another in tallgrass prairie at the USDA Livestock and Forage Experiment Station at El Reno, Okla. The plots were located on a upland prairie site on fine, mixed thermic Udertic paleustolls (USDA 1976). Dominant plants in 3 plots included *Andropogon gerardii, Schizachyrium scoparium, Sporobolus asper, Sorghastrum nutans, Panicum virgatum, Vernonia* spp. and *Ambrosia psilostachya.* Nomenclature follows Correll and Johnston (1979).

Each of the 3 plots was delineated using 3 strands of electrical fencing. Within each plot were two 2.5 × 2.5-m exclosures, also constructed of electrical fencing. No microclimatic differences were found in the plots due to the presence of the fence. Half of each exclosure was left undefoliated while the other half was used for the clipping treatment.

Plants were grazed for 3 days with 20 steers during the third week in June, 1987, and the third week in July (the equivalent of 14 animals/ha as opposed to the recommended stocking rate of 0.5 animals/ha; S. Coleman, pers. comm.). This extremely high stocking rate was used to ensure that all plants within each plot were equally grazed. This was found to be the case since sward height was approximately 40 cm prior to grazing in June and 5–10 cm after grazing. Sward height was approximately 15 cm prior to grazing in July and was approximately 5 cm afterwards. Each plot was grazed to the extent that there was no litter and bare ground was exposed between plants. Sward height in the control plots averaged 52 cm prior to the July defoliation sequence. Litter accumulated to a depth of approximately 5 cm in both the clipped and control plots.

Clipping was done on the day that the animals were removed from a given plot and was done to the same height as the grazed plants. A nylon string "weed-eater" was used for clipping. Leaf blades remaining after each clipping and grazing were approximately 2 cm long. Therefore, most of the photosynthetic area of these plants was sheath tissue immediately after defoliation. Following animal removal from 1 plot, animals were rotated onto the adjacent plot for 3 days of grazing. Following that, animals were rotated onto the final plots for 3 days. This yielded a time series of measurements with sequential plots each having 3 days less time for recovery from grazing or clipping. Gas exchange measurements were taken 1 week and 2 weeks (in the first defoliation sequence only) following cessation of grazing in the first plot.

Gas exchange measurements were taken on the youngest, fully expanded leaves of big bluestem in grazed, clipped, and nondefoliated (control) treatments using a LiCor 6000 (LiCor, Lincoln, Neb.) portable, closed gas exchange system. Eight plants were measured per treatment per plot, yielding a total of 8 leaves per treatment in a plot. Four leaves of each treatment were measured inside each exclosure, yielding 8 leaves per treatment for the 2 exclosures. Leaves were held horizontally by the chamber during the 30-second measurement period. Stomatal conductance, transpiration rates and net photosynthesis were determined along with measurements of relative humidity, quatum flux, leaf temperature, air temperature, and vapor pressure deficits (VPD). Chamber air was well-stirred so that the boundary layer remained constant and negligible during measurements. All gas exchange measurements were taken between 1100 and 1330 CST on each measurement day. All samples were measured within this time frame to minimize variation due to diurnal environmental change.

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Research was funded in part by National Science Foundation Grant BSR 8307117. The author wishes to acknowledge the assistance of the personnel at the USDA Forage and Livestock Experiment Station at El Reno, Okla. Drs. M.M. Caldwell, E.L. Rice, S.L. Collins, and T. Svejcar reviewed an earlier draft of the manuscript.
Manuscript accepted 27 April 1989.

Prior to gas exchange measurements, 4 samples per treatment per plot were taken for gravimetric determination of soil moisture (10–15 cm depth). In addition, in July, samples were taken for determination of soil bulk density.

Tests for significant treatment and data effects were run using ANOVA's. Statistical significance was assumed at $p \leq .05$.

Results

Abiotic Parameters

There were no significant differences in quantum flux, leaf temperature, relative humidity, or soil bulk density between treatments at any date (Table 1). Minor differences in VPD were found in July. Significant differences ($p < .05$) were found in soil moisture in the July and August samples with clipped plots having significantly more moisture than the other treatments (July clipped = 10.48%^{a}, control = 9.68%^{b}, grazed = 9.03%^{b}; August clipped = 0.21%^{a}, control = 0.17^b, grazed = 0.14%^{b}). Values for each month followed by the same letter are not significantly different. It is unlikely that the differences noted in August were biologically important because they were so dry.

Table 1. Average values of incident light (μmole-²s¹), leaf temperature (° C), relative humidity (%) and vapor pressure deficit (mbars) at each sampling date. Values in a row followed by the same letter are not significantly different at $p \leq .05$, Duncans Multiple Range Test.

Parameter	Date	Control	Clipped	Grazed
Light	6/24	992^a	997^a	1100^a
	7/1	1623^a	1597^a	1684^a
	8/4	1591^a	1560^a	1452^a
Temperature	6/24	32.8^a	33.2^a	32.6^a
	7/1	37.1^a	35.9^a	35.6^a
	8/4	37.7^a	38.2^a	37.2^a
Humidity	6/24	30.1^a	28.4^a	29.1^a
	7/1	28.7^a	28.8^a	^{a}31.1^a
	8/4	24.5^a	23.4^a	24.2^a
VPD	6/24	34.2^a	35.8^a	34.7^a
	7/1	45.8^a	43.6^{ab}	40.6^b
	8/4	49.0^a	52.6^a	49.3^a

Gas Exchange

Plants in both defoliation treatments had rates of photosynthesis which were initially depressed relative to the control leaves, but rates increased by day 5 (Fig. 1). After day 3 of the first defoliation sequence, photosynthesis of leaves on the grazed plants was always higher than that of clipped leaves. This difference was significant on days 12 and 15. However, following day 5, the photosynthetic rate of the clipped leaves was never significantly different from the controls. The second defoliation sequence occurred during a seasonal drought. Although rates were much lower than in the first sequence, clipped leaves had the lowest rates of all of the treatments, with this difference being significant on days 11 and 13.

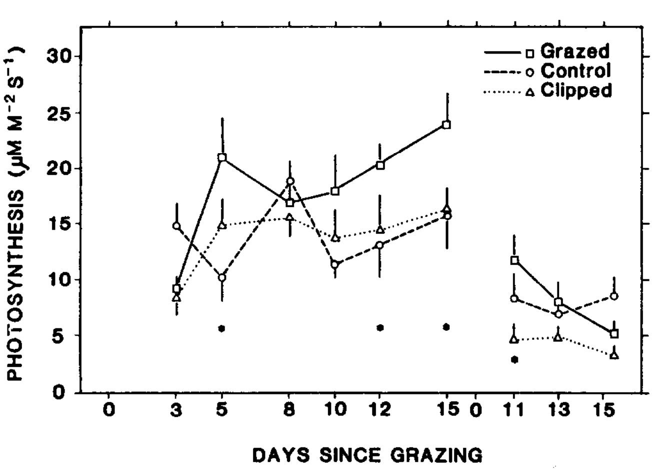

Fig. 1. Time course of photosynthesis after defoliation for both defoliation sequences. Significant ($p \leq .05$) differences between clipped and grazed plants are denoted by an asterisk. Bars represent one standard error of the means plotted for each date and treatment (n = 8).

There were fewer differences between defoliation treatments in stomatal conductances or transpiration rates (Fig. 2). Grazed leaves had significantly greater stomatal conductance than clipped leaves only once. However, both defoliation treatments tended to have greater stomatal conductance values than the control treatment. Transpiration rates were also greater in the defoliated leaves. However, there was no consistent pattern of difference between the clipped and grazed treatments.

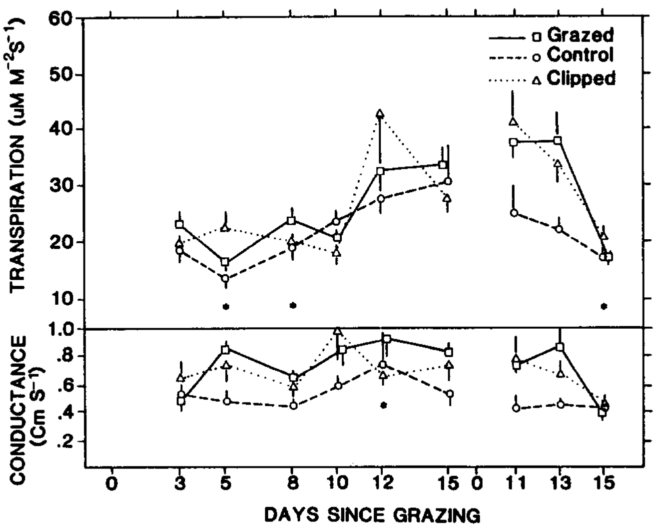

Fig. 2. Time course of stomatal conductance and transpiration after defoliation. Treatment codes and legends are as in Figure 1.

Stomatal sensitivity to humidity (transpiration/VPD) was significantly affected by treatments, with control leaves being significantly less sensitive than either defoliation treatment (grazed mean = 0.65, clipped = 0.64, control = 0.48). There was also a significant date effect, with leaves in July being more sensitive than leaves at other measurement dates. There were no significant interactions between date and treatment.

Multiple regression analysis was conducted on photosynthetic rates for all 3 treatments at all dates to ascertain what factors appeared to be the most highly correlated with photosynthetic rates (Table 2). Grazed leaves showed little correlation with transpiration whereas both clipped and control leaves had negative correlations with transpiration in July. All treatments showed positive, strong correlations with stomatal conductance. Correlations with incident light were always positive but were of less importance to the model than were correlations with stomatal characteristics and indications of water availability (soil moisture and VPD). Thus differences between treatments appear to be how the clipped and control leaves respond to moisture availability.

Discussion

Increased rates of photosynthesis following grazing and clipping were reported in several studies (Vickery 1972, Detling et al. 1979, Painter and Detling 1981, Detling and Painter 1983, Wallace et al. 1984). Some of these studies correlated increased photosynthesis with increased stomatal conductance (Gifford and Marshall 1973, Painter and Detling 1981, Detling and Painter 1983, Wallace et al. 1984). In this study, photosynthesis was also found to be positively correlated with stomatal conductance similar to these cited results.

Table 2. Factors which significantly ($p<.05$) correlated with photosynthesis in each treatment. Correlation coefficients are given for each factor as well as the significance terms for the whole model determined by stepwise multiple regression.

Date	Control*	R^2	p	Clipped	R^2	p	Grazed	R^2	p
6/24	–.34 VPD			9.7 CM			25.4 CM		
	.39 Tran			–1.8 Smst			.0101 QU	.808	.0001
	.011 QU	.901	.0001	.006 QU	.562	.0011			
7/1	42.4 CM			33.6 CM			–1.4 VPD		
	–.9 Tran	.878	.0001	–1 Tran			8.0 CM		
				.006 QU	.613	.0004	2.4 LT	.671	.0001
8/4	–18.2 CM			5.6 CM	.367	.0017	NS		
	–427 Smst	.740	.0001						

*CM = stomatal conductance (cm s^{-1}), Tran = transpiration (mmole H_2O $m^{-2}s^{-1}$), Smst = soil moisture (%), QU = quantum flux (mmole $m^{-2}s^{-1}$), VPD = vapor pressure deficit (mbars), LT = leaf temperature (° C), NS = no significant model found.

However, the increase in photosynthesis over time in the first defoliation sequence was not mirrored in the response of stomatal conductance (Figs. 1, 2). The difference in photosynthesis can not be ascribed solely to differences in conductance. This may be partially explained by the low soil moisture content in the grazed plots since litter may have acted as a mulch in the clipped and control plots. This is contrary to expected results (Wraith et al. 1987).

In the few studies that have explicitly tested the differences between clipped and grazed plants, the greater production or growth of the grazed plants was attributed to differences in leaf display, leaf population age structure, and the nonuniform nature of herbivory (White 1973, King et al. 1984, Parsons et al. 1984). In grazed plants, increases in photosynthesis following grazing have also been attributed to increased incidence of light on previously subtending leaves (Mcnaughton et al. 1981, Caldwell et al. 1983). Caldwell et al. (1983) found that leaves near the interior of bunchgrass canopies exhibited extreme saturation-type light response curves with very low light saturation points. They attributed this to the fact that these leaves developed in a very low light environment. In this study, leaves of the grazed plants were the least shaded since there was extreme canopy reduction and bare ground exposed between plants.

Another method of evaluating the physiological status of a leaf is to examine the ratio of photosynthesis to transpiration (P/T) (Caldwell et al. 1983). They found that leaves that had developed in the sun had higher P/T ratios than did leaves that had developed in the shade. However, I found no such pattern of change in P/T ratios over time following either clipping or grazing (Fig. 3). Unlike Nowak and Caldwell (1984), I did find that leaves of grazed plants had the highest P/T ratios 4 of the 6 measurement days of the first defoliation sequence and were significant greater than leaves of clipped plants 5 out of 6 measurement days. More data will be necessary for a definitive discussion of plant response to canopy structure changes, but these differences indicate that the microclimatic changes in light intensity that accompany ungulate herbivory may be important in plant response.

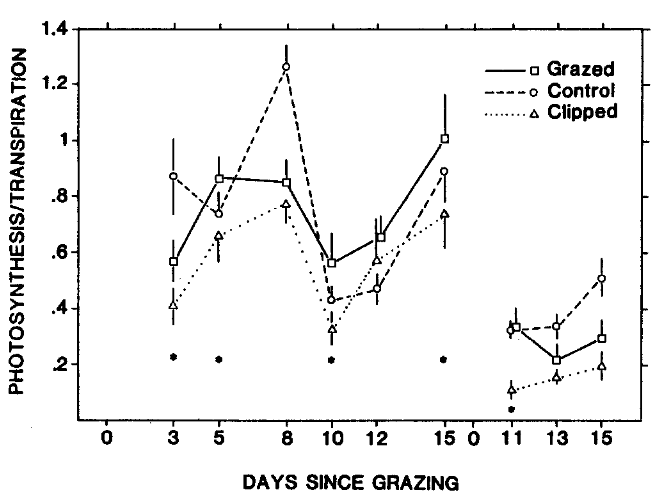

Fig. 3. Time course of the ratio of photosynthesis to transpiration after defoliation. Treatment codes are as in Figure 1.

Additional studies have quantified the defoliation probability for tillers exposed to grazing ungulates (Briske and Stuth 1982). The proportion of tillers defoliated after 33 days of moderate grazing was not 100%, as it would be in the clipped or mowed systems. Although most tillers were defoliated once or twice during this period, plants were not completely defoliated nor were all tillers on a plant grazed at any one time. This would allow for the canopy to be much more open in patches with a greater penetration of light to the base of the plant in those areas. Light penetration models (Sheehy and Cook 1977) have shown increased light intensities in grass canopies with canopy gaps that would occur in differentially grazed systems. Several authors have cited increased light as the reason for high productivity and/or tillering of grazed swards (McNaughton et al. 1981, King et al. 1984, Parsons et al. 1984). In mowed swards, light penetration was actually found to be decreased in one study (Ludlow and Charles-Edwards 1980). In this study, the extremely intense grazing opened the canopy to the point that bare ground was exposed between plants. It would be reasonable to expect, then, that leaves in the grazed plots, would have developed in high light conditions.

In this study, greater rates of photosynthesis may be due to changes in the abiotic environment of the individual leaf. This study was not designed to separate any other effects of grazing animals, i.e., saliva or trampling. Mechanisms do exist for more closely imitating the grazing process via clipping (Stroud et al. 1985), and these should be utilized to test for the effects of animal saliva on plant growth and physiological responses to herbivory.

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Comparison of actual and predicted blue oak age structures

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Abstract

There is increasing interest in understanding the role of management on the current lack of blue oak (*Quercus douglasii* H. & A.) recruitment on California foothill rangelands. Age structure analysis has been suggested to relate when and how much recruitment occurred under past management as an indication of current management effects on recruitment. Previous estimates of blue oak age structure were based on unquantified correlations between age and diameter. Using regression analysis we found that diameter at breast height (DBH) accounted for 42–71% of the variation in tree age at 2 sites. Actual age structures were significantly different than age structures predicted from all regression equations at both sites. We suggest that the use of age structures to infer the role of management on blue oak population dynamics requires direct age measurement.

Key Words: *Quercus douglasii*, age-size relationships, California foothill rangeland

Blue oak (*Quercus douglasii* H. & A.) recruitment since the 1920's has been described as rare on most of its 1 million hectare distribution on California foothill rangelands (Bartolome et al. 1987). As the dominant and often only woody species in the oak-annual grassland savanna, blue oak is considered desirable because it can provide important browse, mast, and cover for wildlife and livestock (McClaran 1986) and increases herbaceous understory production in low rainfall areas (Bartolome 1987). Unlike the more common situation of increased woody species density on western rangelands in the past century and concomitant emphasis on management to curtail recruitment, the lack of blue oak recruitment has stimulated interest in management that is compatible with recruitment. Increased interest in the role of management on recruitment problems of this California endemic have helped stimulate 2 symposia in the last decade (Plumb 1980, Plumb and Pillsbury 1987), proposals for state regulation of fuelwood cutting (Walt et al. 1985), suggestions for reduced livestock grazing, and solicitation of State sponsored research (Bartolome 1987).

Griffin (1977) suggested that current low blue oak recruitment can best be understood by using age structures to describe when and how much past recruitment occurred. Previous age structure studies used unquantified relationships between tree age and diameter, calculated from a subsample of the population, to predict tree ages in the remaining sample population (White 1966,

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Authors wish to thank Charlie Sellers and the staff at Sierra Foothill Range Field Station for field assistance; A. Goldsmith for editorial comments; and J. Helms for providing opitical equipment.

Manuscript accepted 17 May 1989.

Table 1. Correlation coefficients *(r)*, regression equations (age = a + b_1x_1 + b_2x_2) predicting blue oak age at 5 cm height, and goodness-of-fit probability for actual and predicted age structures in 2 central Sierra Nevada sites. Values in parentheses are 1 standard error of the mean.

			Regression Estimates				Goodness-of-fit
Site	N	Independent variable(s)	r	a	b_1	b_2	Smirnov P-value
Campbell	95	DBH	0.66 (0.08)	48.3 (4.3)	0.6 (0.1)		<0.001
		DBH + DBH^2	0.71 (0.07)	28.4 (6.3)	1.5 (0.2)	0.01 (0.01)	<0.001
		$\log_{10}$DBH	0.70 (0.07)	–41.6 (13.1)	75.1 (8.0)		<0.001
Koch	278	DBH	0.84 (0.03)	22.9 (1.8)	3.2 (0.1)		<0.001
		DBH + DBH^2	0.84 (0.03)	22.3 (3.0)	3.3 (0.4)	–0.01 (0.01)	<0.001
		$\log_{10}$DBH	0.74 (0.04)	–14.6 (4.4)	78.1 (4.2)		<0.001

Vankat and Major 1978). This approach was taken because increment core samples were believed to be too difficult or time consuming to obtain. Unfortunately, these authors did not include correlation coefficients, predictive equations, or goodness-of-fit estimates for the relationship between age and size for reference or review. Predicting age structures from size structures through the use of predictive equations from population sub-samples is common, but it has also been criticized for being too inaccurate to reliably describe actual age structures (Harper 1977, Lorimer 1985).

Because current and future research in the role of management on blue oak recruitment will likely focus on age structure analysis, our objective is to evaluate the predictive relationship between blue oak age and size by comparing actual age structures with age structures predicted from age-size relationships.

Materials and Methods

We studied blue oak age structures and predictive age-size relationships on 2 sites within the University of California Sierra Foothill Range Field Station (39° N, 121° W) 30 km east of Marysville, California, in the Sierra Nevada foothills. Station rainfall and temperature patterns are typical of a mediterranean climate, with hot dry summers and cool wet winters that average 73 cm precipitation annually. The two 5-ha study areas were approximately 5 km apart on $\leq$10° slopes, with the Koch site at 500 m elevation and the Campbell site at 300 m. Soils on both sites are Sobrante rocky loam, a mollic haploxeralf developed from granitic parent material. Blue oak cover (from ocular estimates) and basal area on the Koch site was 25% (SE = 4.3) and 13.5 m^2 ha^{-1} (SE = 1.5), and 22% (SE = 3.3) and 62 m^2 ha^{-1} (SE = 8.8) on the Campbell site. On both sites tree height was $\leq$12 m, and over 90% of the trees were blue oak. The pattern of spatial arrangement of the trees was not measured, but we estimated that it was between a contagious and random pattern. Introduced herbaceous annuals, $\leq$1 m tall and 1,000–3,000 kg ha^{-1}, dominated the understory and savanna openings.

In July 1983 and 1984, we measured diameter to the nearest centimeter at 135 cm (breast-height, DBH), 60 cm, and 5 cm aboveground, cut, and removed the cross section at 5 cm aboveground from all blue oak trees in nine 0.05-ha plots on Campbell (N = 95 trees) and six 0.1-ha plots on Koch (N = 278 trees). Plots were located randomly on both study sites. Trees were cut to maximize dating accuracy. We dated each cross-section by counting annual increments along 2 radii (Stokes 1980) after sanding with 200 grit paper.

To describe blue oak age-size relationships at each site, we calculated regression equations and correlation coefficients (Steel and Torrie 1980) with age as the dependent variable and diameter as the independent variable. After assessing a scattergram of the size and age data, and in reference to previous studies (e.g., Leak 1985) we decided to evaluate the age-size relationship using actual diameters and $\log_{10}$ transformation of diameter in separate simple regression analyses, and a curvilinear description with diameter + diameter² as independent variables in a multiple regression analysis. We restricted our sample to trees less than 200 yr because there were only 8 trees older than 200 yr, and these outliers had a significant effect on the regression estimates. We also excluded approximately 10% of the trees from the analysis because they had rotten centers or multiple trunks.

To compare the actual and predicted age structures we assessed the goodness-of-fit for these regression equations. We used the Smirnov test (Lehmann 1975) to evaluate the goodness-of-fit for each equation.

Results and Discussion

Diameter at breast height (DBH) proved to be more strongly related to tree age than diameters taken at lower heights, therefore we will restrict our presentation to results of analyses using DBH. All correlation coefficients (*r*) were different ($p \leq 0.01$) from zero, but only 42–71% (R^2) of the variation in age was associated with DBH. The highest *r* values were with DBH, and DBH + DBH² as the independent variables on the Koch site (Table 1), where all 4 simple regression equations (age = a + b_1x_1) were different for each independent variable at each site. The curvilinear equation, however, was different from the simple DBH equation only at Campbell (Table 1).

All 6 regression equations produced predicted age structures significantly different from the actual age structure (Table 1). In all cases, predicted age structures from the regression equations were more continuous and broadly uneven than the actual age structures at both sites (e.g., Fig. 1).

Low correlation coefficient values and poor goodness-of-fit suggest that blue oak age or age structure cannot be accurately estimated from tree diameter. In addition, our results suggest that blue oak age and diameter relationships vary geographically.

Lorimer (1985) suggested that correlation between tree age and diameter would be better if the stand was broadly uneven aged. Our results agree; we found a higher correlation between blue oak age and diameter in the stand with a greater range of ages (Koch). The lack of improvement in the *r* values when using a curvilinear (DBH + DBH²) equation agrees with Leak's (1985) study of age and diameter relationships in 10 taxa.

Difficulty in predicting tree age from tree size is not surprising (Harper 1977, Lorimer 1985), but ramifications of this problem have focused on accurate dating without much attention to age structure shape. Accurate dating along with relative abundance in each age class (age structure shape) are critical to describing the timing, duration, and reoccurrence of management practices and natural events that might affect an age structure. Therefore the search for management and natural events that affect an age structure will be led astray by both inaccurate dating and shape of age structures. In the case of blue oak, previous age structure estimates generated from age-diameter relationships suggested abundant recruitment occurred between 1880–1920, and management and

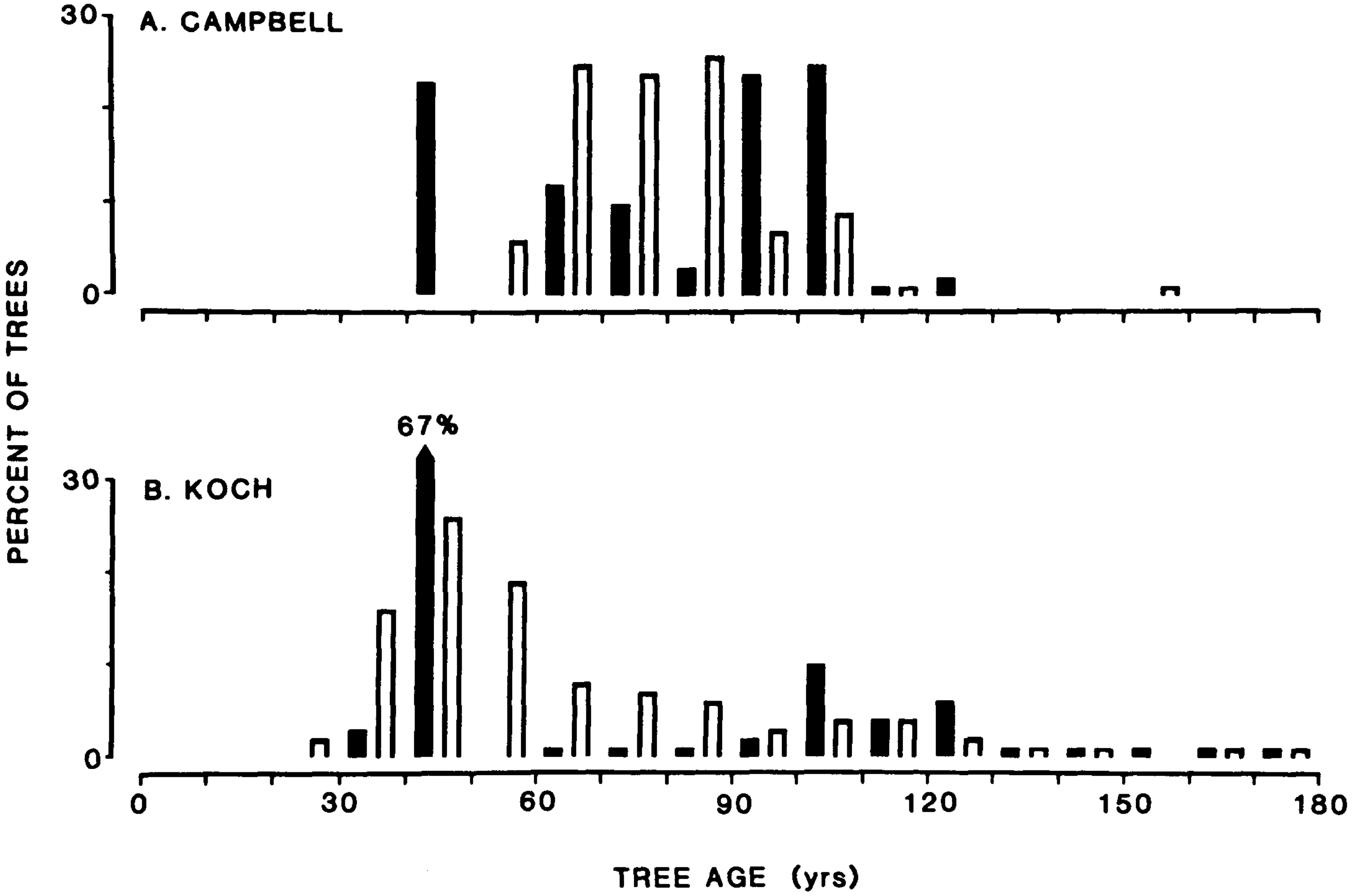

Fig. 1. Actual (solid bar) and predicted (open bar) age structures at both sites as a measure of goodness-of-fit for the linear regression equation with diameter at breast height as the independent variable. Actual and predicted distributions are different for both sites (Table 1).

natural events occurring throughout that 40-yr period, such as increased livestock grazing, decreased fire frequency, or deer population decline were considered to have affected that age structure (White 1966, Vankat and Major 1978). We found that blue oak age structures generated from predictive equations depict a more continuous and broadly uneven age structure than actually occurred. This result suggests that the search for coincident management and natural events should instead focus on events of shorter duration and more sporadic reoccurrence than previously considered.

We conclude that accurate estimates of blue oak age structure cannot be based on predictive age and diameter relationships. Therefore we suggest that future studies of blue oak age structure should be based only on direct measure of tree age from increment cores or tree cutting.

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Herbage production of Mediterranean grassland under seasonal and yearlong grazing systems

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Abstract

Data from 2 consecutive grazing experiments conducted over 7 years on a Mediterranean type grassland were used to calculate forage consumption by herds of beef cattle maintained at different stocking rates and in different grazing systems. In the first experiment the animals were on the experimental range for 8 months of the year; in the second, grazing was yearlong. Total production of herbage mass was estimated from these data and from the residual litter in the paddocks at the end of the dry season. Production of dry herbage mass varied between 2,600 and 3,800 kg/ha, with a mean and SD of 3,060 ± 300 kg/ha. While variation between years was relatively small but significant ($P < .01$), the effect of stocking rate or grazing system (seasonal, yearlong) was smaller and not significant. It is concluded that the attained level of herbage production of Mediterranean grassland on relatively shallow basaltic protogrumosols is not sensitive to total precipitation over a very wide range or to grazing system. It may be dependent on the availablity of nutrients, especially nitrogen, and the seasonal distribution pattern of available soil moisture in a restricted rooting zone.

Key Words: continuous grazing, rotational grazing, forage consumption, supplemental feeding

In order to determine herbage production of rangeland under grazing, it is necessary to solve methodological and logistic problems encountered in estimating long-term intake of forage by the herd and in sampling herbage on large, heterogeneous range units. It is therefore not easy to determine quantitatively the degree to which environmental and management factors limit rangeland productivity in different situations. Annual herbage production has been shown to depend on various environmental factors, in particular precipitation and soil moisture (Le Houerou and Hoste 1977, Murphy 1970), radiation and temperature (Wallach and Gutman 1976), temperature indices like accumulated degree days (George et al. 1988), soil nitrogen, and phosphorus (van Keulen 1975, Penning de Vries and Djiteye 1982, Benjamin et al. 1982). Effects of stocking rate or grazing system on annual herbage production are superimposed on the environmental effects and may interact with them. The effect of defoliation by grazing is dependent not only on the severity of the grazing, but also on the ecology of the habitat (Noy-Meir and Walker 1986). In seasonal ranges, the end of the season can be abrupt when it is caused by photoperiodically induced maturity or by drastic weather change, like the hot, searing winds in the Mediterranean region; or it can depend on the availability and rate of depletion of a resource like water or nutrients. In the first case, increasing grazing pressure should, in theory, reduce primary production; in the second case, not necessarily so (Noy-Meir 1978).

Data obtained over 7 years from grazing trials conducted on rocky basaltic foothill range in a typical Mediterranean type environment were used to analyze effects of grazing system (seasonal and yearlong), grazing method and stocking rate on estimates of herbage production. The objective of the study was to determine the sensitivity of herbage production at the experimental site to differences in grazing management over a period of years. Detailed analysis of animal performance in these experiments is reported elsewhere (Seligman and Gutman 1979, Gutman et al. 1989).

Materials and Methods

Experimental Site

The trial was conducted at the Karei Deshe Experimental Range in the lower Galilee of Israel, situated near the Jordan River and the Kinneret Lake (Sea of Galilee), lat. 32° 55′N, long. 35° 35′E, alt. 150 m. The topography is hilly, with slopes generally less than 10%. The soils are brown basaltic protogrumosols with variable depth but seldom deeper than 60 cm and with a rock cover of about 30% (Gutman 1977, Gutman and Seligman 1979). The vegetation is dominated by hemicryptophytes (forbs and grasses that have a perennial root system but lose most of the shoot during the dry summer) that include *Hordeum bulbosum* L., *Echinops* spp., and *Psoralea bituminosa* L. (Zohary 1972). There are also many annual species, some of which are palatable pasture plants (*Avena sterilis* L., *Bromus* spp., *Trifolium* spp., *Medicago* spp., and many others) while others are palatable for only short periods during the early vegetative stages (e.g., *Scolymus maculatus* L., *Brassica nigra* L., *Echium plantagineum* L.). Annual legumes comprise between 5 and 25% of the herbaceous cover; Hordeum bulbosum and annual grasses often account for more than 40% of cover (Seligman and Gutman 1979).

The rainy season begins in October or November and ends in April. Mean annual precipitation (±SD) during the experiment was 554 ± 169 mm, fluctuating between extremes of 322 and 761 mm. Monthly precipitation is highly variable during the early and late months of the season, less so between December and March (Table 1). Seasonal growth of the range vegetation begins in November to December soon after the first rains. The herbage biomass exceeds 600 kg/ha DM usually by end of January. Growth continues in dependence on moisture and temperature conditions until it peaks during April. By mid-May the herbaceous

Table 1. Monthly precipitation at Karei Deshe during the experimental period (mm).

Year	75/76	76/77	77/78	78/79	79/80	80/81	81/82	Mean	CV (%)
Month[1]									
Oct	0	34	0	31	46	18	0	18	105
Nov	32	180	39	35	72	3	44	58	100
Dec	145	41	202	89	215	163	17	125	62
Jan	77	104	139	66	122	263	30	114	60
Feb	96	53	67	39	128	153	187	103	53
Mar	102	114	136	52	121	107	69	100	30
Apr	51	90	16	10	57	20	11	36	83
Total	503	616	599	322	761	727	358	554	31

[1] During May to September inclusive, there was no significant rain during the study period.

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Manuscript accepted 9 May 1989.

Table 2. Energy concentration of pasture forage and supplementary feeds (Mcal/kg DM).

Feed source	Metabolizable energy CME (gain)	Net energy CNE_m (maint)	Net energy CNE_g (gain)
Green pasture forage	2.3	1.43	0.84
Dry pasture forage	1.6	0.76	0.23
Poultry litter (PL)	1.56		
Wheat Straw (ST)	1.45		
Barley grain (BG)	3.04		

Energy expenditure grazing factor for grazing activity (GRZ) = 1.6

Table 3. Daily energy requirements (Mcal/cow/d) and forage intake (kg/cow/d), derived from NRC (1984).

W = liveweight, kg; G = daily EBW gain, kg/d; t = days after conception

Cows

Variable		Equation
NE for maintenance	NE_m	$= 0.077\ W^{.75}\ GRZ$
NE for gain	NE_g	$= 6.25\ G$
ME for maintenance	ME_m	$= NE_m\ CME/CNE_m$
ME for gain	ME_g	$= NE_m\ CME/CNE_g$
Forage DM intake/cow/day	DMI	$= (ME_m + ME_g - SUP_m - SUP_g)/CME$
Daily ME intake from PL and ST	SUP_m	= PL intake + ST intake
Daily ME intake from BG	SUP_g	= BG intake
Pregnancy	NE_p	$= a \exp(b)$ $a = 0.028\ (0.0149-0.0000407t)$ $b = 0.05883t-0.0000804t^2$

Calves

Variable		Equation
NE for maintenance	NE_m	$= 0.077\ W^{.75}\ GRZ$
NE for gain, medium frame, male	NE_g	$= 0.0493\ W^{.75}\ G^{1.097}$
NE for gain, medium frame, female	NE_g	$= 0.0686\ W^{.75}\ G^{1.119}$

species are dry. During the green season the herbage is of high quality and animals gain rapidly. In the dry seasson, quality is sufficient for maintenance only during the first few months (Table 2).

Experimental Design

Six paddocks, in 2 blocks of 3 each, were available for the experiment. The paddocks were 25.5 to 33.0 ha in size and fenced so as to include equivalent proportions of the different range habitats in each paddock (Gutman and Seligman 1979). Throughout the experimental period, there were 3 grazing treatments. These were replicated twice, once in each block. The data for this study were taken from 2 consecutive experiments conducted at the same site. The first experiment (1976–1977) compared stocking rate and grazing method (continuous and rotational) during a season that began when the germinating pasture reached 500–700 kg/ha green herbage DM usually during January, and terminated at the end of the dry season in September. For about 4 months, between September and January, the animals were removed from the experimental paddocks. The herds for each paddock were reassembled each year, but the paddocks used for each grazing treatment were the same. The grazing treatments were seasonal continuous heavy (SCH), seasonal continuous light (SCL), and seasonal rotational heavy (SRH). The heavy treatments were stocked at 0.9 cows/ha; the light treatment at 0.6 cows/ha. In the rotational system, the paddocks were subdivided into 3 fenced subsections that were rotationally grazed with 3–5 week grazing periods, depending on the herbage growth (Gutman and Seligman 1985). The second experiment (1978 to 1982) used yearlong continuous grazing to compare 3 stocking rates: high (0.83 cows/ha), moderate (0.67 cows/ha), and light (0.50 cows/ha), designated YCH, YCM, and YCL, respectively. The second experiment (1978–1982) began in January 1978 and was terminated at weaning on 19 July 1982. The herds in each stocking rate treatment stayed in their paddocks throughout the experiment except when taken to a central corral for weighing or veterinary treatment.

Animals

The cows were crosses and backcrosses between local (Balady) cows and Brahman, Hereford, and Simmental bulls. They were small and weighed on the average of 340 kg. They were allocated between treatments so as to achieve evenly composed herds with equivalent initial weight and age structure. During the 'seasonal' grazing experiment, the herds were randomly assembled each year so that there was no carry-over effect of animal response from one year to the next. During the 'yearlong' grazing experiment, herds remained in the paddocks throughout the 5-year grazing trial. From July onwards, cows were supplemented ad libitum with poultry litter fed from large troughs to which all animals had free access. After the early rains, barley grain was mixed with poultry litter (20% barley) and straw was given in daily rations that varied with stocking rate. Supplementation ceased when green pasture became well established, usually between the middle and end of January (Tables 2 and 4). No supplements were given in the last year because the experiment terminated at weaning before the supplementary feeding period. In the seasonal experiment all cows were with calf at least at the beginning of the year.

In the yearlong experiment cows were all with calf only in the first year, after which the calving rate depended on the breeding

Table 4. Supplementary feed given to experimental herds (kg/ha).

	Supplementary feed								
	Poultry litter			Barley grain			Straw		
Seasonal grazing system									
Treatment[1]	SCH	SCL	SRH	SCH	SCL	SRH	SCH	SCL	SRH
1976	14	9	14	0	0	0	0	0	0
1977	27	20	27	0	0	0	0	0	0
Mean	20	15	20	0	0	0	0	0	0
Yearlong grazing system									
Treatment[1]	YCH	YCM	YCL	YCH	YCM	YCL	YCH	YCM	YCL
1978	1130	690	570	36	21	11	240	29	4
1979	860	590	400	70	48	37	310	0	0
1980	960	720	610	140	110	91	330	85	0
1981	1280	730	580	140	64	45	370	100	0
1982[2]	0	0	0	0	0	0	0	0	0
Mean	1060	680	540	96	60	46	310	54	1

Analysis of variance (CH and CL treatments only)

Variable Source	Poultry litter F-value	Poultry litter PR>F	Barley grain F-value	Barley grain PR>F
System	1284.7	.0001	—	—
Stocking rate	87.2	.0001	21.6	.0007
r^2	0.99		0.62	
CV (%)	7		31	
n	24		16	

[1] See Study Area and Methods.

[2] Experiment terminated on 19 July 1982, before any supplements were given.

[3] 1978 to 1981

performance of the cows in each experimental paddock. Bulls (grade Simmental) were with the cows between November and May. Calves generally were weaned between July and August. Pregnancy tests (by rectal palpation) were conducted after the last weaning and about 3 months after the bulls were removed from the herds. Cows in the yearlong experiment were replaced to maintain stocking rates only after skipping 2 consecutive breeding seasons or because of mortality.

Estimate of Forage Consumption and Herbage Production

The cows and calves were weighed during the experiment at 1- to 2-month intervals after withdrawal from water or feed for 18 hours. The normative consumption of pasture forage was calculated from net energy requirements of cows and calves for maintenance, physiological status, and live weight gain according to NRC standards (NRC 1984) using the equations shown in Table 3. Maintenance requirement was corrected to account for grazing activity by multiplication with a grazing factor (GRZ) of 1.6, as obtained in an experiment with sheep (Benjamin et al. 1977). The energy requirements used to calculate dry range forage consumption in the dry season were corrected for supplementary feed consumed during the period (Table 4). Forage intake was then calculated from net energy concentrations for maintenance and gain for green and dry range forage. These values were derived from estimates of metabolizable energy of local range vegetation (Table 2).

Amount of remaining dry herbage in each paddock was estimated at the end of the dry season in October before the first rains of the following rainy season. Estimates were based on calibrated ocular estimates (Tadmor et al. 1975) along permanent transects in the experimental paddocks; the herbage mass in 300 25 × 25-cm quadrats in each paddock was estimated and 30 (every tenth quadrat) were clipped for calibration.

Statistical Analysis

The comparison between seasonal and yearlong grazing systems in this experiment cannot be conclusive because the systems were studied consecutively on the same range and not in parallel. Consequently, year effects overlap grazing system effects. Despite this problem, the grazing system is analysed as a separate factor because of the large differences between the systems: seasonal pasture utilization vs. yearlong, newly assembled herds each year vs. permanent herds, negligible supplementation vs. heavy supplementation. In addition, the 2 systems were compared on the same range in the same paddocks. Therefore, in the analysis of herbage consumption and production, year effects and system effects were analyzed separately. In order to facilitate the analysis, only systems that were comparable in both systems were included: SCL, SCH, YCL, and YCH. Data from the SRH and YCM treatments that were excluded from the statistical analysis are presented in Tables 3 to 5 for comparison.

Analysis of variance was calculated with the SAS (1985) general linear model (GLM) procedure. In the analysis, systems (seasonal and yearlong), stocking rates (high and low), year, and interactions were taken into account. Several versions of the model were tried but most interaction terms were not significant. In the final model only significant interactions and interactions of special interest were included. For each variable analyzed, the coefficient of determination (r^2), the coefficient of variation of the residual sum of squares (CV), and the number of observations (n) are presented. In the analysis of animal responses, each individual animal in a year is an observation; hence, n is in the hundreds. In the analysis of herbage consumption and production, each paddock in a year is an observation; hence n=28.

Table 5. Animal performance under seasonal and yearlong grazing systems.

	Cow live weight[2] (kg/cow)			Calf weaning wt (kg/calf)			Weaned LW production (kg/ha)[3]		
Seasonal grazing system									
Treatment[1]	SCH	SCL	SRH	SCH	SCL	SRH	SCH	SCL	SRH
1976	326	315	306	211	200	190	108	61	91
1977	331	338	312	211	214	200	116	79	95
Mean	329	327	309	211	207	195	112	70	93
Yearlong grazing system									
Treatment	YCH	YCM	YCL	YCH	YCM	YCL	YCH	YCM	YCL
1978	342	362	391	211	206	217	92	74	60
1979	333	339	377	187	190	215	136	89	83
1980	328	322	349	166	178	202	104	93	85
1981	349	334	365	176	165	184	99	77	55
1982	349	321	348	182	151	182	88	79	82
Mean	340	336	366	184	178	200	104	82	73

Analysis of variance (CH and CL treatments only)

Variable	Cow live weight		Calf weaning wt.		Weaned LW/ha	
Source	F-value	Pr>F	F-value	Pr>F	F-value	Pr>F
System	17.5	0.001	18.2	.0001	0.1	.7533
Stocking rate	11.3	.0001	2.4	.1200	23.8	.0001
SR * SYST	6.1	.0136	6.7	.0102	0.6	.4625
r^2	0.06		0.07		0.51	
CV (%)	17		18		21	
n	542[4]		466[4]		28[5]	

[1] See Study Area and Methods.

[2] Cow liveweight at weaning.

[3] In years 1976, 1977 and 1978, weaned LW production on range = weaning wt. – wt on entry into the experiment.

[4] Individual animal observations.

[5] Whole paddock observations.

Results

In the seasonal grazing experiment, the cows consumed only small amounts of supplement (poultry litter in summer) while in the yearlong experiment, massive supplementation with poultry litter, barley, and straw were required, particularly in autumn and early winter. The amounts consumed increased with stocking rate (Table 4).

Mean cow weight per treatment at weaning varied between extremes of 310 and 390 kg/cow (Table 5). The cows in the seasonal experiment were slightly smaller than those in the yearlong experiment. The mean calf weights at weaning were similar at the beginning of each experiment, but on the average were lower in the yearlong experiment (Table 5). This can be ascribed to the fact that during the seasonal experiment the cows with calves were all pre-selected for early calving whereas in the yearlong experiment, later birth dates led to lower weaning weights. Overall, grazing treatment differences accounted for only 6 to 7% of the variation in cow and calf weight at weaning. Consequently, weaned calf weight per unit area was determined largely by stocking rate, which accounted for more than 50% of the variation. Differences between systems were not significant. During the driest year (1979), herbage production was average and animal production per unit area was the highest it had been during the whole experimental period (Table 6). An important factor that determined weaned liveweight production per unit area was the weaning rate. This, together with the fact that pasture inadequacy was partially made up with supplementary feed, contributed to the poor correlation between calf liveweight per unit area and herbage production or precipitation.

In each year the animals were in the paddocks for a shorter period during the seasonal experiment compared to the yearlong experiment. Consequently, the calculated mean annual pasture consumption per ha for equivalent stocking rates (CH and CL) was lower ($P<0.01$), and unused herbage at the end of the grazing season was higher ($P<0.05$) during the seasonal grazing experiment (Table 6). The mean total dry herbage production from the range, calculated by summing the forage consumption and residual herbage, was strikingly similar in both experiments at about 3,000 kg/ha (Table 6). Differences between treatments were very small and not significant. Differences between years were significant, mainly because of a particularly productive year in 1978, the first year of the yearlong, continuous grazing experiment.

Table 6. Annual forage consumption, residual herbage at the end of the dry season and total dry matter production in the experimental treatments (kg/ha DM).

	Forage consumption			Residual litter			Total production		
Seasonal grazing system									
Treatment[1]	SCH	SCL	SRH	SCH	SCL	SRH	SCH	SCL	SRH
1976	2200	1420	2020	900	1610	1130	3100	3030	3150
1977	2270	1720	2190	660	1230	1000	2930	2950	3190
Mean	2240	1570	2100	780	1420	1070	3010	2990	3170
Yearlong grazing system									
Treatment[1]	YCH	YCM	YCL	YCH	YCM	YCL	YCH	YCM	YCL
1978	2840	2670	2280	810	1080	1570	3650	3750	3850
1979	2610	2360	2160	500	560	820	3110	2920	2980
1980	2710	2170	1960	400	540	1010	3110	2710	2970
1981	2060	1820	1930	550	770	1280	2610	2590	3210
1982[2]	1960	1460	1320	1020	1170	1500	2980	2630	2820
Mean	2440	2100	1930	650	820	1230	3090	2920	3160

Analysis of variance (CH and CL treatments only)						
Variable	Forage consumption		Residual litter		Total production	
Source	F-value	Pr>F	F-value	Pr>F	F-value	Pr>F
System	16.2	.0012	7.6	.0154	1.5	.2416
Stocking rate	76.6	.0001	134.7	.0001	0.3	.6018
Year	15.9	.0001	14.8	.0001	7.1	.0017
SR * SYST	1.8	.1788	1.3	.3050	1.3	.3170
r^2	0.93		0.94		0.76	
CV(%)	8		14		8	
n	28		28		28	

[1] See Study Area and Methods

[2] Grazed up till 19 July 1982.

Discussion

Herbage production as estimated in the present study does not include plant material that was lost by decomposition or removed by other herbivores (insects, rodents, game). The calculation of herbage consumption by the beef herd, even though validated at the experimental site, is based on assumptions, such as the grazing factor, that add an element of uncertainty to the estimate. In addition, the measurement of residual herbage is subject not only to sampling error but is also affected by weathering and trampling of the dry material. An independent estimate of herbage production on the site during 1969–1973 was published by Gutman (1977). The vegetation was harvested from plots that were undisturbed by grazing or clipping until the end of the growing season. The mean dry matter yield (±SD) for the 5 years was 3,100±503 kg/ha. The yields ranged between 2,490 and 3,650 kg/ha. These data do not account for leaf death and non-domestic herbivory, so they too are probably underestimates. However, they are direct measurements of above-ground ungrazed herbage production and at least confirm that the calculated data from the grazed plots are reasonable.

Studies in a drier Mediterranean site but where the soil is deep and there are no rocks, have shown that herbage production from native annual vegetation with 400 mm of annual precipitation, and with adequate plant nutrients, can produce 9,000 kg/ha (van Keulen 1975, Benjamin et al. 1982). This would indicate that potential, climate-limited production in the study region is much higher than that observed in the present study. It must be concluded that soil resources, including restricted soil depth, are probably the dominant factor determining growth. This conclusion is supported by the fact that in the study area, fertilizer application, particularly nitrogen, has been shown to increase herbage production by almost 3 tons/ha dry matter, i.e., nearly double that measured in the present study (Gutman 1977). Basaltic protogrumosols are not deficient in phosphorus (Koyumdjisky and Dan 1969), but nitrogen availability can vary with mineralization, leaching, and N-fixation by the highly variable annual legume component (Seligman and Gutman 1979).

The CV of the yields (uncorrected for treatment or year effects) from the clipped plots was 16.2% compared with 11.2% for that estimated from the grazed paddocks. Both these values are low when compared with other similar regions (Murphy 1970, Duncan and Woodmansee 1975, Le Houerou and Hoste 1977, Noy-Meir and Walker 1986). The CV of precipitation was 31% for total annual precipitation and between 30 and 105% for monthly precipitation (Table 1), values that are much larger than the variation in herbage production. In addition, correlation between total annual precipitation and total annual herbage production was low and not significant, even though the pattern of growth and the timing of the beginning and end of each season was determined mainly by precipitation distribution. The observed variation in total herbage production could also be explained by the seasonal distribution of precipitation and the duration of dry spells in the rainy season. These factors determine for how long a period in each season both soil moisture and soil nitrogen in a restricted rooting zone are optimal for plant growth. George et al. (1988) have shown that inter-annual variation in herbage production of California annual grasslands is related to accumulated degree days during the growing season. This relationship may explain the variation in the current experiment but could not be checked because of insufficient data. Degree days would not explain why the maximum herbage production at the study site is so much lower than potential herbage production under prevailing climatic conditions.

The lack of sensitivity of primary production to stocking rate and to grazing system needs clarification. If growth under the study conditions is determined mainly by a limited soil resource such as plant nutrients or moisture in a restricted rooting zone then it could be relativey independent of grazing regime because slower growth will cause a slower resource use and a longer growing season. This would be true unless growth rate and leaf area accumulation was reduced by grazing to so low a level that the growing season would be terminated before the vegetation utilized the available growth limiting plant nutrients (or moisture) in the soil (Noy-Meir 1978). For the latter to happen, stocking rates would have to be considerably higher than those that were imposed. At the heaviest stocking rate, 0.9 cows/ha, and with mean green season herbage consumption rates of 11 kg/cow/d (Holzer, unpublished data), the maximum defoliation rate of about 10 kg/ha/d would be reached when green herbage availability ceased to limit intake at about 600 kg/ha DM, usually about 6 to 8 weeks after germination (Gutman 1977). With a relative growth rate of 4%, which is common during the early growth stages, the absolute growth rate at this stage is already 24 kg/ha, and increases as herbage accumulates. Hence, for most of the season, growth rate of the vegetation considerably exceeds defoliation rates even at the heaviest stocking and leaf biomass should always be well above the critical threshold for net growth

(Noy-Meir 1975). Thus, even though the total amount of forage consumed by the herd varied with stocking rate, the total amount of herbage produced, did not.

Conclusion

We conclude that in the study area, where mean annual precipitation is more than 500 mm per annum, the interannual variability of herbage production of native Mediterranean-type grasslands growing on relatively shallow, rocky soil, was much lower than the variability of precipitation. Total annual herbage production was not particularly sensitive to total annual precipitation, grazing system, or to stocking rates between 0.5 and 0.9 small cows per ha. The highest herbage production achieved was much lower than potential production under prevailing climatic conditions, so production level must have been determined mainly by the seasonal patterns of nutrient and soil moisture availability in a restricted rooting zone.

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Comparison of the copper and molybdenum status of yearling steers grazing reclaimed mined-land and native range

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Abstract

Spoil material replaced after strip mining for lignite coal may differ from the original top soil with respect to concentrations of copper (Cu) and molybdenum (Mo), consequently levels of these elements may be affected in plants grown on this soil. The objective of the study was to compare the Cu and Mo status of yearling steers grazing mined-land and native range forage to determine whether mined-land grazed steers were more prone to molybdenosis and/or Cu deficiency. Vegetation samples were collected from both mined-land and native range pastures. Copper was marginal and Mo was slightly high, for beef cattle, in forage obtained from both study sites. Blood serum and liver biopsy samples were taken from yearling steers at the initiation and termination of grazing on reclaimed mined-land and native range in 1978, 1979, 1982, and 1983. For the 4 years, there was no significant difference between forage sources with respect to Cu and Mo levels in the liver or Mo levels in the serum. However, serum Cu was slightly ($P<.10$) lower in steers grazing on mined-land. Liver Cu levels were marginal in steers grazing on either mined-land or native range. Initial liver Mo levels were slightly above normal but did not increase to levels expected if animals were consuming a diet excessively high in Mo. No symptoms of Cu deficiency or molybdenosis were observed during the course of the study. However, marginal serum, liver and forage Cu levels measured suggest that central North Dakota ranchers should be alert to the possibility of a Cu deficiency, whether cattle are grazing reclaimed mined-land or native range.

Key Words: strip mining, copper deficiency, molybdenosis

Strip mining for lignite coal is an on-going activity in North Dakota and other northern Great Plains states. Following reclamation, the land, in many cases, is seeded to a perennial forage crop and used for grazing. Because spoil material with unsuitable concentrations of copper (Cu) and molybdenum (Mo) is within reach of the plant's roots, it has been suggested by Erdman et al., (1978) that a potential exists for molybdenosis in cattle and sheep grazing these forages. Sweet clover *(Melilotus officinalis)* sampled by Erdman et al. (1978) contained >5 mg/l Mo at 5 of 8 mine sites sampled in the northern plains. Copper and Mo levels in individual forage species reported by Newman and Munshower (1984) were highest in forage grown on bare spoils. Molybdenum levels were higher for legumes than for grass, but no values were reported >10 mg/l, the level suggested by Kubota (1975) above which molybdenosis may occur. Underwood (1977) reported that connective tissue changes occurred in sheep grazing pastures containing from 5–20 mg/l Mo, but Ward (1978) indicated the minimum toxic Mo level on fresh pasture was 20 mg/l. Ward (1978) also suggested that molybdenosis may occur when the Cu:Mo ratio is less than 2:1.

Soils containing high concentrations of Mo are generally found in Nevada and California (Kubota 1975). However, metabolic problems similar to molybdenosis were reported in cattle grazing forage grown on spoil materials containing high Mo and Cu levels exposed as a result of a clay mining operation in Missouri (Ebens et al. 1973). Molybdenosis also has been reported in southwest North Dakota resulting from soil contamination by a uraniferous lignite coal ashing plant (Christianson and Jacobson 1970). While forage Mo and Cu levels may be indicative of the potential for a toxicity problem, the Committee on Mineral Nutrition (1973) indicated that liver and, to a lesser extent, serum were the most appropriate materials to examine for molybdenosis or Cu deficiency.

Although Cu and Mo levels in forage grown on reclaimed mined-land have been reported, animal data assessing the potential for molybdenosis are lacking. Thus, the objective of this study was to measure Cu and Mo levels in yearling steers grazing reclaimed mined-land forage and adjacent native range to determine whether mined-land forage presented a health hazard to grazing cattle.

Materials and Methods

The study area, located near Center, North Dakota, consisted of a reclaimed strip mined-land site and adjacent native range. The mined site had been stripped for lignite coal during the late 1960's. Pre-mining soils were classified as Cabba (loamy, mixed, calcareous, frigid, shallow Typic Ustorthents) and Sen (fine-silty, mixed Typic Haploborolls). Spoil materials were characterized physically and chemically by Bauer et al. (1976). Five years before initiation of the Cu-Mo study, the mined area was reshaped and covered with clay loam topsoil to a thickness of 9.7 cm. The area was seeded to a mixture of 'Lincoln' smooth bromegrass (*Bromus inermis* Leyss.), 'Nordan' crested wheatgrass [*Agropyron desertorum* (Fisch. Ex Link) Schult.], intermediate wheatgrass [*Agropyron intermedium* (Host) Beauv.], 'Vernal' alfalfa (*Medicago sativa* L.), and yellow sweetclover (*Melilotus officinalis* Lam.) Vegetation on the native range site was primarily blue grama (*Bouleloua gracilis* Lagasca ex Griffiths) and sedges (*Carex* spp.).

In 1978 and 1979, 3 steers were assigned to graze on reclaimed mined-land and 3 on native range each year, for a total of 12 steers (3 steers/pasture for 2 years). Utilization of both pastures was approximately 80%. In 1982 and 1983 a different set of pastures consisting of 4 mined-land, and 2 native range, were used to facilitate replication of pastures. Two of the mined-land pastures had previously been lightly utilized (35%) and 2 had had a combination of moderate (47%) and heavy (93%) use (Hofmann and Ries 1988). These grazing treatments resulted in species and forage production carryover effects among pastures, thus, in the study reported here, light and heavy utilization mined-land pastures refers to previous grazing treatments. In 1982 and 1983, all mined-land and native pastures were stocked at the same rate. Drinking water for the cattle used in the study was not available at the study site, thus it was hauled as needed from the Northern Great Plains Research Laboratory 50 km away.

In 1982, one steer was assigned to each of the 6 pastures for a total of 6 steers, while in 1983 two steers were assigned to each of the 6 pastures for a total of 12 steers. Steers were blood sampled and liver biopsied at initiation and termination of each grazing period: on 22 May and 8 August, 1978, 1 June and 3 August, 1979,

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The authors wish to thank Mr. Terrence R. Shuler, chemist, USDA-ARS, Human Nutrition Research Center, Grand Forks, North Dakota, for his contribution to molybdenum analysis of the samples.

Manuscript accepted 21 March 1989.

Table 1. Copper and molybdenum levels averaged over sampling dates for forage grown on reclaimed mined-land and native range in 1982 and 1983.

	Copper			Molybdenum			Cu:Mo Ratio[1]		
Year	Native	Mined-LU[2]	Mined-HU[2]	Native	Mined-LU	Mined-HU	Native	Mined-LU	Mined-HU
	mg/l (dry basis)			mg/l (dry basis)					
1982[3]	2.8^a	3.0^a	4.5^b	1.3	1.2	1.4	2.8^a	2.6^a	3.7^b
1983	3.2	3.2	3.6	1.6	1.4	1.6	2.2	2.7	2.7

[1] All ratios show only the first value of the ratio, the second value is 1 in all cases.

[2] Mined-LU = mined-land previous history light utilization (35%).
Mined-HU = mined-land previous history moderate (47%) and heavy utilization (93%).

[3] Pasture means averaged over sampling dates for an element or ratio with different letters, differ ($P < .10$) according to Student-Neweman-Keuls' Test.

24 May and 24 September, 1982, and 19 May and 3 October, 1983. No data were collected in 1980 and 1981. Serum was separated from whole blood samples and frozen until it could be analyzed. Liver samples were kept on ice as they were collected, then rinsed with deionized water and frozen until analysis could be completed.

Forage samples were obtained in July, 1978, and June and August, 1979, by hand-clipping plants and plant parts similar to those being grazed. Random grab samples of forage were obtained from 0.9 by 3.0-m cutter bar mower strips (1/pasture) on 15 June, 21 July, 18 August, and 4 October in 1982 and on 1 June, 2 August, and 27 September 1983. Samples were also collected from ungrazed exclosures in the pastures at the same time by the same method. Forage samples were dried at 70° C and ground through a 1-mm screen prior to analysis. Serum, liver, and forage samples were prepared for analysis according to procedures outlined by Fick et al. (1976). Copper was determined by atomic absorption spectrophotometry and Mo was analyzed by flameless atomic absorption spectrophotometry using a graphite furnace. Changes in serum and liver Cu and Mo levels between initial and final samples were analyzed in order to correct for differences in initial values between animals.

Animal data for 1978 and 1979 were analyzed together as a randomized complete block by analysis of variance, with pastures considered fixed and years random. Data for 1982 and 1983 and for all 4 years together were analyzed in the same manner. Utilization rates were most comparable between native range and lightly utilized mined-land pastures in 1982 and 1983; thus only data from these pastures were used when all 4 years were analyzed together. Forage data were analyzed for 1982 and 1983 separately as a randomized complete block with pastures considered fixed and sampling times considered random. Treatment means, when there were more than 2, were compared with the Student-Newman-Keul's Test. Data were considered significant at the 10% level of probability.

Results and Discussion

Forage

In July 1978, Cu and Mo levels in forage from grazed mined-land and native range were 6.2 and 1.6 mg/l, and 7.8 and 0.6 mg/l, respectively. In 1979, forage Cu from grazed mined-land and native range was 10.0 and 10.7 mg/l, respectively, in June and 11.4 and 2.8 mg/l, respectively, in August. Forage Mo on mined-land was 2.7 and 3.0 mg/l in June and August 1979, respectively, but on native range it was only about 1/4 as high.

Forage Cu and Mo levels did not vary significantly ($P > 0.1$) among sampling dates in either 1982 or 1983; thus only pasture means are presented in Table 1. However, the Cu:Mo ratios did differ significantly among all 4 sampling dates averaged over pastures (June, 3.7:1, July, 2.9:1, August, 1.4:1 and October, 4.2:1) in 1982. The Cu:Mo ratio for August was well below the 2:1 ratio suggested by Ward (1978) as a threshold was well below which Cu deficiencies were likely to occur. In 1982 the forage Cu levels and the Cu:Mo ratio (Table 1) were higher on the heavily utilized mined-land pasture than either native range or the lightly utilized mined-land pastures. Forage Cu and Mo levels averaged over sampling dates from the exclosures were 3.9 and 1.2 mg/l and 2.4 and 1.0 mg/l, respectively, from mined-land and native range. These values were comparable to levels in grazed forage (Table 1).

In 1983 there were no significant differences in Cu or Mo levels or in Cu:Mo ratios among pastures (Table 1) or sampling dates (data not shown). Molybdenum levels tended to be higher and the Cu:Mo ratios lower than in 1982. Forage Cu and Mo levels were only about 60% as high as levels reported by Erdman et al. (1978) for yellow sweet clover collected at a mine site near Beulah, ND. Forage Cu levels for 1982 and 1983 ranged from 1.6 to 6.6 mg/l, with most values in the 3 mg/l range (Table 1). The National Research Council (1984) suggests that diet Cu levels lower than 3 to 5 mg/l may result in subnormal plasma and liver Cu levels.

Table 2. Copper and molybdenum levels in the serum and liver of yearling steers grazing on mined-land and native range, average of 1978 and 1979 samples.

	Serum				Liver[1]			
Pasture	Initial	Final	Change	SE[2]	Initial	Final	Change	SE
				Copper (mg/l)				
Mined	0.87	0.65	–0.22	0.02	34.1	24.1	–10.0	0.3
Native range	0.85	0.78	–0.07	0.02	41.1	20.5	–20.6[3]	0.3
Mean	0.86	0.72			37.6	22.3		
				Molybdenum (mg/l)				
Mined	0.09	0.04	–0.05	0.002	4.9	4.8	–0.1	0.4
Native range	0.08	0.01	–0.07	0.002	5.1	3.9	–1.2	0.4
Mean	0.08	0.02			5.0	4.4		

[1] Levels are expressed on a dry matter basis.

[2] Standard error the mean = $\frac{\sqrt{EMS}}{N}$, where EMS = error mean square used to test pastures and N = the number of values/mean.

[3] Means in the same column for the same element differ ($P < .10$) according to Student-Newman-Keuls' Test.

Table 3. Copper and molybdenum levels in the serum and liver of yearling steers grazing on mined-land and native range, average of 1982 and 1983 samples.

	Serum				Liver[1]			
Pasture	Initial	Final	Change	SE[2]	Initial	Final	Change	SE
				Copper (mg/l)				
Mined-LU[3]	0.42	0.30	–0.12	0.04	27.0	19.0	– 8.0	4.6
Mined-HU[3]	0.52	0.50	–0.02	0.04	27.2	16.8	–10.4	4.6
Native range	0.54	0.58	+0.04	0.04	29.4	48.9	+19.5	4.6
Mean	0.50	0.46			27.9	28.2		
				Molybdenum (mg/l)				
Mined-LU	0.03	0.09	+0.06	0.02	6.4	6.8	+ 0.4	0.7
Mined-HU	0.04	0.04	0.00	0.02	5.1	7.4	+ 2.3	0.7
Native range	0.04	0.12	+0.08	0.02	5.2	5.7	+ 0.5	0.7
Mean	0.04	0.08			5.6	6.6		

[1] Levels are expressed on a dry matter basis.

[2] Standard error the mean = $\frac{\sqrt{EMS}}{N}$, where EMS = error mean square used to test pastures and N = the number of values/mean.

[3] Mined-LU = mined-land previous history light utilization (35%).
Mined-HU = mined-land previous history moderate (47%) and heavy utilization (93%).

Animals

Mean serum Cu levels for 1978 and 1979 were not significantly different between steers grazing on mined-land and steers grazing on native range (Table 2). Initial and final serum Cu levels were in the adequate range (>0.65 mg/l) according to the Committee on Mineral Nutrition (1973). Mean initial liver Cu levels for steers grazing on both mined-land pastures and native range were marginal (<50 mg/l) Committee on Mineral Nutrition 1973). During the approximately 70-day grazing season, liver Cu declined for steers in both pastures, but decline was greatest ($P<.10$) for steers on native range. Final liver Cu levels for steers on both mined-land and native range were near the severe deficiency level (<20 mg/l) (Committee on Mineral Nutrition 1973). The average liver Cu level for mature cattle is 200 mg/l with a range of 23 to 409 mg/l, according to Underwood (1977), with liver Cu ranging from 3 to 32 mg/l with a mean of 11.5 mg/l for mature cattle that are Cu deficient. Tejada (1984) reported that the critical liver Cu level ranged between 25–75 mg/l.

Serum and liver Mo in 1978 and 1979 tended to decrease during the grazing period, but there was no significant difference between steers grazing on mined-land and native range (Table 2). The critical liver Mo reported by Tejada (1984) was 4 mg/l. Initial and final liver Mo levels ranged from 3.9 to 5.1 mg/l for steers on both pastures. Underwood (1977) stated that adult sheep and cows retained Mo concentrations to 25–30 mg/l in their livers when they were ingesting moderately large amounts of the element. These levels rapidly returned to a normal range of 2–4 mg/l when excessive levels of Mo were removed from the diet. This suggests that liver Mo for steers used in this study may have been slightly above normal, but that forage Mo was not high enough to cause a further increase in liver Mo levels.

In 1982 and 1983 (Table 3) serum Cu in steers did not change significantly among pastures during the approximately 124-day grazing season. Liver Cu also did not change significantly between steers grazing mined-land and native range, but there was a trend for liver Cu to increase in steers grazing native range and to decline in steers grazing on mined-land. Mean final liver Cu levels from steers grazing on mined-land were below the 20 mg/l level suggested by the Committee on Mineral Nutrition (1973) as the level below which severe deficiency and usually clinical Cu deficiency signs appear. In 1978 and 1979 serum and liver Mo appeared to decrease slightly during the 70-day grazing period, but in 1982 and 1983 over a 124-day grazing season, the reverse appeared to be true. However, there was no significant difference among pastures, and liver Mo levels were in the same range as in 1978 and 1979.

Combined data for the 4 years (Table 4) show a significantly greater decline in serum Cu in steers grazing on the mined-land than in steers grazing on native range. Mean liver Cu over the 4 years tended to decline more for steers on mined-land during the grazing period, but results were not significant. In 1978 and 1979 the decline in liver Cu was greatest for steers on native range, while in 1982 and 1983 liver Cu appeared to increase in steers grazing on native range and decrease in steers grazing the mined-land pastures. Liver Cu was quite variable in our study: levels for individual

Table 4. Summary of copper and molybdenum levels in the serum and liver of yearling steers grazing on mined-land and native range, average of 1978, 1979, 1982, and 1983 samples.

	Serum				Liver[1]			
Pasture	Initial	Final	Change	SE[2]	Initial	Final	Change	SE
				Copper (mg/l)				
Mined	0.64	0.48	–0.16	0.02	30.6	21.6	–9.0	4.6
Native range	0.70	0.68	–0.02[3]	0.02	35.3	34.7	–0.6	4.6
Mean	0.67	0.58			32.9	28.1		
				Molybdenum (mg/l)				
Mined	0.06	0.06	0.00	0.01	5.7	5.8	+0.1	0.4
Native range	0.06	0.07	+0.01	0.01	5.2	4.8	–0.4	0.4
Mean	0.06	0.06			5.4	5.3		

[1] Levels are expressed on a dry matter basis.

[2] Standard error the mean = $\frac{\sqrt{EMS}}{N}$, where EMS = error mean square used to test pastures and N = the number of values/mean.

[3] Means in the same column for the same element differ ($P<.10$) according to Student-Newman-Keuls' Test.

animals ranged from 17 to 73 and from 8 to 82 mg/l at the initial sampling times in 1978 and 1979 and 1982 and 1983, respectively. Termination values were only slightly less variable. The range in liver Cu was greater than had been anticipated and no doubt contributed to the variability of the results. However, the values were all on the lower end of the concentration scale reported for normal liver Cu and the range in values reported in the literature suggest that these results may not be unusual. Mean initial and final liver Cu values for the 4 years were in the area considered marginal (<50 mg/l) by the Committee on Mineral Nutrition (1973), regardless of the pasture grazed.

Data suggest that yearling steers in this study had liver Cu and Mo levels that, according to literature, were in the marginal range with respect to prevention of Cu deficiency. However, the change in serum or liver Cu or Mo levels during the grazing periods used in the study were not consistent among years, even though forage on both mined-land and native range was marginally low in Cu and marginally high in Mo for beef cattle. The relatively constant liver Mo levels, however, suggest that dietary Mo levels on either mined-land or native range were not excessive.

High concentrations of dietary sulfur (S) may enhance the adverse affect of Mo on Cu availability (Smart et al. 1981). Langlands et al. (1981) indicated that with sheep, when Mo concentrations exceeded 10 mg/l, S had a greater adverse affect on the availability of Cu than when Mo concentrations were less than 5 mg/l. In the study reported here forage Mo concentrations were generally in the 1–3 mg/l range; thus it is unlikely that S played any significant role in Cu availability.

No animals used in this study showed any symptoms of Cu deficiency, molybdenosis or impaired performance, and the rancher whose land was used for the study had never observed Cu deficiency symptoms in his animals. However, Cu deficiencies have been documented with cattle grazing native range in North Dakota and the marginal nature of Cu levels in forage and animal tissues reported in this study suggest that ranchers in central North Dakota should be alert to the possibility of a Cu deficiency, whether their cattle are grazing on native range or on reclaimed mined-land.

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Estimates of critical thermal environments for mule deer

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Abstract

Mule deer *(Odocoileus hemionus hemionus)* can be thermally stressed under a wide range of ambient conditions. We developed a model that provides examples of the combinations of wind, solar radiation, and air temperature that may result in thermally critical environments for standing, full-fed adult mule deer during winter in snow-covered and snow-free, open habitats, and in meadows in summer. Critical thermal combinations of environmental variables are shown as 3-dimensional surfaces and tables. Animal size, age, pelage characteristics, and ground cover (height and albedo) further affect the energy costs for thermoregulation by mule deer. The need for habitat managers to consider the provision of thermal cover to reduce heat or cold stress in mule deer depends on the combinations of environmental variables in a particular habitat and geographic location. Implications, limitations, and management considerations of our estimates are discussed.

Key Words: energetics, *Odocoileus*, standard operative temperature, thermal cover, thermoregulation

Field observations suggest that wild ungulates select cover, bedding sites, and postures for apparent thermal benefits (Beall 1974, Leckenby 1977). Thermal cover now is considered an important component of ungulate habitat (Black et al. 1976), although few studies have quantified the thermal environments experienced by animals and much of the information on movements or habitat selection cannot be used to distinguish between animal preference and requirement. Bioenergetics research on captive animals has identified physiological mechanisms that allow wild ungulates to cope with climatic stress and has defined many of their energetic requirements (e.g., Parker and Robbins 1984, Renecker and Hudson 1986). Increased knowledge of the interactions between weather variables and animal responses is needed if thermal conditions are to be considered in habitat-management (Thomas et al. 1979).

In most studies, air temperature (T_a) alone has been used to describe the thermal environments experienced by animals. Standard operative temperature (T_{es}) (Bakken 1980, 1981), however, more appropriately describes the effective temperature experienced by animals outdoors by integrating effects of air temperature, wind speed, and incident radiation into a single variable describing the animal's thermal environment. Thermal conditions of different habitats for a species may then be compared with a common thermal index. Effects of precipitation, however, are not included in this index.

Thermoregulation is an animal's ability to regulate body temperature within acceptable limits despite large variations in ambient conditions. Over a thermoneutral range of environmental temperatures, an animal's resting metabolic rate remains relatively constant and independent of environmental conditions (e.g., Parker and Robbins 1985). As the animal approaches the lower limit of this thermoneutral zone (TNZ) or lower critical temperature (LCT), it increases the thermal resistance of the hair coat by piloerection and that of the tissue by peripheral vasoconstriction. When physical regulation of body temperature reaches a maximum, chemical regulation occurs. Energy metabolism must increase to maintain acceptable body temperature and prevent impairment of tissue function. Above the upper limit of the thermoneutral zone, or upper critical temperature (UCT), metabolic rate increases and is usually associated with hyperthermia. To minimize energy costs for thermoregulation by a wildlife species, habitat management could provide thermal cover to ameliorate environmental conditions when standard operative temperatures are less than LCT's and greater than UCT's.

Although the concept of critical thermal environments has already been proposed (Moen 1968a), wildlife managers currently place little emphasis on thermal constraints. Our specific objectives are to: (1) present a model that provides examples of thermally critical environments for mule deer in winter and summer based on standard operative temperature; and (2) describe these environments in tabular and graphical format. With this information, managers will be better able to determine whether thermally critical environments are commonly experienced by mule deer in specific habitat conditions.

Methods and Theory

To examine the effects of weather on ungulates in the wild, we generated a thermal model to assess physiological responses of mule deer to various combinations of micrometeorological variables (see Appendix 1 for general equations).

Calculation of Operative Temperature

Thermal environments of mule deer initially were quantified using the equation for operative temperature (T_e), presented by Campbell (1977:94):

$$T_e = T_a + \frac{r_e\,(R_{abs} - \epsilon_s \sigma T_a^4)}{\rho c_p} \qquad (1)$$

where the temperature experienced by the animal (T_e) includes air temperature and the effects of wind and radiation. These effects incorporate r_e, the animal's resistance to convective and radiative heat transfer; R_{abs}, the solar and thermal radiation absorbed by the animal; $\epsilon_s \sigma T_a^4$, thermal emittance of the animal's surface at air temperature; and ρc_p, the volumetric specific heat of air. Preliminary estimates of T_e for mule deer (Parker and Gillingham 1987) incorporated the influence of wind on coat resistance but underestimated the effects of high wind speeds. Therefore, a wind-chill corrected or standard operative temperature (T_{es}), based on theory developed by Bakken (1981), was used to better estimate the animal's thermal environment:

$$T_{es} = T_b - \frac{r_{HBS} + r_{es}}{r_{Hb} + r_e} \bullet (T_b - T_e) \qquad (2)$$

where T_b is the animal's body temperature, r_{Hb} is the thermal resistance of skin and pelage to heat flow under natural outdoor wind speeds (u), and r_{Hbs} and r_{es} are the values of r_{Hb} and r_e under low convective conditions ($u \leq 1$ m/s).

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Research was funded in part by the Science Council of British Columbia through a grant to F.L. Bunnell. The insights and contributions by G.S. Campbell are greatly appreciated. Helpful comments on this manuscript were provided by R.T. Bowyer.

Manuscript accepted 16 March 1989.

Physiological Measurements

Using the energetic measurements made on animals under outdoor conditions from Parker (unpubl.) and Parker and Robbins (1984), we employed nonlinear regression techniques (Dixon 1981) to describe the relationships between ambient conditions and body temperature, and thermal resistance of mule deer at low wind speeds ($u \leq 1$ m/s). Animal whole body resistance was partitioned into tissue and coat components. Tissue resistance was assumed to be an inversely linear function between vasoconstriction at lower critical temperature (170 s/m) and vasodilation at upper critical temperature (50 s/m) (Webster 1974). Coat resistance was calculated as the difference between whole body and tissue resistances. At wind speeds greater than 1 m/s, we assumed that coat resistance decreased 8% with each m/s increase in wind speed, as noted for caribou, wolf, and rabbit (Campbell et al. 1980).

Adult animals were assumed to weigh 67 kg (Parker 1983). In winter, LCT was fixed at −19° C and upper temperature was +2.5° C (Parker and Robbins 1984:1418). In summer, lower and upper critical limits were +5° and 23.5° C, respectively (Parker and Robbins 1984:1419).

Effects of Wind

Wind speeds, standardly measured at 3 m above the ground, were extrapolated to animal height (Campbell 1977:38). This height was assumed to be the height of mid-rib cage, which varies as a function of body weight for mule deer (Parker 1987). The average 'crop' height (grass, shrubs, snow) in which the animal was standing was fixed at 0.1 m for this analysis. A characteristic dimension, or representative distance over which the wind travels on the animal's surface (Campbell 1977:65) was computed as the average of the animal's length and diameter (Parker 1987).

Effects of convection, forced (resulting directly from wind speed) and free (occurring because of thermal gradients between the animal and its environment), were assessed prior to determining the animal's resistance to convective heat transfer. Usually one or the other process dominates, and we used only the resistance for the dominant process (Campbell 1977:70). Resistance to free convection was calculated from the temperature difference between the air and the animal's skin surface in the sun or shade; this resistance occurred over the characteristic dimension of the animal.

Effects of Solar and Thermal Radiation

We separated short-wave irradiance into direct and diffuse components using factors to incorporate differences between potential and measured direct radiation and the amount of absorption of the solar beam by atmospheric moisture and ozone (Wesley and Lipschutz 1976, Campbell 1981). Reflected short-wave radiation was estimated using surface albedos of 0.80 for snow, 0.20 for a field in summer, and 0.26 for matted grass in winter (Lowry 1969:133). Angle of solar elevation was defined by the interaction among solar declination, geographic latitude, time of day, and time of solar noon (Paltridge and Platt 1976, Campbell 1981). Total short-wave radiation absorbed by the animal was then calculated assuming a shadow area equal to 1/3 of the animal's surface area and short-wave absorptivity values of 0.7 and 0.8 in summer and winter pelage, respectively (W. Porter, pers. comm.).

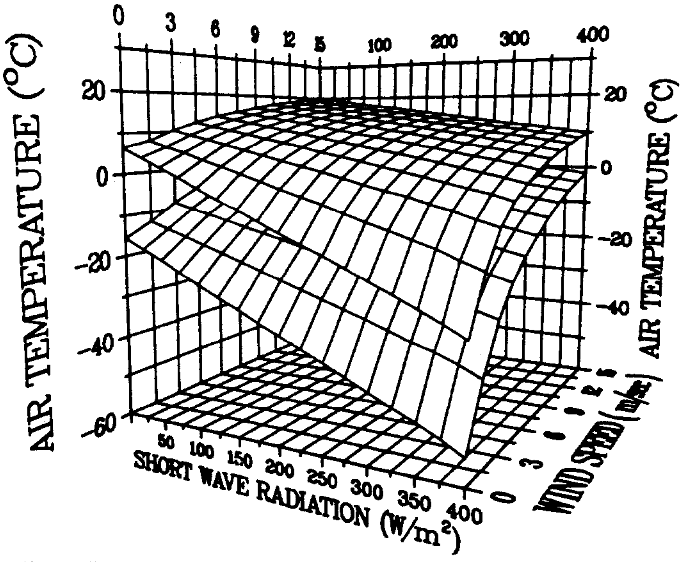

Fig. 1. Three-dimensional surfaces of predicted lower (T_{es} = -19° C) and upper (T_{es} = 2.5° C) thermally critical environments for full-fed, adult mule deer standing in snow-covered, open habitats in winter.

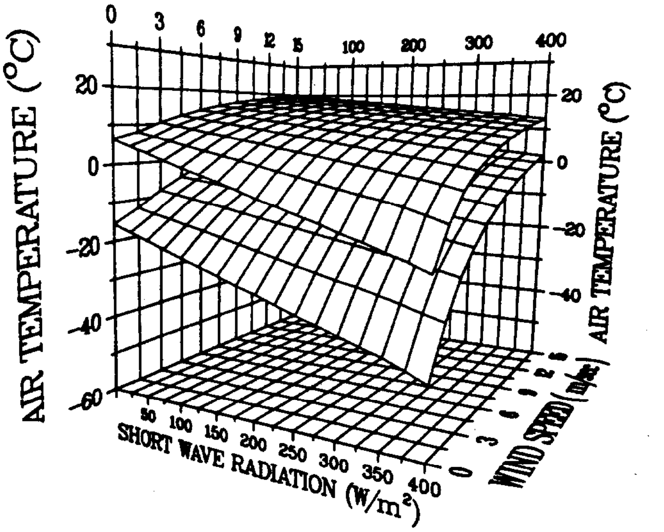

Fig. 2. Three-dimensional surfaces of predicted lower (T_{es} = -19° C) and upper (T_{es} = 2.5° C) thermally critical environments for full-fed, adult mule deer standing in snow-free, open habitats in winter.

In the calculation of long-wave radiation absorbed by the animal, we employed a clear sky emissivity based on air temperature (Moen 1968b:340), a ground emissivity of 0.97 (K.L. Parker, unpubl. data), and an animal emissivity of 1.0, as demonstrated for caribou *(Rangifer tarandus)* (Monteith 1973). Because of the extreme variability of thermal energy flux from animal surfaces

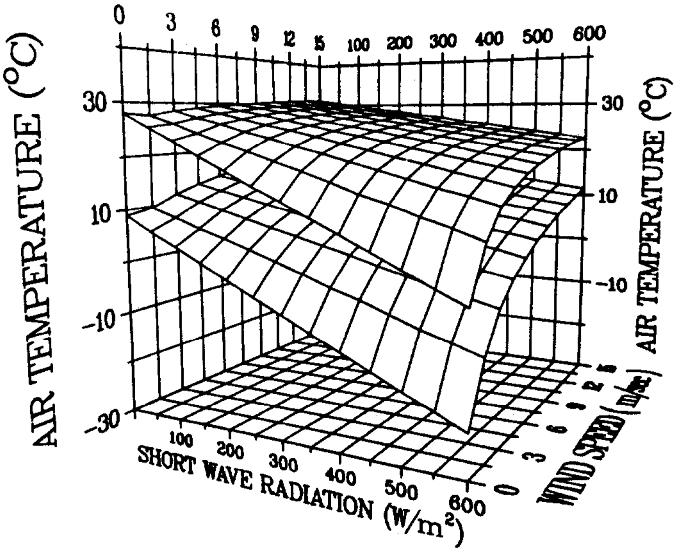

Fig. 3. Three-dimensional surfaces of predicted lower (T_{es} = 5° C) and upper (T_{es} = 23.5° C) thermally critical environments for full-fed, adult mule deer standing in meadowed habitats in summer.

when exposed to ambient conditions (Moen 1973:88, 1974, Moen and Jacobsen 1974) and because these interactions between environmental variables and surface temperatures have not been thoroughly quantified, we assumed that the animal's outer surface temperature equalled air temperature.

Model Inputs and Outputs

T_{es} was determined for combinations of air temperature (−20 to +20° C in winter, 0 to 40° C in summer), wind speed (0 to 15 m/s), and short-wave radiation (0 to 400 W/m² in winter, 0 to 800 W/m² in summer) at 46.83° N, 117.20° W (Pullman, Washington). Predictions were made under no sun conditions and at a maximum angle of solar elevation (time of day = time of solar noon) in midsummer (Julian day = 200) and midwinter (Julian day = 49) under conditions with and without snow. These predictions and planes of lower and upper critical temperatures are presented in tabular and 3-dimensional formats. Graphical output was produced using Displa Integrated Software System and Plotting Language (ISSCO 1987).

Results

Predicted Standard Operative Temperatures

Incident solar radiation raises the standard operative temperature (T_{es}) experienced by an animal and wind speed decreases the effective environment (Tables 1-3). In winter, the high reflectance of solar radiation from snow increases standard operative temperatures up to 9° C from those experienced on bare ground at midday under the same air temperature, still air, and high solar level conditions (Table 1, 2). Wind speeds of 5 m/s can eliminate most of the thermal effects of maximum solar levels. In summer, incident solar levels may be twice as high as those occurring in winter (Table 3). The relative effects of these high solar loads at midday with minimal wind, however, are comparable to those in snow-covered winter habitats and may raise standard operative temperatures 30°

Table 1. Predicted standard operative temperatures (T_{es}) for full-fed, adult mule deer standing in snow-covered open habitats in winter. T_a is air temperature; u is wind speed at 3 m; u_a is wind speed at animal height; SW is short-wave radiation.

T_a (°C)	u (m/s)	u_a (m/s)	SW (W/m²)	T_{es} (°C)
−25	0	0.0	0	−28.2
−25	0	0.0	100	−18.9
−25	0	0.0	200	−10.2
−25	0	0.0	300	−2.0
−25	0	0.0	400	6.5
−25	5	3.7	0	−44.5
−25	5	3.7	100	−39.1
−25	5	3.7	200	−33.8
−25	5	3.7	300	−28.9
−25	5	3.7	400	−23.7
−25	10	7.5	0	−59.4
−25	10	7.5	100	−54.6
−25	10	7.5	200	−49.8
−25	10	7.5	300	−45.5
−25	10	7.5	400	−40.9
−25	15	11.2	0	−72.8
−25	15	11.2	100	−68.2
−25	15	11.2	200	−63.5
−25	15	11.2	300	−59.2
−25	15	11.2	400	−55.1
−20	0	0.0	0	−23.3
−20	0	0.0	100	−14.2
−20	0	0.0	200	−5.6
−20	0	0.0	300	2.5
−20	0	0.0	400	10.8
−20	5	3.7	0	−38.1
−20	5	3.7	100	−32.9
−20	5	3.7	200	−28.0
−20	5	3.7	300	−23.1
−20	5	3.7	400	−18.0
−20	10	7.5	0	−51.7
−20	10	7.5	100	−47.1
−20	10	7.5	200	−43.0
−20	10	7.5	300	−38.8
−20	10	7.5	400	−34.3
−20	15	11.2	0	−64.0
−20	15	11.2	100	−59.5
−20	15	11.2	200	−55.8
−20	15	11.2	300	−52.1
−20	15	11.2	400	−47.9
−15	0	0.0	0	−18.4
−15	0	0.0	100	−9.4
−15	0	0.0	200	−1.0
−15	0	0.0	300	7.3
−15	0	0.0	400	15.2
−15	5	3.7	0	−31.9
−15	5	3.7	100	−27.0
−15	5	3.7	200	−22.1
−15	5	3.7	300	−17.2
−15	5	3.7	400	−12.2
−15	10	7.5	0	−44.6
−15	10	7.5	100	−40.5
−15	10	7.5	200	−36.3
−15	10	7.5	300	−32.1
−15	10	7.5	400	−27.6
−15	15	11.2	0	−56.1
−15	15	11.2	100	−52.3
−15	15	11.2	200	−48.6
−15	15	11.2	300	−44.7
−15	15	11.2	400	−40.5
−10	0	0.0	0	−13.5
−10	0	0.0	100	−4.7
−10	0	0.0	200	3.7
−10	0	0.0	300	11.8
−10	0	0.0	400	19.9
−10	5	3.7	0	−25.9
−10	5	3.7	100	−21.1
−10	5	3.7	200	−16.2
−10	5	3.7	300	−11.4
−10	5	3.7	400	−6.2
−10	10	7.5	0	−37.8
−10	10	7.5	100	−33.7
−10	10	7.5	200	−29.5
−10	10	7.5	300	−25.4
−10	10	7.5	400	−20.9
−10	15	11.2	0	−48.7
−10	15	11.2	100	−45.0
−10	15	11.2	200	−41.1
−10	15	11.2	300	−37.3
−10	15	11.2	400	−33.1
−5	0	0.0	0	−8.6
−5	0	0.0	100	0.1
−5	0	0.0	200	8.4
−5	0	0.0	300	16.4
−5	0	0.0	400	24.3
−5	5	3.7	0	−19.9
−5	5	3.7	100	−15.1
−5	5	3.7	200	−10.3
−5	5	3.7	300	−5.3
−5	5	3.7	400	0.0
−5	10	7.5	0	−31.0
−5	10	7.5	100	−26.9
−5	10	7.5	200	−22.8
−5	10	7.5	300	−18.6
−5	10	7.5	400	−13.3
−5	15	11.2	0	−41.3
−5	15	11.2	100	−37.5
−5	15	11.2	200	−33.7
−5	15	11.2	300	−29.8
−5	15	11.2	400	−25.0
0	0	0.0	0	−3.7
0	0	0.0	100	4.9
0	0	0.0	200	13.0
0	0	0.0	300	20.9
0	0	0.0	400	28.7
0	5	3.7	0	−13.9
0	5	3.7	100	−9.2
0	5	3.7	200	−4.1
0	5	3.7	300	1.0
0	5	3.7	400	6.2
0	10	7.5	0	−24.1
0	10	7.5	100	−20.0
0	10	7.5	200	−15.5
0	10	7.5	300	−10.7
0	10	7.5	400	−5.5
0	15	11.2	0	−33.7
0	15	11.2	100	−30.0
0	15	11.2	200	−25.6
0	15	11.2	300	−20.9
0	15	11.2	400	−15.6
5	0	0.0	0	1.1
5	0	0.0	100	9.7
5	0	0.0	200	17.7
5	0	0.0	300	25.5
5	0	0.0	400	33.1
5	5	3.7	0	−7.8
5	5	3.7	100	−2.8
5	5	3.7	200	2.2
5	5	3.7	300	7.2
5	5	3.7	400	12.4
5	10	7.5	0	−17.0
5	10	7.5	100	−12.3
5	10	7.5	200	−7.6
5	10	7.5	300	−2.9
5	10	7.5	400	2.3
5	15	11.2	0	−25.7
5	15	11.2	100	−21.0
5	15	11.2	200	−16.2
5	15	11.2	300	−11.5
5	15	11.2	400	−6.3

Table 2. Predicted standard operative temperatures (T_{es}) for full-fed, adult mule deer standing in snow-free open habitats in winter. T_a is air temperature; u is wind speed at 3 m; u_a is wind speed at animal height; SW is short-wave radiation.

T_a (°C)	u (m/s)	u_a (m/s)	SW (W/m²)	T_{es} (°C)
-25	0	0.0	0	-28.2
-25	0	0.0	100	-21.7
-25	0	0.0	200	-15.5
-25	0	0.0	300	-9.3
-25	0	0.0	400	-3.0
-25	5	3.9	0	-44.9
-25	5	3.9	100	-41.2
-25	5	3.9	200	-37.5
-25	5	3.9	300	-33.9
-25	5	3.9	400	-30.0
-25	10	7.7	0	-60.2
-25	10	7.7	100	-56.9
-25	10	7.7	200	53.5
-25	10	7.7	300	-50.2
-25	10	7.7	400	-46.8
-25	15	11.6	0	-73.9
-25	15	11.6	100	-70.7
-25	15	11.6	200	-67.5
-25	15	11.6	300	-64.3
-25	15	11.6	400	-60.8
-20	0	0.0	0	-23.3
-20	0	0.0	100	-17.0
-20	0	0.0	200	-10.8
-20	0	0.0	300	-4.7
-20	0	0.0	400	1.5
-20	5	3.9	0	-38.5
-20	5	3.9	100	-34.8
-20	5	3.9	200	-31.4
-20	5	3.9	300	-28.0
-20	5	3.9	400	-24.1
-20	10	7.7	0	-52.5
-20	10	7.7	100	-49.1
-20	10	7.7	200	-46.3
-20	10	7.7	300	-43.4
-20	10	7.7	400	-40.2
-20	15	11.6	0	-65.0
-20	15	11.6	100	-61.8
-20	15	11.6	200	-59.2
-20	15	11.6	300	-56.6
-20	15	11.6	400	-53.6
-15	0	0.0	0	-18.4
-15	0	0.0	100	-12.1
-15	0	0.0	200	-6.1
-15	0	0.0	300	-0.1
-15	0	0.0	400	6.0
-15	5	3.9	0	-32.2
-15	5	3.9	100	-28.9
-15	5	3.9	200	-25.5
-15	5	3.9	300	-22.1
-15	5	3.9	400	-18.3
-15	10	7.7	0	-45.3
-15	10	7.7	100	-42.4
-15	10	7.7	200	-39.6
-15	10	7.7	300	-36.7
-15	10	7.7	400	-33.4
-15	15	11.6	0	-57.1
-15	15	11.6	100	-54.5
-15	15	11.6	200	-51.9
-15	15	11.6	300	-49.2
-15	15	11.6	400	-46.2
-10	0	0.0	0	-13.5
-10	0	0.0	100	-7.3
-10	0	0.0	200	-1.1
-10	0	0.0	300	4.6
-10	0	0.0	400	10.6
-10	5	3.9	0	-26.2
-10	5	3.9	100	-22.9
-10	5	3.9	200	-19.5
-10	5	3.9	300	-16.2
-10	5	3.9	400	-12.4
-10	10	7.7	0	-38.5
-10	10	7.7	100	-35.6
-10	10	7.7	200	-32.8
-10	10	7.7	300	-29.9
-10	10	7.7	400	-26.6
-10	15	11.6	0	-49.7
.10	15	11.6	100	-47.1
-10	15	11.6	200	-44.4
-10	15	11.6	300	-41.8
-10	15	11.6	400	-38.8
-5	0	0.0	0	-8.6
-5	0	0.0	100	-2.5
-5	0	0.0	200	3.6
-5	0	0.0	300	9.2
-5	0	0.0	400	15.1
-5	5	3.9	0	-20.2
-5	5	3.9	100	-16.9
-5	5	3.9	200	-13.6
-5	5	3.9	300	-10.3
-5	5	3.9	400	-6.3
-5	10	7.7	0	-31.6
-5	10	7.7	100	-28.8
-5	10	7.7	200	-25.9
-5	10	7.7	300	-23.0
-5	10	7.7	400	-19.8
-5	15	11.6	0	-42.2
-5	15	11.6	100	-39.5
-5	15	11.6	200	-36.9
-5	15	11.6	300	-34.2
-5	15	11.6	400	-31.2
0	0	0.0	0	-3.7
0	0	0.0	100	2.3
0	0	0.0	200	8.4
0	0	0.0	300	13.9
0	0	0.0	400	19.7
0	5	3.9	0	-14.2
0	5	3.9	100	-10.9
0	5	3.9	200	-7.5
0	5	3.9	300	-4.0
0	5	3.9	400	0.0
0	10	7.7	0	-24.7
0	10	7.7	100	-21.9
0	10	7.7	200	-19.0
0	10	7.7	300	-15.6
0	10	7.7	400	-11.9
0	15	11.6	0	-34.6
0	15	11.6	100	-32.0
0	15	11.6	200	-29.3
0	15	11.6	300	-26.1
0	15	11.6	400	-22.3
5	0	0.0	0	1.1
5	0	0.0	100	7.1
5	0	0.0	200	13.1
5	0	0.0	300	18.6
5	0	0.0	400	24.5
5	5	3.9	0	-8.0
5	5	3.9	100	-4.6
5	5	3.9	200	-1.1
5	5	3.9	300	2.4
5	5	3.9	400	6.4
5	10	7.7	0	-17.5
5	10	7.7	100	-14.2
5	10	7.7	200	-10.9
5	10	7.7	300	-7.6
5	10	7.7	400	-3.9
5	15	11.6	0	-26.5
5	15	11.6	100	-23.1
5	15	11.6	200	-19.8
5	15	11.6	300	-16.5
5	15	11.6	400	-12.7

C from nighttime conditions. Under the same environmental conditions in both seasons (e.g., $T_a = 0°$ C, u = 0 m/s, SW = 400 W/m²), the standard operative temperature experienced by the animal is greater in winter because of the greater insulation and absorptivity to solar radiation provided by its winter pelage.

Lower and Upper Critical Temperatures

Environmental conditions between the predicted surfaces of lower (LCT) and upper critical temperatures (UCT) represent optimum thermal environments for mule deer (Figs. 1-3). Increased energy expenditures for thermoregulation would occur above and below these surfaces. Variations in the steepness of the surfaces represent the sensitivity of the boundary between an animal's critical and noncritical thermal environment to different weather variables. In winter, the range of air temperatures in which animals exist most comfortably (i.e., the width of the thermoneutral zone) under conditions of minimal wind is ≈22° C with no solar gain and 24–25° C with full solar loads (400 W/m²; Figs. 1-2). Increasing wind speeds to 15 m/s decreases the thermoneutral zone to ≈11° C, regardless of incident solar levels. In summer, high wind speeds (15 m/s) reduce the thermoneutral zone by 8–10° C from still air conditions (Fig. 3).

Discussion

Implications of Predicted Thermal Environments

Predicted thermal environments for mule deer provide insight into the contributions of solar radiation and wind to the standard operative temperatures experienced by animals, seasonal differences in these contributions, the importance of snow relative to solar reflectivity and the wind speed profile, and the importance of reduced radiative heat input from a clear sky at night.

Particular importance of solar radiation to mule deer at cold temperatures on snow-covered surfaces during winter is demonstrated by animals that are not thermally stressed until T_a's fall to approximately -53° C when solar radiation levels are high (400

Table 3. Predicted standard operative temperatures (T_{es}) for full-fed, adult mule deer standing in open habitats in summer. T_a is air temperature; u is wind speed at 3 m; u_a is wind speed at animal height; SW is short-wave radiation.

T_a (°C)	u (m/s)	u_a (m/s)	SW (W/m^2)	T_{es} (°C)	T_a (°C)	u (m/s)	u_a (m/s)	SW (W/m^2)	T_{es} (°C)	T_a (°C)	u (m/s)	u_a (m/S)	SW (W/m^2)	T_{es} (°C)
0	0	0.0	0	–3.7	10	5	3.7	400	10.9	20	10	7.5	800	24.4
0	0	0.0	200	6.5	10	5	3.7	600	16.2	20	15	11.2	0	5.0
0	0	0.0	400	16.0	10	5	3.7	800	17.7	20	15	11.2	200	9.0
0	0	0.0	600	24.9	10	10	7.5	0	–4.5	20	15	11.2	400	13.4
0	0	0.0	800	27.5	10	10	7.5	200	–0.2	20	15	11.2	600	18.7
0	5	3.7	0	–11.7	10	10	7.5	400	4.1	20	15	11.2	800	20.2
0	5	3.7	200	–5.9	10	10	7.5	600	8.6	25	0	0.0	0	20.7
0	5	3.7	400	–0.4	10	10	7.5	800	9.9	25	0	0.0	200	30.2
0	5	3.7	600	4.8	10	15	11.2	0	–8.8	25	0	0.0	400	39.1
0	5	3.7	800	6.1	10	15	11.2	200	–4.9	25	0	0.0	600	47.1
0	10	7.5	0	–18.5	10	15	11.2	400	–1.0	25	0	0.0	800	49.4
0	10	7.5	200	–13.4	10	15	11.2	600	3.0	25	5	3.7	0	18.1
0	10	7.5	400	–8.4	10	15	11.2	800	4.2	25	5	3.7	200	23.6
0	10	7.5	600	–4.1	15	0	0.0	0	11.0	25	5	3.7	400	29.1
0	10	7.5	800	–2.8	15	0	0.0	200	20.7	25	5	3.7	600	34.4
0	15	11.2	0	–24.0	15	0	0.0	400	29.7	25	5	3.7	800	36.1
0	15	11.2	200	–19.2	15	0	0.0	600	38.4	25	10	7.5	0	14.9
0	15	11.2	400	–14.3	15	0	0.0	800	40.5	25	10	7.5	200	20.1
0	15	11.2	600	–10.4	15	5	3.7	0	6.4	25	10	7.5	400	25.3
0	15	11.2	800	–9.3	15	5	3.7	200	11.5	25	10	7.5	600	30.5
5	0	0.0	0	1.2	15	5	3.7	400	16.7	25	10	7.5	800	32.0
5	0	0.0	200	11.2	15	5	3.7	600	22.2	25	15	11.2	0	12.1
5	0	0.0	400	20.5	15	5	3.7	800	23.9	25	15	11.2	200	17.4
5	0	0.0	600	29.3	15	10	7.5	0	1.8	25	15	11.2	400	22.6
5	0	0.0	800	31.9	15	10	7.5	200	6.2	25	15	11.2	600	27.7
5	5	3.7	0	–5.3	15	10	7.5	400	10.6	25	15	11.2	800	29.3
5	5	3.7	200	0.0	15	10	7.5	600	15.1	30	0	0.0	0	25.5
5	5	3.7	400	5.2	15	10	7.5	800	16.7	30	0	0.0	200	34.9
5	5	3.7	600	10.5	15	15	11.2	0	–2.0	30	0	0.0	400	43.7
5	5	3.7	800	12.1	15	15	11.2	200	1.9	30	0	0.0	600	51.6
5	10	7.5	0	–11.1	15	15	11.2	400	6.0	30	0	0.0	800	53.8
5	10	7.5	200	–6.5	15	15	11.2	600	10.0	30	5	3.7	0	24.5
5	10	7.5	400	–2.2	15	15	11.2	800	11.2	30	5	3.7	200	29.9
5	10	7.5	600	2.2	20	0	0.0	0	15.8	30	5	3.7	400	35.2
5	10	7.5	800	3.5	20	0	0.0	200	25.4	30	5	3.7	600	40.5
5	15	11.2	0	–15.7	20	0	0.0	400	34.6	30	5	3.7	800	42.3
5	15	11.2	200	–11.5	20	0	0.0	600	42.8	30	10	7.5	0	22.8
5	15	11.2	400	–7.7	20	0	0.0	800	45.1	30	10	7.5	200	27.9
5	15	11.2	600	–3.8	20	5	3.7	0	12.3	30	10	7.5	400	33.0
5	15	11.2	800	–2.6	20	5	3.7	200	17.3	30	10	7.5	600	37.7
10	0	0.0	0	6.1	20	5	3.7	400	22.8	30	10	7.5	800	39.1
10	0	0.0	200	16.0	20	5	3.7	600	28.4	30	15	11.2	0	21.4
10	0	0.0	400	25.1	20	5	3.7	800	30.0	30	15	11.2	200	26.6
10	0	0.0	600	34.0	20	10	7.5	0	8.3	30	15	11.2	400	31.7
10	0	0.0	800	36.3	20	10	7.5	200	12.7	30	15	11.2	600	36.3
10	5	3.7	0	0.6	20	10	7.5	400	17.5	30	15	11.2	800	37.4
10	5	3.7	200	5.7	20	10	7.5	600	22.8					

W/m^2) and effects of wind are minimal (Fig. 1). Even at T_a's of –30° C, the first direct beam radiation at sunrise will stop shivering by mule deer almost immediately and elevate skin temperatures equal to those at +30° C in summer (Parker and Robbins 1984). Radiant temperatures of the surface of mule deer pelage may change 18° C between shaded and unshaded conditions (Parker and Harlan 1972). In contrast, upper critical temperatures actually may be exceeded at –25° C (T_a) for animals on snow surfaces with minimal wind speeds and high solar levels (400 W/m^2) (Fig. 1, Table 1).

In high elevation mountain habitats when air temperatures fall to freezing (0° C) in late summer, solar levels must exceed 175 W/m^2 for adults to remain in thermoneutral environments (Fig. 3). As such, nighttime poses lower thermally critical conditions in still air. In the extreme case, when freezing air temperatures occur at midday, solar radiation levels greater than 550 W/m^2 may induce heat stress. Hence, a singular change in solar radiation from minimal to average daily loads will cause standard operative temperatures for mule deer to range from cold-stressed to heat-stressed environments.

In both seasons, under conditions of dark, calm, and no wind, an animal radiates more heat to the environment than it gains. It consequently senses the environment to be colder than air temperature (e.g., Table 1, adult in snow in winter: T_a = –20° C, u = 0, SW = 0, T_{es} = –23.3° C). In the model, this occurs because the long-wave radiation absorbed by the animal is less than its long-wave emittance. Data for white-tailed deer *(Odocoileus virginianus)* suggest that animal surface temperatures (T_r) are greater than air temperatures under still, no wind conditions (T_a = 0.0 to –30.0° C, T_r = 6.6 to –21.8° C; Moen 1968b). Because this model assumed an outer coat temperature equal to air temperature, net radiative heat loss and an estimate of the resistance of free convection by mule deer may be slightly greater than predicted here and their operative thermal environment would be even colder.

Wind also significantly affects the mule deer's thermal environment. The range of temperatures within the thermoneutral zone under no wind conditions in winter declines 50% when wind speeds reach 15 m/s; similarly, in summer a 43% decrease occurs. Increasing wind speeds (0 to 15 m/s) have the greatest effect on lower critical environments with high solar radiation levels; effects are least on upper thermally critical limits during no sun conditions (Figs. 1-3).

The wind speed experienced by an animal is slightly less when it stands in snow (or a meadow) that is 0.1 m deep than when on bare ground because the wind speed profile, which increases exponentially with increasing height above the ground (Campbell 1977:39), does not begin until 0.1 m above the substrate. Standard operative temperatures experienced by fawns would be slightly colder than those experienced by adults (Tables 1-3). Even though smaller animals (with lower rib-cage heights) have the advantage of being in the lower-velocity portion of a wind speed profile (Moen and Jacobsen 1975), their characteristic dimension relative to body weight (Parker 1987) and larger surface area to volume ratio result in higher susceptibility to convective heat losses.

Limitations of Estimating Thermally Critical Environments

Critical temperatures for mule deer were determined for standing, full-fed, healthy animals. Thermal stress for animals in the field may be adjusted slightly by behavior, diet, and body condition. For example, lying postures potentially reduce heat loss through the extremities and may decrease LCT's for moose *(Alces alces)* by more than 10° C (Renecker et al. 1978). In contrast, locomotory costs in reindeer may substitute for some thermoregulatory expenditures (Nilssen et al. 1984), even though convective heat losses would be greater for moving than for stationary animals. Fasting pronghorn *(Antilocapra americana)* reach critical thermal environments at air temperatures 12–15° C higher than those on ad libitum intake (Wesley et al. 1973). For free-ranging mule deer in poor body condition or on limited food intake in winter, lying postures would minimize energy expenditures for activity, and, because of the insulative qualities of snow, reduce thermoregulatory costs. A reduced food intake or quality-limited diet, however, also would reduce heat produced by the animal. Therefore, lower critical temperatures for free-ranging mule deer would probably approach −19° C, as used in this model, and also determined by Mautz et al. (1985), by accumulative effects of food and posture. Regardless of the absolute value chosen to represent the boundary between thermoneutrality and thermally critical environments, the relative effects of air temperature, wind speed, and solar radiation should be as shown in the surfaces generated by our analysis.

Weight-specific metabolic rates of fawns may be significantly higher than those of adults depending on age of the animal (Parker and Robbins 1984). As such, feed intake per unit weight must be higher for fawns. Young animals would be affected indirectly to a greater extent by thermal constraints than would adults.

Convective heat losses, as estimated in this model, are based on a static nature of the animal's hair coat. For animals in winter, wind speeds up to 15 m/s reduce coat resistance to ≈35% of still-air values, which is only slightly more than the insulation determined for deer pelts by Moote (1955). Winter pelage of deer provides poor insulation from wind, particularly in comparison to arctic species, because it is less dense and easily compressed. At some undetermined wind speed, however, this maximum protective insulation of the hair coat, regardless of its relative quality, will be disrupted. Studies using animal models with sheep and cattle pelts indicate that external insulation is partially destroyed because of a breakdown and/or separation of the hair fibers at wind speeds greater than 11 m/s (Ames and Insley 1975). If these data are applicable to live animals, coat resistance would be reduced greatly from that predicted by this model and standard operative temperatures at wind speeds greater than 11 m/s would be much colder. Unfortuntely, actual micrometeorological measurements of high wind speeds have not been related to metabolic requirements of mule deer.

Conductive heat losses have not been included in this model. In snow-covered habitats in winter, the insulation provided by the animal's winter pelage and the snow may minimize heat losses. For animals lying on cold, poorly insulated ground without snow or during early spring and summer conditions, conduction may aggravate cold stress and may be one of the more important ways of heat loss (Gatenby 1977). Standard operative environments would be colder than predicted herein if the heat lost by conduction (but conserved by lying) exceeded heat lost by convection (and expended during standing).

The transitions between different thermal environments (the animal's transient state) is a more difficult variable to incorporate in thermal models (Campbell 1977:96, Parker and Robbins 1985). Animals are not static components of their environment. Because of activity patterns and movements, a variety of non-uniform microsites are encountered. Large animals, with low surface area to volume ratios and a large thermal resistance, are able to endure long exposures to environments outside acceptable operative conditions before significant changes in body temperature occur. Smaller animals respond more quickly to environmental changes and consequently may benefit to a greater degree, at least in the short term, by the provision of thermal cover.

Influences of Vegetative Cover

We have modelled the interactions of weather variables as they affect the operative temperatures experienced by adult mule deer. The animal's metabolic response to a given T_{es} is the same no matter what habitat it is in. It is unlikely, however, that abiotic variables measured in open areas are equivalent to those measured simultaneously under forested canopies. Vegetative structures (and hence, the concept of thermal cover) modify the abiotic components of open areas (temperature, windspeed, radiation) and have been addressed by Bunnell et al. (1986).

From a very general standpoint, compared with an open area, a forested habitat is often cooler (−2° C) in summer and warmer (+2° C) in winter, may reduce windspeeds by 85%, receives only 20% of total incoming short-wave radiation, and traps more long-wave radiation at night (Bunnell et al. 1986). Recognizing that there are additional complexities (e.g., changes in albedo, snow depths, and turbulence factors), but simplistically assuming only the above differences between open and forested areas, we compared estimates of T_{es} between the 2 areas during winter and summer. T_{es} was significantly altered in these simulations. For example at −10° C with windspeeds of 10 m/s under snow conditions during winter, mule deer are thermally stressed regardless of solar radiation level (Table 1). T_{es} in forested habitats would be 15° C warmer than in open habitats because of reduced windspeeds, thereby eliminating thermal stress. Similarly in summer, under calm conditions and 20° C, forested areas may provide shaded areas that are 20° C cooler than open areas by reducing high solar levels. Shrub-steppe communities will have less profound global effects on altering weather variables, but scattered trees or shrubs, rocks, or topological formations may, nonetheless, provide improved microclimates for deer.

Further studies are needed to compare concurrent measurements of micrometeorological variables in open and forested areas; modelling efforts to predict the environmental conditions imposed by vegetative structures from weather measurements in open areas would be extremely valuable and could then be linked with this model to predict whether or not an animal is thermally stressed.

Conclusions

Management of mule deer and their habitats should integrate the behavioral, physiological, and microclimatic factors that cause changes in habitat use over the year. Maintaining a healthy, productive deer population depends on how well and how often the physiological needs of the individuals are met or exceeded (Leckenby 1977). This model has addressed only one component of the individual's energy balance—thermoregulation. Effective management also must consider the relative contributions of activity, diet, and sociality to energy requirements and subsequent population status.

An animal's habitat choice may not directly reflect thermal conditions (see Bunnell et al. 1986:17-24). During summer, the thermoregulatory cost of remaining in the open may be counterbalanced by opportunities for increased energy intake from abundant and high quality forage. In winter, however, at a time of decreased forage resources and increased locomotory costs in snow, it is less likely that animals will leave thermal cover on the comparatively rarer chance of finding sufficient energy intake to meet additional thermoregulatory requirements. Thermal cover serves to reduce heat loss or gain and becomes physiologically important when its presence is necessary to maintain a positive energy balance (Moen 1968b). Daily thermoregulatory costs during winter are often of longer duration than periodic locomotory costs and can be a constant drain on an individual's reserves. The energy expended during thermal stress in summer may reduce what is available for lactation, growth, fattening, and movement (Leckenby 1977). Thermal stress in both seasons, therefore, may influence immediate survival of the individual, and production and future survival of its offspring.

Management guidelines for the provision of thermally neutral habitats for mule deer should delineate the range of standard operative temperatures that occur in habitats occupied by deer. Specifically measured micrometeorological variables are necessary for a better understanding of habitat influences on weather conditions and for the prediction of standard operative temperatures. The calculations of T_{es} should incorporate region-specific geographical coordinates, average snow depths and vegetation heights, and average size of animals. Physiological responses of the animal to T_{es} are incorporated in this model to determine if animals are thermally stressed. Two questions should then be asked: (1) how often do animals encounter thermally critical environments during each season? (or to what degree could thermoregulation influence habitat selection?), and (2) if critical environments are often encountered, is thermal cover available to ameliorate existing thermal conditions or are food and water resources adequate to offset heat losses and gains? (or should silvicultural or management prescriptions be used to generate suitable thermal cover, food, or water resources?). Habitat management for thermal cover would be helpful under those conditions in which individuals are without large energy reserves and for which added energetic constraints would negatively influence population status.

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Appendix 1: Calculation of standard operative temperature (T_{es}) experienced by an animal

$$T_{es} = T_b - \frac{r_{Hbs} + r_{es}}{r_{Hb} + r_e} \cdot (T_b - T_e) \qquad \text{(Bakken 1981)}$$

where:

$$T_e = T_a + \frac{r_e(R_{abs} - \epsilon_s \sigma T_a{}^4)}{\rho c_p} \qquad \text{(Campbell 1977:94)}$$

and: T_e = operative temperature (°C)
T_a = air temperature (°C)
r_e = equivalent resistance to convective and radiative heat transfer ($s \cdot m^{-1}$)
R_{abs} = solar (SW) and thermal radiation (LW) absorbed by the animal ($W \cdot m^{-2}$)
$\epsilon_s \sigma T_a{}^4$ = thermal radiation emitted by the animal ($W \cdot m^{-2}$)
ρc_p = density of the air (ρ)·specific heat (c_p) (1200 $J \cdot m^{-3} \cdot °K^{-1}$; Campbell 1977:9)
T_b = body temperature (°C)
r_{Hb} = whole body thermal resistance ($s \cdot m^{-1}$)
r_{Hbs} = r_{Hb} under low convective conditions ($u \leq 1\ m \cdot s^{-1}$)
r_{es} = r_e under low convective conditions ($u \leq 1\ m \cdot s^{-1}$)

SHORT-WAVE RADIATION ABSORBED (SW):

$$SW = a_s(A_p/A \cdot S_p + 0.5 \cdot S_d + 0.5 \cdot SWGR)$$

where: a_s = absorptivity to shortwave radiation (0.70 in summer, 0.80 in winter; W. P. Porter pers. comm.)
Ap/A = ratio of shadow area on a surface perpendicular to the solar beam (0.3; Campbell 1977:80)
S_p = direct beam radiation on surface perpendicular to beam ($W \cdot m^{-2}$)
S_d = diffuse short-wave radiation ($W \cdot m^{-2}$)
SWGR = reflected short-wave radiation from ground ($W \cdot m^{-2}$)

Incident Short-Wave Radiation

$$S_p = S_b / \sin\theta$$
$$S_d = \alpha(\beta S_{po} \sin\theta - S_T)/(1 - \alpha)$$
$$S_d = S_T \text{ for } S_T < 0.5 \cdot S_{po} \sin\theta$$
$$S_T = S_b + S_d$$

where: S_b = incident beam radiation ($W \cdot m^{-2}$)
S_T = total incident short-wave radiation (beam + diffuse; $W \cdot m^{-2}$).
S_{po} = solar constant of extra-terrestrial flux density (1360 $W \cdot m^{-2}$; Campbell 1977:55)
α = scalar incorporating differences between potential direct radiation and solar constant (0.64; Wesley and Lipschutz 1976)
β = scalar incorporating absorption of solar beam by moisture and ozone (0.79; Wesley and Lipschutz 1976)
θ = solar angle (degrees);

and: TLA = TD + LONGC + EQ (Paltridge and Platt 1976)
EQ = $0.000075 + 0.001868 \cdot \cos(\phi) - 0.032077 \cdot \sin(\phi) - 0.014615 \cdot \cos(2\phi) - 0.040849 \cdot \sin(2\phi)$
LONGC = +4 min for each °E and −4 min for each °W of standard meridian
δ = $0.006918 - 0.399912 \cdot \cos(\phi) + 0.070257 \cdot \sin(\phi) - 0.006758 \cdot \cos(2\phi) + 0.000907 \cdot \sin(2\phi) - 0.002697 \cdot \cos(3\phi) + 0.001480 \cdot \sin(3\phi)$
Sinθ = $\sin\delta + \sin(\text{lat}) + \cos\delta\cos(\text{lat}) \cdot \cos(15(\text{TLA-TSN}))$

where: TSN = time of solar noon
TLA = local apparent time
TD = clock time
LONGC = longitudinal correction
EQ = equation of time
δ = solar declination
lat = latitude
ϕ = $2 \cdot \pi \cdot J/365$
J = Julian day

Reflected short-wave radiation from ground

$$SWGR = \text{Albedo} \cdot S_T$$

where: Albedo = 0.8 for snow; 0.20 for typical field; 0.26 for matted grass (Lowry 1969:133)

LONG-WAVE RADIATION ABSORBED (LW):

$$LW = a_L(0.5 \cdot \epsilon_{sky} \sigma T_a{}^4 + 0.5 \cdot \epsilon_{gr} \sigma T_a{}^4)$$

where: σ = Stephan Boltzman constant ($5.67 \cdot 10^{-8}\ W \cdot m^{-2} \cdot °K^{-4}$)
a_L = absorptivity to long-wave radiation (1.0 for caribou; Monteith 1973)
ϵ_{sky} = emissivity of sky (see Moen 1968:340)
ϵ_{gr} = emissivity of ground (0.97; Parker unpubl.)
$T_a{}^4$ = air temperature in °K ($(T_a + 273)^4$)

LONG-WAVE RADIATION EMITTED FROM ANIMAL (L_{oe}):

$$L_{oe} = \epsilon_s \sigma T_a{}^4$$

where: ϵ_s = emissivity of surface (1.0 for caribou, Monteith 1973)
$T_a{}^4$ = air temperature in °K ($(T_a + 273°)^4$)

THERMAL RESISTANCE BETWEEN OUTER SURFACE AND ENVIRONMENT (r_e):

$$1/r_e = 1/r_{Ha} + 1/r_r$$
$$r_r = \rho c_p / 4\underline{\epsilon_s \sigma T}_a{}^3$$
$$r_{Ha} = 307\sqrt{d/u} \cdot 0.7$$
$$r_{Hasun} = 840[d/(T_{s(sun)} - T_a)]^{0.25}$$
$$r_{Hashade} = 840[d/(T_{s(shade)} - T_a)]^{0.25}$$
$$Z_{pd} = 0.77h$$
$$Z_m = 0.13h$$
$$u^* = u(k)/(\ln(Z_u + Z_m - Z_{pd})/Z_m)$$
$$u_a = (u^*/k) \cdot \ln((Z - Z_m - Z_{pd})/Z_m)$$

where: r_e = thermal resistance of skin and pelage to heat flow
r_r = resistance to long-wave radiative transfer
r_{Ha} = resistance to forced convective heat transfer
r_{Hasun} = resistance to free convection in sun
$r_{Hashade}$ = resistance to free convection in shade
d = characteristic dimension of animal [(length + width)/2; Parker 1987)
0.7 = turbulence factor (Campbell 1981)
Z_{pd} = zero plane of displacement or distance from height zero to average height of heat exchange (Campbell 1977:38)
h = average 'crop' height (grass, shrubs, snow)
Z_m = momentum roughness parameter for uniform surfaces or length of drag at momentum exchange surfaces (Campbell 1977:39; see Bussinger (1975) for more complex surfaces)
Z_u = height of wind measurement (standard is 3m)
k = von Karman's constant (0.4; Campbell 1977:38)
Z = animal height (assumed to be rib cage; Parker 1987)
u = wind speed, $m \cdot s^{-1}$
u* = friction velocity
u_a = wind speed extrapolated to animal height ($m \cdot s^{-1}$)
T_s = skin temperature (from Parker and Robbins 1984)

BODY TEMPERATURE (T_b):

$T_b = 37.95 + 6.0/(1 + e^{-0.103(Te-53.65)})$ in winter (from Parker and Robbins 1984)

$T_b = 38.18 + 6.0/(1 + e^{-0.153(Te-51.01)})$ in summer (from Parker and Robbins 1984)

WHOLE BODY THERMAL RESISTANCE (R_{HBs})

$r_{HBs} = 857.9 - 29.9T_e - 0.19T_e^2 + 0.006T_e^3$ in winter (from Parker and Robbins 1984)

$r_{HBs} = 603.29 - 4.62T_e - 0.30T_e^2$ in summer (from Parker and Robbins 1984)

$r_{Hcs} = r_{HBs} - r_{Ht}$

$r_{Ht} = 63.95 - 5.58T_e$ in winter (Webster 1974)

$r_{Ht} = 204.43 - 6.49T_e$ in summer (Webster 1974)

where: r_{Hcs} = thermal resistance of the coat under low convective conditions ($u \leq 1$ m/s)

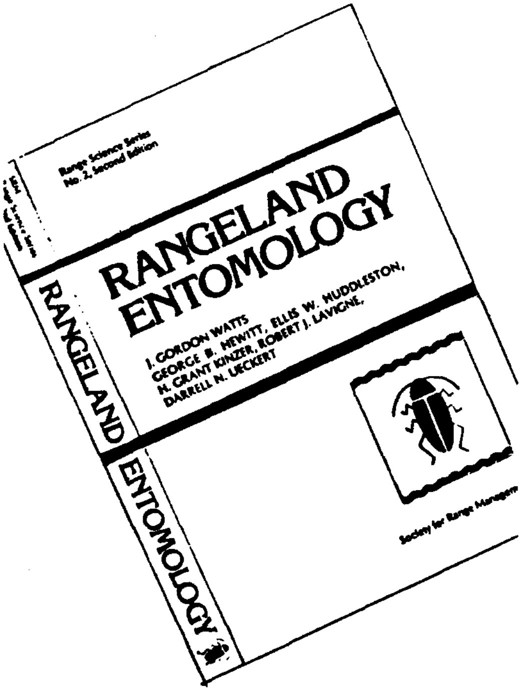
r_{Ht} = thermal resistance of the tissue

WHOLE BODY THERMAL RESISTANCE TO OUTDOOR WIND SPEEDS:

$r_{Hb} = r_{Ht} + r_{Hc}$

$r_{Hc} = r_{Hcs}/(1.0 + 0.08u_a)$ (Campbell et al. 1980)

where: r_{Hc} = thermal resistance of the coat under outdoor wind speeds



Technical Notes

A comparison of two furrow opener-depth control assemblies for seeding forage grasses

T. LAWRENCE AND F.B.DYCK

Abstract

Seed from 45 strains of grass were sown with 2 drills fitted with different furrow openers and depth control devices. Standard (34-cm diameter) double disk openers (Kirchman (Lilliston Melroe)) fitted with depth control bands 2 cm wide and 5 cm smaller in diameter than the disk were used to seed 1 trial at a seeding depth of 2.5 cm. This seeding was compared to forage crop stands obtained from a drill fitted with an experimental opener using 2 disks of unequal diameter, the larger (38 cm diameter) running vertical and the smaller (28 cm diameter) angled at 7°. The center for mounting the small disk is 5 cm below and 2.5 cm behind the large disk, thus the bottoms of the disks are on the same horizontal plane. Seeding depths of 2.5 cm and 6.25 cm were accomplished by an adjustable rubber-tired depth gauge wheel assembled beside the large disk. At the 2.5 cm depth of seeding, the large-small disk opener assembly resulted in superior forage establishment compared to that obtained with the standard double disk assembly. Comparing either opener-depth control assembly set to seed at 2.5 cm depth with the large-small disk assembly set to seed at 6.25 cm depth confirmed the value of shallow seeding of forage crops to overcome establishment problems.

Key Words: furrow opener-depth control assemblies, forage emergence, seeding depth, Altai wild ryegrass, Russian wild ryegrass, intermediate wheatgrass, crested wheatgrass, tall wheatgrass

Observations made in producers' fields and experimental plots over the past 30 yr indicate that 80-90% of forage crop stand failures in the arid prairies can be attributed to seeding too deeply (Lawrence 1979). In an arid environment where dryland forages are adapted, lack of soil surface moisture or inappropriate seeding equipment are reasons for seeding at a depth greater than is commonly recommended. Double disk-type openers and other drills without depth controls are widely used to seed forage crops with variable success.

Methods

This study reports on a comparison between 2 furrow openers with depth control assemblies for seeding forage crops. Two Swift Current self-propelled 6-row plot seeders (McLaughlin and Dyck 1986) were fitted with different furrow openers and depth control devices. Drill I was fitted with the standard commercial (34 cm diameter) double disk opener assembly (Kirchman (Lilliston Melroe)) with a 2 cm wide depth control band on each disk. The depth control bands were 5 cm smaller in diameter than the disks. (Fig. 1). Drill II was fitted with an experimental opener using 2 disks of unequal diameter, the larger (38 cm diameter) running vertical and the smaller (28 cm diameter) angled at 7 ° toward the larger disk (Dyck 1982, Dyck and Tessier 1986). The center for mounting the small disk is 5 cm below and 2.5 cm behind the large disk, so that

Table 1. Emergence of various grass strains as influenced by type of furrow opener-depth control assemblies and depth of seeding.

		Emergence—No. seedlings/m		
		Drill I	Drill II	
Grass	Strain	2.5-cm depth	2.5-cm depth	6.25-cm depth
Altai wild ryegrass	Sc A 3751	33	47	16
	Sc A 3752	26	58	23
	Sc A 3753	37	50	28
	Sc A 3754	32	54	31
	Sc A 3757	29	48	29
	Sc A 3758	21	37	7
	Sc A 3772	25	44	28
	Sc A 3773	29	34	33
	Sc A 3803	31	43	24
	Sc A 15011	34	52	26
	Sc A 15012	24	37	33
	Prairieland	28	47	38
Russian wild ryegrass	Sc R 3751	48	82	14
	Sc R 3742	34	47	11
	Sc R 3753	30	50	18
	Sc R 3761	28	44	16
	Sc R 3762	36	63	42
	Sc R 3793	37	52	22
	Sc R 17040	28	68	20
	Swift	54	65	12
	Mayak	32	46	22
	Cabree	28	47	5
	Idaho 100	28	50	12
	Sc R 4N 721	27	28	9
	Sc R 4N 722	20	30	10
	Sc RN 3761	35	50	10
Intermediate wheatgrass	Sc I 3701	39	56	26
	Sc I 3702	48	87	42
	Sc I 3711	44	52	24
	Sc I 3712	42	56	14
	Sc I 3713	34	53	30
	Sc I 3714	36	50	22
	Sc I 3715	30	40	15
	Sc I 3731	35	63	38
	Sc I 3732	20	42	41
	Sc I 3734	35	45	24
	Sc I 3761	36	41	34
	Sc I 3762	40	41	22
	Sc I 3763	29	51	30
	Clarke	32	41	21
	Chief	15	38	11
Crested wheatgrass	Commercial	70	94	16
Tall wheatgrass	Orbit	30	42	18
	Test Mean	34	51	22
	LSD (P=.05)	16	23	20
	SEM%	17	16	32

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Manuscript accepted 24 May 1989.

the bottoms of the disks are on the same horizontal plane. A single rubber-tired semipneumatic wheel 5 cm wide and 33 cm in diameter was mounted on a separate bracket beside the large disk to form an adjustable depth control gauge wheel (Fig. 2).

Three, 3-replicate randomized block tests including 12 strains of Altai wild ryegrass, *Leymus angustus* (Trin) Pilger; 14 strains of Russian wild ryegrass, *Psathyrostachys juncea* (Fisch.) Nevski; 15 strains of intermediate wheatgrass, *Thinopyrum intermedium* (Host) Barkworth and D.R. Dewey; 1 strain of each diploid crested wheatgrass, *Agropyron cristatum* (L.) Gaertner, tall wheatgrass, *Thinopyrum elongatum* (Host) D.R. Dewey were sown consecutively over a 2-day period on a test area. One test was sown with drill I at a depth of 2.5 cm and the other with drill II at 2.5 cm and 6.25 cm deep. Plots consisted of 2 rows 30 cm apart and 6 m long. The tests were seeded in May 1983 on fallow land described as a Swinton silty loam to loam soil (Ayres et al. 1985).

Results and Discussion

At the 2.5 cm depth of seeding, the large-small disk arrangement with adjustable depth gauge wheel resulted in a significantly superior forage crop emergence (t = 11.11, *P* = .0001) to that obtained with the standard double disk with attached depth bands. Comparing the double disk opener assembly seeding at 2.5 cm depth with the large disk-small disk at 6.25 cm depth, stands of forage crop were superior using the former assembly (t = 6.97, *P* = .0001). Similarly, comparing the forage plant emergence from the 2.5 cm depth with that from the 6.25 cm depth, using the large disk-small disk assembly showed the superiority of shallow seeding with the same opener (t = 13.04, *P* = .0001). An observation made in the field during the course of this study suggests that a possible reason for poorer stands from deep seeding may be poor refilling of the seeding trench and consequent poor packing of soil around the seed.

It was concluded that the large-small disk assembly resulted in superior stands of forage crops at recommended seeding depths. Subsequent seedings of numerous forage tests using the large-small disk assembly have confirmed the superiority of this device for improving stand establishment.

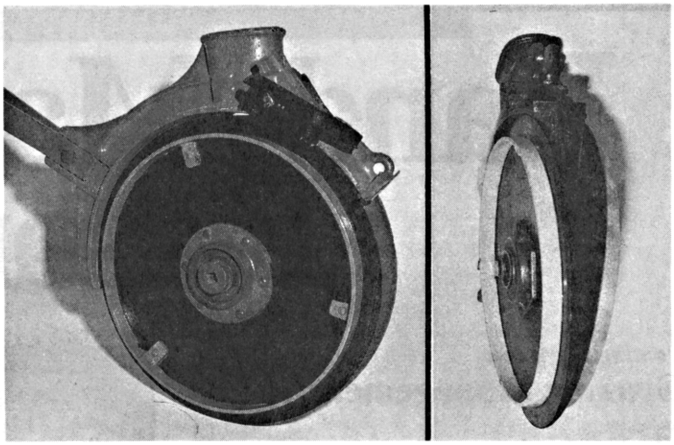

Fig. 1. Standard double disk opener fitted with depth control bands.

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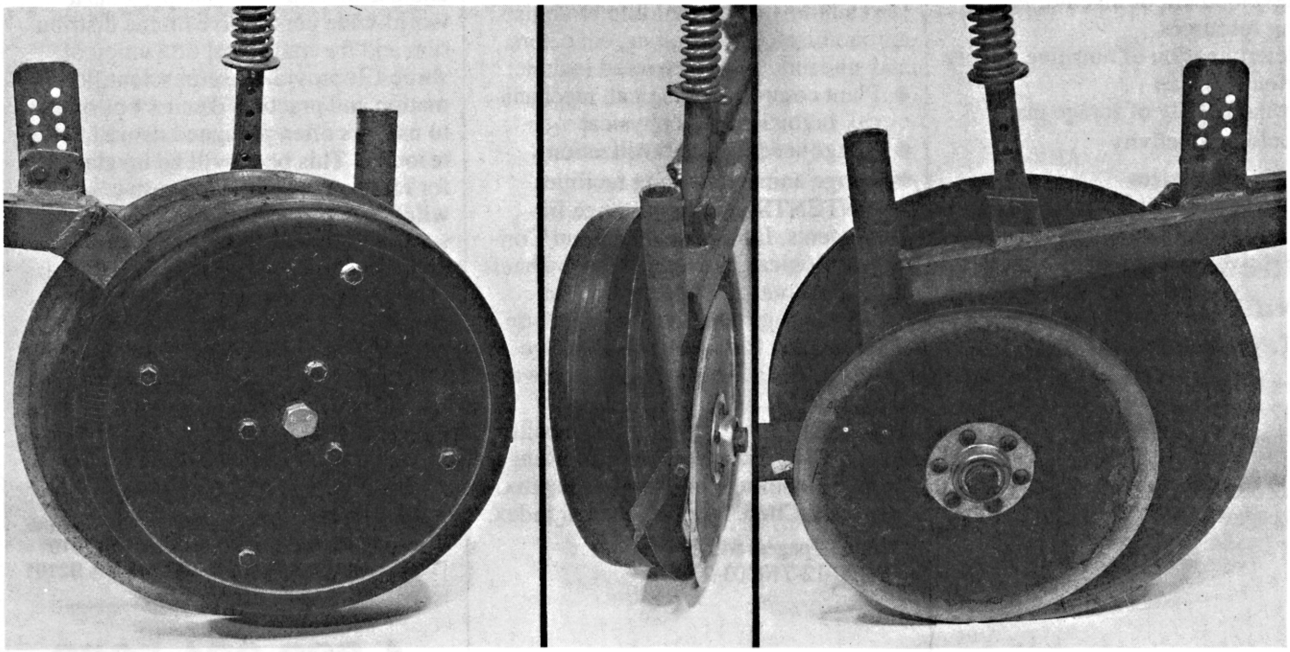

Fig. 2. Large-small double disk opener assembled with an adjustable rubber-tired depth gauge wheel.

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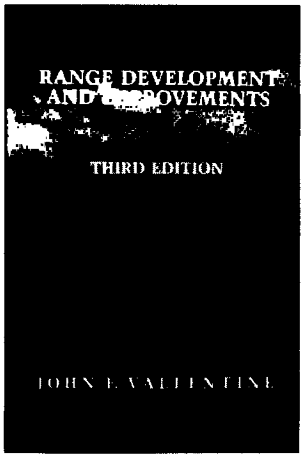

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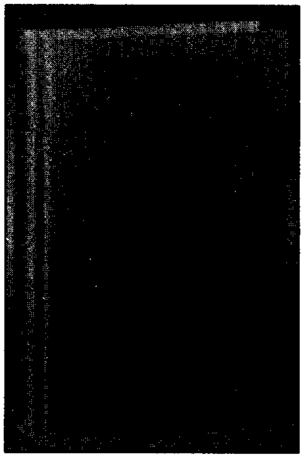

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Book Reviews

From Sagebrush to Sage: The Making of a Natural Resource Economist. by Marion Clawson. 1987. Ana Publications, 4343 Garfield St., NW Washington, D.C. 20007. 476p. $20.00 (Paper).

"From Sagebrush to Sage" is an extremely enjoyable book to read which should be of interest to many individuals within the resource management profession. For those who have pondered the ideas expressed by Marion Clawson in his numerous papers and books, this autobiography provides an opportunity to gain a better understanding of this unique man who has contributed so much to natural resource policy and natural resource economics. All readers, including those who have known the man for a number years, will enjoy reading this book and learning more about him and his work as well as his philosophy of life.

The book is divided into two sections—recollections and reflections. Recollections is composed of 12 chapters which chronicle the many and varied aspects of Marion Clawson's life from his roots in turn of the century towns and mining camps of Nevada through his life in the 1980's. Each chapter covers roughly a decade in his life or a specific period within his professional career. Early chapters are devoted to discussions of growing up in the early 1900's. Many of the discussions within these chapters will remind readers of the reflections of their own parents and grandparents. Subsequent chapters focus on a combination of Clawson's professional and personal life. The author includes a variety of information about himself and his family, his interactions with others and his management style. Specific chapters are devoted to his years with the Bureau of Land Management (BLM), Resources for the Future (RFF) and the Society for International Development (SID). Each of these chapters includes an introduction to these organizations as well as discussions of Clawson's role in their evolution.

In part two of the book—reflections—Marion Clawson comments on a wide range of topics including "Life and Death", "Comforts of Living and Concepts of Poverty", "Sex", "Science", "Government", "More for Me", "Optimum Inequality" and "Is there a Purpose To It All". These chapters provide additional insights into this unique individual, while adding an element of humor and a taste of his personal philosophy to the book.

In summary, Marion Clawson's autobiography is an excellent book, well worth the time required to read it. It is interesting, informative, and makes a meaningful contribution to the history of resource policy.—*Keith A. Blatner,* Department of Forestry and Range Management, Washington State University.

Cyprus: A Chronicle of Its Forests, Land and People. By J.V. Thirgood. 1987. University of British Columbia Press (Cloth). 371 p.

In his foreword to this meticulous history of the forests of Cyprus, a former Conservator says it all:

> The author has traced in considerable detail the earlier forest history of Cyprus and the progress, through the eighty years of the British Administration and the first twenty-five years of the Republic, of forest protection and management, starting with the demarcation of forest reserves and the gradual elimination of forest misuse....

Dr. Thirgood has indeed compiled a detailed, scholarly and thoroughly researched account of the administration, environment, politics and sociology of the forests of the island of Cyprus. From the verdant beginnings in the early mists of their history, the Cyprus forests have suffered over-use, neglect and, particularly with the advent of the omnivorous goat, abuse to such an extent that the first forester employed there could write:

> Summing up: the forests of the island are in a deplorable state, and their ruin is hastened daily from the fact that the action gets more destructive on account of its yearly being concentrated on a narrower area. There is no more time to remedy the situation by simple remedies, only energetic measures may be of some use, and there must be no hesitation in their application, as the whole future prosperity of the island depends on this.

Just 110 years ago a British colonial administration set about halting further destruction and instituting a programme of rehabilitation. Bedevilled by inadequate surveys; complex, archaic and dishonest tenures ("Be he Christian or Mussulman, the Cypriot peasant is convinced that wood, like air and water, has no other master than the God who made it. It seems as natural to him to go where he will and cut wood as to drink in the brook hard by when he is thirsty"); meagre funding, and the ubiquitous goat, it was no easy or straightforward task. Slowly, patiently and persistently progress was achieved despite many setbacks. Applied silviculture control of arson and natural fires, grazing management and, above all, strict control of goats meant that when, in 1960, officials of the nearly independent Republic assumed office, they took over a forest-in- being and on the mend if not yet fully restored. Their predecessors had, wisely, addressed the social and economic challenges as well as the simply technical ones.

This tradition of thoughtful management of the whole forest resource for the continuing good of the local community has been zealously continued by a succession of dedicated Cypriot foresters despite political obstacles, some of them huge. Tourism has lately become an increasingly important use of the forest estate which must be accommodated along with more traditional practices.

While details of the Cyprus experience may not hold fascinating interest for the North American forest or range manager, the underlying significance is real and pertinent. A forest nearing total destruction has been recovered by sensitive application of a well-constructed consistent and long-term policy, despite early opposition. It has gained acceptance and support by a majority of the local populace; the grass-roots without which sustained health is impossible.

Are we going to take Dr. Thirgood's message to heart or must we too reach the brink of disaster before mending our profligate ways? The lesson is clearly spelled out—now we must respond.—*R.M. Strang,* White Rock, B.C.

Natural vegetation of Oregon and Washington. 1988. Jerry Franklin and C.T. Dyrness. Oregon State University Press, Corvallis, OR 97331-6407. $22.95 plus $2 shipping. (paper) 452p.

Originally published by the U.S. Forest Service in 1973, it quickly became the "classic volume on regional ecology" for these Pacific Northwest States. The original printing soon was exhausted, and it has remained out of print for several years. Oregon State University has undertaken reprinting to fill the current need. This is an excellent reproduction, limited almost entirely to the original volume in content, but with the addition of new preface, comments, and bibliographic supplement. The authors note that significant contributions have been made to the ecologic understanding of the region since 1973, but their workload in new directions has precluded a complete updating of the volume at this time. The bibliographic supplement provides help to the reader by adding 100 recent citations to the more than 400 listed in the original.

The authors divide the region into major physiographic and geologic provinces as background information to the reader, and major vegetational areas (forest and steppe) are subdivided into zones for individual treatment. Environmental features, species composition, successional patterns, and special types are discussed for each of the forest zones. Descriptions of steppe vegetation of eastern Washington and Oregon are essentially lifted from publications of R.F. Daubenmire. (Franklin is a student of Daubenmire). The book is filled with more than 200 unusually beautiful photographs, showing useful detail for field recognition of zonal vegetation and aspect. Soil descriptions are also unusually good.

This book provides by far the outstanding ecological treatment of the Pacific Northwest Region. It should be in the library of all who have interest, but especially responsibility, for land management, in the region. From a range manager's point of view, I only wish the authors had had as much interest in the steppe areas as in the forest.—*Grant A. Harris,* Washington State University, Pullman.

Population Ecology of the Mallard, VIII, Winter Distribution Patterns and Survival Rates of Winter Banded Mallards. By James D. Nichols and James E. Hines. 1987. U.S. Fish and Wildlife Service, Matomic Building, Room 148, Washington, D.C. 20240. 154 p.

This book addresses questions about winter distribution patterns of North American mallards, *Anas platyrhynchos*. It includes descriptive information and hard data on winter distribution patterns, survival rates, and band recovery data, as well as a band recovery model and population ecology on the migratory wild mallard. If you are looking for facts, this is the book for you!

The authors divided primary wintering range of the mallard into 45 minor and 15 major reference areas. Data were collected by banding mallards during the winter from 1950–1977. Distribution patterns are shown for each reference area by plotting subsequent recovery distributions. Survival rates were estimated from winter banding data and mallard recovery. Data include female versus male survival rates by reference area.

The objectives of this publication were to:

—develop a set of winter reference areas and to present descriptive data on band recovery distributions for mallards banded in these areas

—draw inferences about certain potential sources of variation in winter distribution patterns of mallards

—estimate survival and recovery rates of winter-banded mallards and to investigate potential sources of variation in these rates

—compare survival rate estimates based on preseason and winter banding data

The data collected for this report were extensive. They include nearly 2,000,000 bandings from preseason and winter periods and more than 300,000 recoveries. A ready reference of people and agencies who have banded more than 1,000 wild mallards (1922–1982) is provided in the appendix.

For those working with wild mallards and other migratory waterfowl, this book is an excellent reference. And now with the heated controversy of lead versus steel shot for waterfowl hunting, if you are in the middle of this battle, this book is a must for your library.—*Don Rees,* Paso Robles, California.

The Physiology of Plants Under Stress. By Maynard G. Hale and David M. Orcutt (with a chapter by Laura K. Thompson). John Wiley & Sons, Inc., 605 Third Ave, New York, NY 10158-0012. 1987. 206 p.

There is hardly a field of scientific inquiry more relevant to those concerned with grazing or reclamation than the topic of plant physiological stress. *The Physiology of Plants Under Stress* is, as the authors state in the preface, a graduate student text. Judging from the content, the course for which it is designed is a beginning graduate survey preparing agriculturally oriented students for more specific readings and research on plant stress.

The authors have wisely devoted the first chapter to elucidating conflicting terminology that has appeared in research publications on plant stress. The next seven chapters deal [successively] with individual stresses; these chapters are entitled: "drought stress"; "drought resistance"; "temperature stress"; "nutrient stress"; "salt stress"; "irradiation stress"; and "allelochemical stress". Two chapters follow, dedicated to specific topics in cell physiology: "the effects of stress on membranes"; "the role of phytohormones in stressed plants." In the final chapter, "stress tolerance through biotechnology", both plant growth regulators and genetic engineering are discussed as methods for infusing economically important species with stress resistance or tolerance. For the classroom, the authors have supplemented each chapter with some pertinent discussion questions. A short glossary has been compiled, a helpful addition given the broad subject matter.

Whereas plant stress is a vast topic requiring discussions of biochemistry, physics, and physiology, several chapters are very brief (only six full pages are devoted to salt stress). The authors chose to limit in-depth explanations of physiological mechanisms, and avoided almost entirely the presentation of quantitative models. In addition, too few graphics were used to clarify discussions of cellular phenomena, chemical exchange, and functional change. The authors omitted stress and response to defoliation (neither *grazing* nor *defoliation* are listed in the index). In my latter point, it is more than personal bias [as a range scientist] that compels me to level this criticism; research on plant responses to defoliation has yielded information that is pertinent not only to range and pasture management, but agriculture and forestry, as well. Applied scientists recognize that theories of plant response to partial harvests, insect herbivory, as well as to large herbivore grazing, should influence management and research decisions.

Although the authors have done well to unite the different elements of plant stress physiology between a single set of book covers, in this edition they have not cultivated the material to a depth attractive to a wide readership. In addition, without mention of herbivory, the book is not very useful to range science students.—*Richard P. Cincotta,* Los Angeles, California.

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