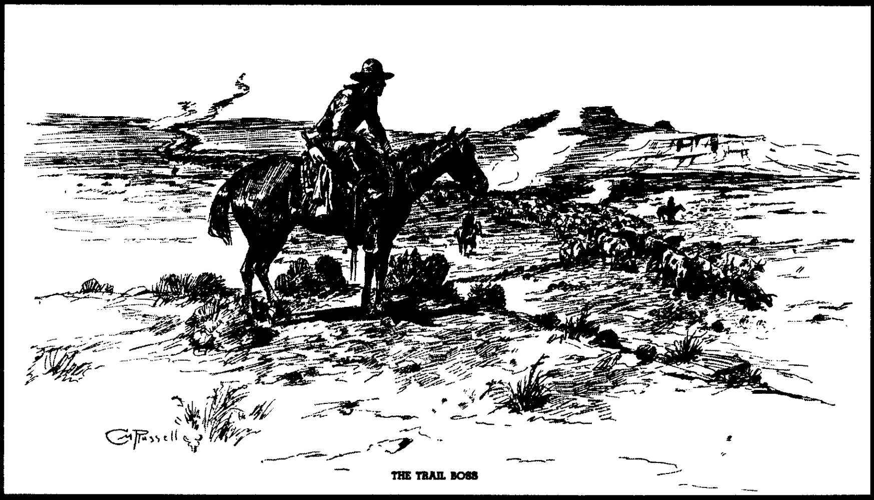
JOURNAL OF RANGE MANAGEMENT

USPS 282-460



PUBLICATION OF THE
SOCIETY FOR RANGE MANAGEMENT

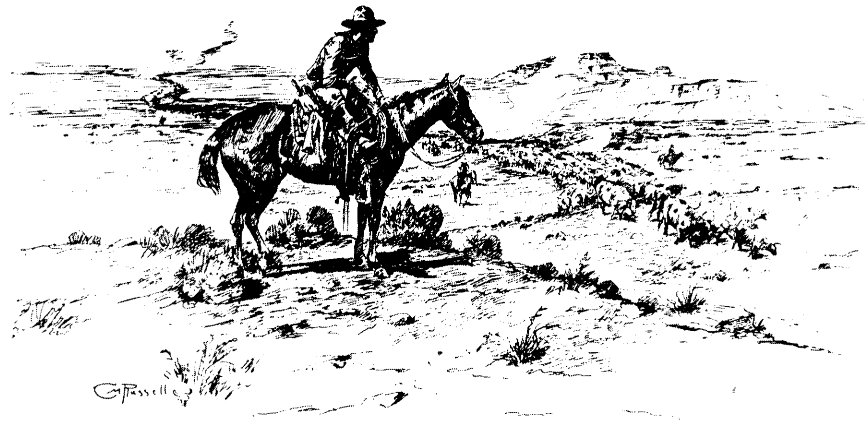
VOL. 32, NO. 1
JANUARY 1979

SOCIETY FOR RANGE MANAGEMENT

Contribution Policy

The Society for Range Management may accept donations of real and/or personal property, subject to limitations imposed by State and Federal Law. All donations shall be subject to control by the Board of Directors and their discretion in utilization and application of said donations. However, consideration may be given to the donor's wishes concerning which particular fund account and/or accounts the contribution would be applied.

We recommend that donor consult Tax Advisors in regard to any tax consideration that may result from any donation. Donations may be made by bequests, legacies, devises or transfers from private individuals, partnerships, corporations, foundations, sections, organizations, estates and trusts, or a memorial fund established as an expression of remembrance to members of real and/or personal property. Donations can be sent to the Society for Range Management, Executive Secretary, 2760 West Fifth Avenue, Denver, Colorado 80204.



THE TRAIL BOSS

The **Society for Range Management**, founded in 1948 as the *American Society of Range Management*, is a nonprofit association incorporated under the laws of the State of Wyoming. It is recognized exempt from Federal income tax, as a scientific and educational organization, under the provisions of Section 501(c)(3) of the Internal Revenue Code, and also is classed as a public foundation as described in Section 509(a)(2) of the Code. The name of the Society was changed in 1971 by amendment of the Articles of Incorporation.

The objectives for which the corporation is established are:

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

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

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

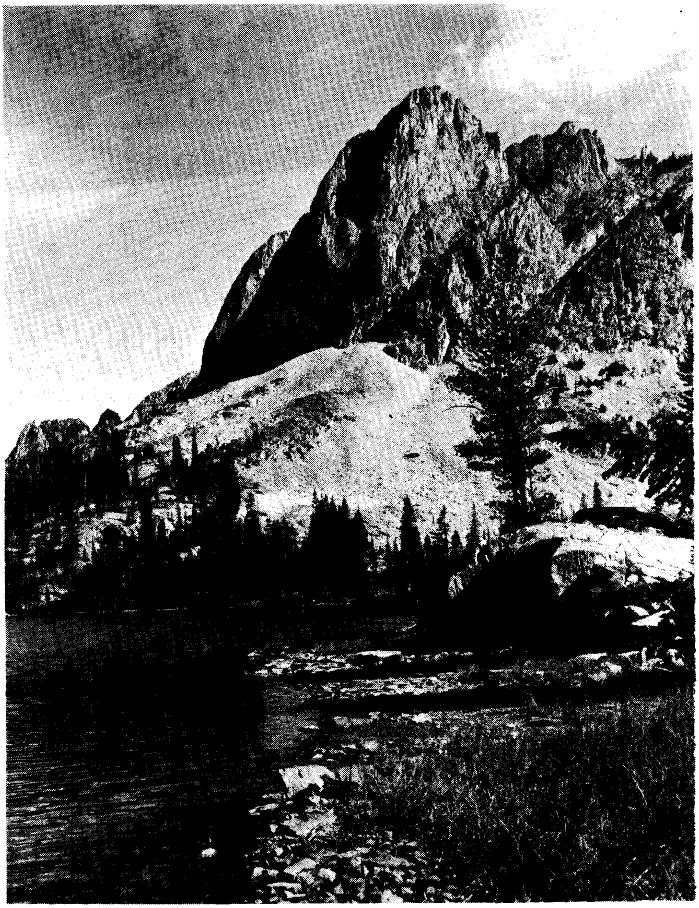
—to create a public appreciation of the economic and social benefits to be obtained from the range environment; and

—to promote professional development of its members.

Membership in the Society for Range Management is open to anyone engaged in or interested in any aspect of the study, management, or use of rangelands. Please contact the Executive Secretary for details.

The **Journal of Range Management** serves as a forum for the presentation and discussion of facts, ideas, and philosophies pertaining to the study, management, and use of rangelands and their several resources. Accordingly, all material published herein is signed and reflects the individual views of the authors and is not necessarily an official position of the Society. Manuscripts from any source—nonmembers as well as members—are welcome and will be given every consideration by the editors. Submissions need not be of a technical nature, but should be germane to the broad field of range management. Editorial comment by an individual is also welcome and, subject to acceptance by the editor, will be published as a "Viewpoint."

You are cordially invited to see IDAHO
With the Summer Meeting of
the Society for Range Management.
July 16–17, 1979



Alice Lake in the Sawtooth Wilderness near Stanley, Idaho

Convention Headquarters—*Ramada Inn, Pocatello, Idaho*
Tour Site—*Phosphate Mine Reclamation near Soda Springs, Idaho*

Watch for the Idaho Section booth at Casper.

JOURNAL OF RANGE MANAGEMENT

Published bimonthly—January, March, May, July, September, November—by the
Society for Range Management
2760 West Fifth Avenue
Denver, Colorado 80204

INDIVIDUAL SUBSCRIPTION is by membership in the Society for Range Management.

LIBRARY or other INSTITUTIONAL SUBSCRIPTIONS, on a calendar year basis, are $22.00 postpaid to all countries. Payment from outside the United States should be remitted in US dollars by international money order or draft on a New York bank.

CHANGE OF ADDRESS notices should be sent to the Managing Editor, 2760 West Fifth Ave., Denver, CO 80204, no later than the first day of the month of issue. Copies lost due to a change of address cannot be replaced unless adequate notice is given. To assure uninterrupted service, provide your local postmaster with a *Change of Address Order* (POD Form 3575), indicating thereon to guarantee forwarding postage for second class mail. POSTOFFICE: Please return entire journal with address change.

BUSINESS CORRESPONDENCE, concerning subscriptions, advertising, reprints, back issues, and related matters, should be addressed to the Managing Editor, 2760 West Fifth Ave., Denver, CO 80204.

EDITORIAL CORRESPONDENCE, concerning manuscripts or other editorial matters, should be addressed to the Editor, Dep. Animal and Range Sciences, New Mexico State Univ., Las Cruces 88003.

INSTRUCTIONS FOR AUTHORS appear each year in the March issue; copies of these instructions are available from the editor.

SECOND CLASS POSTAGE paid at Denver, Colorado.

TABLE OF CONTENTS: Vol. 32, No. 1, January 1979

ARTICLES

TECHNICAL NOTES

BOOK REVIEWS

Executive Secretary Vacancy Announcement

The position of Executive Secretary of the Society for Range Management will be vacant on March 1, 1979. The position description and search procedures will be finalized on February 14, 1979, during the annual meeting of the Society in Casper, Wyoming. A general description of the position follows:

The Society for Range Management is an organization incorporated under the laws of the State of Wyoming and governed by the "Articles of Incorporation" and the "Bylaws". The Executive Secretary is the chief administrative officer of the Society and also serves as corporate secretary and treasurer.

The responsibilities of the Executive Secretary assigned in the Bylaws are:

Article IV. SECTION 6. The executive secretary shall be accountable to the Board of Directors, and under the general supervision of the president. He will be expected to attend all meetings of the Board of Directors and of the Society, and shall be responsible for a record of the business conducted at such meetings. He shall supervise the Society's offices and its employees, maintain suitable membership records, reporting monthly to each Section the membership changes within that Section, conduct the correspondence of the Society, and keep full records of the same. The executive secretary shall also serve as treasurer and fiscal agent for the Society, collecting all dues payable to the Society and Sections, and all other monies due to the Society, depositing the same in the name of the Society, and making such expenditures as are authorized by an approved budget. He shall be responsible for maintaining suitable books of account, which shall be independently audited periodically as directed by the Board of Directors, prepare annual and interim financial reports for the Board of Directors, and be responsible for all financial or other reports required by law. The executive secretary also shall present an operational report of the Society at the annual meeting and perform such other duties as the Board may assign to him from time to time. He may be bonded in a suitable amount as decided by the Board of Directors and at the Society's expense.

In addition to the responsibilities assigned in the Bylaws, the Executive Secretary shall supervise Society employees, and assist the Board of Directors, Editors, committees, and appointed representatives, thus serving as coordinating officer for Society affairs and exercising leadership for policies and programs approved by the Board of Directors.

The position is at the Society's headquarters in Denver, Colorado. Salary will be commensurate with experience and qualifications. Initial contract will be for one year. Subsequent contracts may be for longer periods as negotiated with the Board of Directors.

The final position description and the procedures for nomination and application will be mailed to each Society member and others, including those who have inquired about the position, as soon after the Casper meeting as is practicable. All inquiries, nominations or applications should be sent to:

Dr. S. Clark Martin, Chairman of the Search Committee
2143 E. Minton Dr.
Tempe, Arizona 85282
ph: (602) 261-4365   (602) 839-8837

The approximate schedule for filling the position is:

April 1, 1979—Deadline for nominations
April, 20, 1979—Deadline for receiving applications
June, 1979—Approximate selection date

Botanical Composition of Central Texas Rangeland Influences Quality of Winter Cow Diets

JERRY W. STUTH AND DONALD R. KIRBY

Abstract

Winter diets of dry, pregnant cows were investigated on a Blackland range site in mid- and high-poor condition. Under similar amounts of available forage, an advanced successional stage, i.e. change in species composition within a range condition class, resulted in increased dietary protein (CP), digestible organic matter (DOM) and phosphorus (P). A slightly larger abundance of cool-season grasses on the pasture in higher poor condition allowed the animals to select a diet adequate in CP, DOM and P approximately 3 weeks earlier in spring than on the mid-poor condition pasture.

The typical wintering program of Central Texas producers involves concentration of livestock in rangeland pastures that have good winter accessibility. Stocking pressure is high and the animals derive most of their required nutrients from hay, protein supplement, and free choice minerals. The result is a severely overgrazed and trampled pasture in poor range condition. The severity of this problem can be lessened with minor changes in successional status of the rangeland pasture.

The complex relationships between range condition and animal nutrition must be recognized by the range manager interested in animal production (Gates 1972). Range condition is defined as the current productivity of a range relative to what a particular range is naturally capable of producing (Kothmann 1974). Gates (1972) has noted that ambiguities can arise when using the term in reference to vegetation quality or quantity. Changes in ecological condition of rangelands represent changes in both species present and/or biomass produced. An increase in range condition generally represents an increase in quantity and/or quality of forage available to the grazing animals. Studies have shown that levels of biomass can mask the affect of species composition on dietary quality due to greater animal selectivity of plant parts (Goebel and Cook 1960; Cook et al. 1965; Kothmann 1968). However, Goebel and Cook (1960) found diets to vary between condition classes. Demarchi (1973) noted that poor condition sites tended to be higher in total protein, cellulose, and phosphorus.

Little information exists on quality differences as affected by successional status within a given condition class. Generally, when production values are similar between two areas, dietary quality is dependent upon species composition. Therefore, intra-class range condition differences due to successional status of a given range site should have some impact on diet quality of animals. It was the purpose of this paper to determine the influence of changes in species composition on winter diets of cows grazing a summer-deferred, poor condition Blackland range site (U.S. Dep. Agr. 1976) in central Texas.

Authors are assistant professor and research technician, respectively, Texas Agricultural Experiment Station, Range Science Department, Texas A&M University System, College Station 77843.

This paper is published with approval of the director, Texas Agricultural Experiment Station, as TA-13922.

The authors wish to express appreciation to Mr. Samuel S. Pegues, Farms Manager, and other research personnel of the Texas Agricultural Experiment Station at McGregor, Texas, for their assistance and care of the fistulated cows used in this study.

Manuscript received January 13, 1978.

Study Area and Procedures

The study was conducted during the winter of 1976-1977 (December 17—April 1) on the Texas Agricultural Experiment Station Research Center at McGregor, Tex. Two, 44-hectare pastures with 4-hectare subdivisions in mid-poor and high-poor ecological condition were utilized as study sites. The soil series common to both pastures was a Houston black clay, which forms a Blackland range site (U.S. Dep. Agr. 1976). Average annual precipitation for the area is 83.9 cm (33 inches) (NOAA 1976). Peak rainfall occurs in May and September. Winter precipitation for the study period averages 34 cm (13.4 inches). The station recorded 46 cm (18.1 inches) during the study period.

In its pristine condition, this range site supported a true prairie vegetation. Little bluestem (*Schizachyrium scoparium*) dominates the plant community at climax with yellow indiangrass (*Sorghastrum nutans*) and big bluestem (*Andropogon gerardii*) as subdominant species. As retrogression occurs, silver bluestem (*Bothriochloa saccharoides*) and meadow dropseed (*Sporobolus asper*) are initial increasers. If continuous, heavy use occurs, buffalograss (*Buchloe dactyloides*), purple threeawn (*Aristida purpurea*), Texas grama (*Bouteloua rigidiseta*) and Halls panicum (*Panicum hallii*) will come to dominate the site (U.S. Dep. Agr. 1976).

Species composition was determined immediately after the first killing frost in late November 1976. Species composition was determined using a pace transect method (Stuth and Dahl 1974). Five, 100-point transects were randomly located in each pasture.

Both pastures were deferred during the growing season and stocked at approximately 3.25 ha/animal units (au) from December 15 to April 1. Access was provided to the subdivision in each pasture at all times except during diet collection periods. To monitor stocking pressure between subdivisions, available above-ground biomass was determined at each collection period. All vegetation within 20, 0.25-m^2 plots was clipped at ground level and dried at 100°C for 48 hours.

The dietary sampling technique was similar to that described by Cook (1964) and Van Dyne and Torell (1964). Four, esophageally cannulated cows were grazed approximately 1 hour in the early morning during six collection periods from December 17, 1976 to April 1, 1977. The cows were fasted approximately 12 hours prior to sample collections. Sample collections for the two pastures were made on consecutive days by rotating the cows. The cows were maintained throughout the study on TAM wintergreen (*Phalaris stenoptera*) and native pastures located on the McGregor Research Center.

Table 2. Mean standing crop (kg/ha) and associated confidence intervals of forage on mid-poor and high-poor condition pastures on a Blackland range site grazed during the winter.

	Condition Class			
Date	Mid-poor	C.I.	High-poor	C.I.
December 17, 1976	2030[1]	±374	2242	±318
January 11, 1977	1656	±185	1698	±272
January 28, 1977	1492	±288	1300	±191
February 18, 1977	1012	±202	1216	±255
March 14, 1977	980	±177	764	±156
April 1, 1977	628	±154	658	±161

[1] Standing crop did not differ significantly between pastures at any sampling date ($P<0.05$).

Forage Availability

To evaluate nutritional differences it was critical that stocking pressures be maintained as near equal as possible between pastures. Standing crop of forage was maintained at reasonably comparable levels throughout the study (Table 2). Thus, compositional effects on diets were reflected while biomass differences were minimal. The pattern of utilization obtained in this study is typical of utilization on ranches in central Texas.

Dietary Quality

Dietary Crude Protein

Crude protein was generally higher in the forage ingested by animals grazing the high-poor condition pasture (Table 3). If 5.9% and 9.2% crude protein are used as required levels for maintenance of a 1000-lb pregnant or lactating cow, respectively (NRC 1976), then only the period from mid-December to mid-January was deficient in the high-poor condition pasture. Deficient CP levels were extended into February on the mid-poor condition pasture. Available forage was assumed not to be limited.

A rapid increase in dietary protein was observed during February, when cool-season species began active growth. The high-poor condition pasture exhibited the response 3 weeks earlier than did the mid-poor condition pasture. Initiation of growth of cool-season species depends primarily on winter and early spring temperatures. The significantly larger percentage of both perennial and annual cool-season grasses in the high-poor condition pasture probably accounted for the earlier increase in CP observed there (Table 1). Crude protein content of the diet averaged 2.5% higher for the entire sampling period in the high-poor condition pasture as compared to the mid-poor condition pasture ($P<0.05$). All CP values were significantly different between pastures and among dates ($P<0.05$).

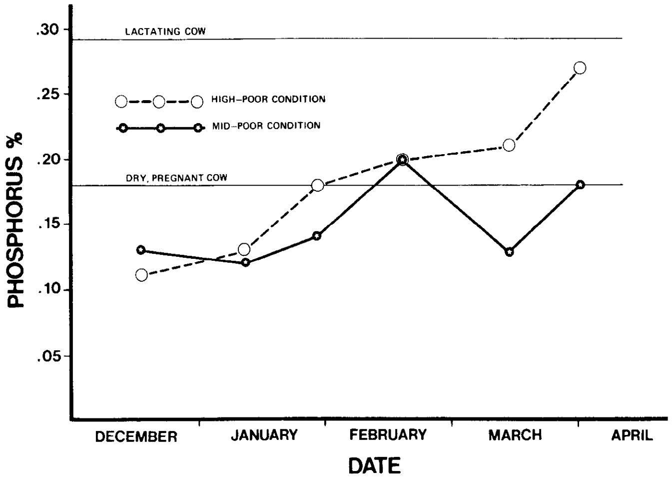


Fig. 2. *Phosphorus (%) in diets of cows on mid-poor and high-poor condition pastures of a Blackland range site grazed during the winter of 1976-77. Dietary phosphorus requirement for lactating and dry, pregnant cows is provided.*

Digestible Organic Matter

Percent DOM was generally higher in the high-poor condition pasture during mid-winter (Table 3). DOM levels were lowest in diets for both pastures in February, a period with low standing crop and little growth of cool-season plants. The greatest differences in DOM between pastures were in March and April, a period when the spring "flush" of cool-season grasses, primarily Japanese brome (*Bromus japonicus*), little barley (*Hordeum jubatum*), rescuegrass (*Bromus unioloides*) and Texas wintergrass, occurred. Average DOM was 10% higher in the high-poor condition pasture than in the mid-poor condition pasture ($P<0.05$). All DOM values were significantly different between pastures for each sampling date ($P<0.05$).

Phosphorus

Phosphorus levels were similar between pastures until mid-January (Fig. 2). After February, phosphorus content of the diets was higher in the high-poor condition pasture. Dietary phosphorus levels declined during March on the mid-poor condition pastures. It appeared that utilization of cool-season species exceeded growth, thereby, reducing their contribution to the cows' diets. Differences in dietary phosphorus were most evident in March and April.

Table 3. Percent dietary crude protein (CP) and percent digestible organic matter (DOM) of mid-poor and high-poor condition pastures on a Blackland range site grazed during the winter.

	CP				DOM			
Date	High-poor	C.I.	Mid-poor	C.I.	High-poor	C.I.	Mid-poor	C.I.
December 17, 1976	6.07	±0.11[1,2]	4.67	±0.06	58.4cd	±0.3[1,3]	51.9f	±0.5
January 11, 1977	5.65	±0.03	6.42	±0.04	60.0c	±0.4	55.3e	±0.9
January 28, 1977	9.29	±0.06	5.28	±0.08	55.7e	±0.5	57.8d	±0.6
February 18, 1977	8.37	±0.05	8.50	±0.05	45.9g	±1.4	42.7h	±3.8
March 14, 1977	15.24	±0.04	8.77	±0.04	71.2b	±5.3	45.4g	±1.3
April 1, 1977	16.04	±0.33	11.81	±0.07	76.3a	±2.4	55.2e	±0.6
Mean	10.11		7.58		61.3		51.4	

[1] All values are significantly different between pastures ($P<0.05$).
[2] All values are significantly different among dates × pastures ($P<0.05$).
[3] DOM values followed by a common letter are not significantly different (<0.05).

Fig. 1. *Esophageally cannulated cows grazing the mid-poor condition pasture with the high-poor condition pasture in background.*

Forage samples were oven-dried at 60°C for 48 hours and ground in a Wiley mill to pass a 1-mm screen. Crude protein (CP) was determined using micro-Kjeldahl procedures as outlined by the Association of Official Agricultural Chemists (1960). Digestible organic matter (DOM) was determined using in vitro digestion followed by Neutral Detergent Fiber digestion as outlined by Ellis (1970). Phosphorus (P) content of the diet samples was determined in duplicate by the forage testing division of the Texas Agricultural Analytical Services using atomic emissions spectrophotometry (AOAC 1975). An attempt to reduce salivary P contamination of the diet samples was made by hand squeezing to remove saliva. Hoehne et al. (1967) reported P contamination nearly eliminated in squeezed samples. Phosphorus values represent averages of composited samples by date over animals analyzed in duplicate.

Chi-square analysis was used to determine significant difference in species composition between pastures. The Student's *t*-test was used to evaluate differences in available biomass between pastures. A two-way analysis of variance was used to test differences in CP and DOM ($O<0.05$). Means were compared using Duncan's multiple range test (Bruning and Kintz 1968).

Results and Discussion

Species Composition

Compositional analysis of the vegetation indicated significant species differences occurred between pastures (Table 1). However, when range condition was determined from Soil Conservation Service guides, the pastures were found to have identical scores. The determination of mid- or high-poor condition was based upon presence and amounts of dominant and subdominant species in relation to known successional stages as previously described. The high-poor condition pasture was dominated by meadow dropseed with Texas wintergrass forming a strong subdominant. Both species were significantly higher in amounts present than on the mid-poor condition pasture. Other subordinate species in the high-poor condition pasture included buffalograss, common Bermudagrass (*Cynodon dactylon*), purple threeawn, and cool-season annual grasses. Only the annual cool-season grasses had a greater abundance in the high-poor condition pasture than in the mid-poor condition pasture.

Buffalograss was the dominant species in the mid-poor community, with common Bermudagrass, Texas wintergrass, Halls panicum, meadow dropseed, and purple threeawn being important subordinants. Only purple threeawn did not differ significantly between pastures. Twenty-five percent of the composition in the high-poor condition pasture consisted of cool-season species which provided green forage during the winter while cool-season species constituted only 17% composition in the mid-poor condition pasture.

Table 1. Species composition (%) of mid-poor and high-poor condition summer deferred pastures on a Blackland range site grazed during the winter (December 17, 1976).

Species		Condition Class	
Common name	Scientific name	Mid-poor	High-poor
Buffalograss	*Buchloe dactyloides*	31	7**
Common Bermudagrass	*Cynodon dactylon*	14	4**
Texas wintergrass	*Stipa leucotricha*	13	18*
Halls panicum	*Panicum hallii*	11	1**
Meadow dropseed	*Sporobolus asper var. drummondii*	11	51**
Purple threeawn	*Aristida purpurea*	10	8ns
Silver bluestem	*Bothriochloa saccharoides*	2	1†
White tridens	*Tridens albescens*	2	4†
Windmillgrass	*Chloris verticillata*	1	3†
Texas grama	*Bouteloua rigideseta*	<1	–†
K.R. bluestem	*Bothriochloa ischaemum* var. *songaricus*	2	–†
Annual cool-season grasses		3	6*
Annual cool-season forbs		<1	1†
Total cool-season species		17	25
SCS Range Condition Score		15	15

*–P<0.05 ns–not significant
**–P<0.01 †–not analyzed (<5% composition)

Phosphorus levels were deficient for a non-lactating, pregnant cow (NRC 1976) in both pastures until late January. However, neither pasture would have met the phosphorus needs of lactating cows (0.28%) throughout the study period. By early April both pastures were providing adequate phosphorus levels for dry, pregnant cows (0.18%).

Conclusions

CP, DOM and P in diets of fistulated cows were influenced by differences in species composition on two ranges differing in condition, even though standing crop of forage was approximately the same. The plant community in a higher successional stage provided diets higher in quality throughout the winter months and furnished critical nutrients earlier in late winter and spring. The important role of cool-season species was evident in these findings. A small increase (8%) in contribution of cool-season species to a plant community could mean a 3 to 4 week shorter supplementation period for protein, energy, and phosphorus. The findings would be applicable to a poor condition Blackland range site.

Literature Cited

Association of Official Agricultural Chemists. 1960. Official Methods of Analysis (9th ed.) Ass. Off. Agr. Chem., Washington, D.C.

Association of Official Analytical Chemists. 1975. Spectroscopic methods. J. Ass. Off. Anal. Chem. 58:421-422.

Bruning, J.L., and B.L. Kintz. 1968. Computational Handbook of Statistics. Scott, Foresman and Co., Glenview, Ill. 269 p.

Cook, C.W. 1964. Symposium on nutrition of forages and pastures: Collecting forage samples representative of ingested material of grazing animals for nutritional studies. J. Animal Sci. 23:265-270.

Cook, C.W., M.M. Kothmann, and L.E. Harris. 1965. Effect of range condition and utilization on nutritive intake of sheep on summer ranges. J. Range Manage. 18:69-73.

Demarchi, D.A. 1973. Relationship of range quality to range condition in the Chilcotin Region, British Columbia. J. Range Manage. 26: 345-348.

Ellis, W.C. 1970. The in vitro determination of true and apparent digestibility of forages. Dep. Animal Science, Texas A&M University, College Station. Mimeo. 4p.

Gates, D.H. 1972. The use of range condition in rangeland ecosystem evaluation and management planning. U.S.-Australia Range Workshop. Adelaide, Australia. 33 p.

Goebel, C.J., and C.W. Cook. 1960. Effect of range condition on plant vigor, production and nutritive value of forage. J. Range Manage. 13:307-313.

Hoehne, O.E., D.C. Clanton, and C.L. Streeter. 1967. Chemical changes in esophageal fistula samples caused by salivary contamination and sample preparation. J. Anim. Sci. 26:628-631.

Kothmann, M.M. 1968. The botanical and nutrient content of the diet of sheep grazing on poor condition pasture as compared to good condition pasture. Ph.D. Diss. Texas A&M Univ., College Station. 60 p.

Kothmann, M.M. (ed.). 1974. A glossary of terms used in range management. Soc. Range Manage. Denver, Colo. 36 p.

National Oceanic Atmospheric Administration. 1976. Climatological data for Texas—Vol. 81. U.S. Dept. Commerce. Washington, D.C.

National Research Council. 1976. Nutrient requirements of domestic animals; No. 4. Nutrient requirements of beef cattle. National Academy of Science. Washington, D.C. 55 p.

Stuth, J.W., and B.E. Dahl, 1974. Evaluation of rangeland seedings following mechanical brush control in Texas. J. Range Manage. 27:146-149.

U.S. Dep. Agriculture. 1976. Range site descriptions for Texas-Blackland Site-Area 16. Soil Conservation Service. Temple, Texas. 4 p.

Van Dyne, G.M., and D.T. Torell. 1964. Development and use of the esophageal fistula: A review. J. Range Manage. 17:7-19.

Aerial Census of Wild Horses in Western Utah

MILTON N. FREI, J. SCOTT PETERSON, AND J. RON HALL

Abstract

The accuracy of aerial censuses in estimating absolute density of wildlife populations varies widely. Aerial censusing of wild horses was done to compare the effects of experience and aircraft type. The difference between aircraft types was not found to be statistically significant, while observer experience was significant at the 5% level. The variability caused by these factors places considerable uncertainty on projections of rate of increase based upon a comparison of two or more aerial censuses.

Aerial survey is the only practical means of counting larger animals in wilderness terrain (Fuller 1950), but is, at best, a rough method of estimating the size of a population (Caughley 1974). The literature contains no information on aerially censusing wild horses, but there is a wealth of data concerning large mammals. The various factors which affect the accuracy of aerial counts include variables related to observer (experience, fatigue, individual variation), animal (density, color, size, diurnal behavior pattern), technique (transect width, speed, height), physiography (terrain, vegetation), weather (clouds, turbulence, snow cover, light conditions), and equipment (aircraft type, pilot). In an aerial census of moose in 1-square mile enclosures, LeResche and Rausch (1974) found that seasoned observers without recent counting experience are as inaccurate as unseasoned observers. The accuracy of aerial censuses in estimating absolute density of wildlife populations varies from 29 to 88% (Caughley 1977).

In recent years, aerial censusing of wild horse populations has indicated that populations are experiencing phenomenal growth. Heady and Bartolome (1977) indicate an increase in numbers from 66 to 120 and 225 on the Three Fingers and from 94 to 113 and 150 on the Jackies Butte horse management areas in Oregon for the consecutive years of 1972, 1973 and 1974, respectively. The above authors state that "although inaccurate counting and addition of adults to the herds cannot be ruled out in either area, the major increase reflects natural reproduction. The data for Jackies Butte are believed accurate and they suggest a reproductive rate of 60% in 3 years or 20% per year." Two other examples of published data on rate of increase include an increase of 28%, 29%, and 18% for 1973, 1974, and 1975 respectively, in Idaho's Challis Planning Unit (U.S. Dep. Interior 1975) and 30% and 22% for 1974 and 1975, respectively, in California's Susanville District (U.S. Dep. Interior 1976).

Authors are range conservationist, Bureau of Land Management, Denver Federal Center Denver, Colorado 80225; range conservationist, Botany and Plant Pathology, Colorado State University, Fort Collins, Colorado 80523; and wild horse specialist Bureau of Land Management, Winnemucca, Nevada 89445.

The authors would like to thank Dr. Frederick K. Martinson, who provided technical assistance in statistical analysis of the data.

Manuscript received January 16, 1978.

The aerial surveys in the Challis Planning Unit were made by fixed-wing aircraft in 1973-74 and by helicopter in 1975. The type of aircraft used in the Susanville District was not identified.

It is our contention that a large portion of the above increases can be attributed to the noncompensating errors naturally inherent in aerial surveys. The present study is not intended to give an absolute count of a population, since aerial surveys of large mammals consistently underestimate densities (Golley and Buechner 1968; Bergerud 1963; LeResch and Rausch 1974; Gilbert and Grieb 1957). The purpose was to evaluate differences in the results of wild horse aerial censusing with regard to (1) the experience of personnel and (2) the type of aircraft used, particularly as related to projections of wild horse population increase.

Study Area

The study area is situated on the Dugway Proving Grounds in west-central Utah (Fig. 1). The specific study sites within this area were the Granite Mountain and a portion of the Cedar Mountains with elevations ranging from 1,342 to 2,140 meters. These two areas were selected because the wild horse populations were isolated due to topography. The areas were geographically dissimilar, particularly in size and terrain. Granite Mountain occupies approximately 110 km² and resembles a butte. The slopes are rocky and very steep, with most horse activity on the adjacent flats. The Cedar Mountains, in comparison, have relatively accessible slopes, with many canyons along the range. This site comprises approximately 330 km² with horse activity observed throughout.

Vegetation on Granite Mountain consisted of plant species common to the northern desert shrub community. Big sagebrush (*Artemisia tridentata*), black sagebrush (*Artemisia nova*), shadscale (*Atriplex confertifolia*) and winterfat (*Ceratoides lanata*) were the common shrubs in the area. Grasses and forbs included wheatgrass (*Agropyron* spp.), galleta (*Hilaria jamesii*), cheatgrass (*Bromus tectorum*), scarlet globemallow (*Sphaeralcea coccinia*), and lupine (*Lupinus* spp.). Visibility of horses not limited due to the open terrain and lack of trees.

Cedar Mountain was dominated by a juniper woodland, which was interspersed with open sagebrush parks along the ridges and canyon bottoms. Open flats bordered both sides of the mountain and contained vegetation common to the northern desert shrub community. Trees and shrubs included utah juniper (*Juniperus osteosperma*), big sagebrush, rubber rabbitbrush (*Chrysothamnus nauseosus*), shadscale, and black sagebrush. Wheatgrass, cheatgrass, galleta, Indian ricegrass (*Oryzopsis hymenoides*), scarlet globemallow, bladderpod (*Lesquerella* spp.) and tansymustard (*Descurainia* spp.) were common grasses and forbs. Visibility of horses was limited due to density of vegetation and complexity of topography.

All flights over the study area were conducted during the period February 28 through March 7, 1977. The Cedar Mountains were covered with a light blanket of snow during all flights conducted with the Jet-Ranger helicopter. Patchy snow conditions were encountered during all other flights. Light conditions were excellent to good for 16

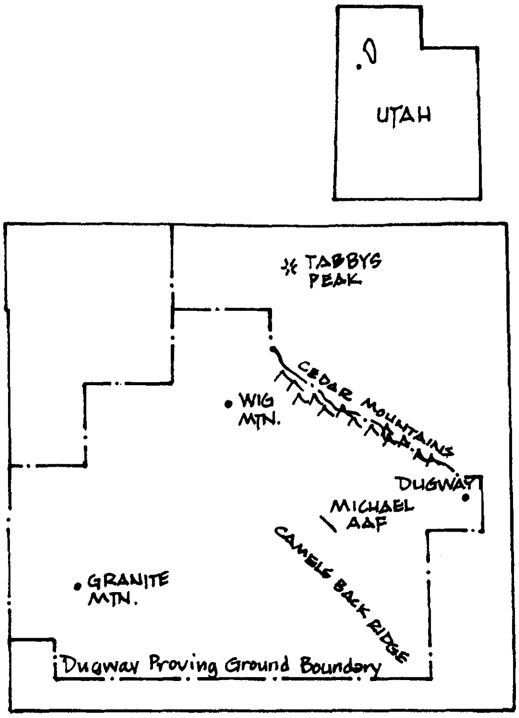


Fig. 1. *Location map of study area.*

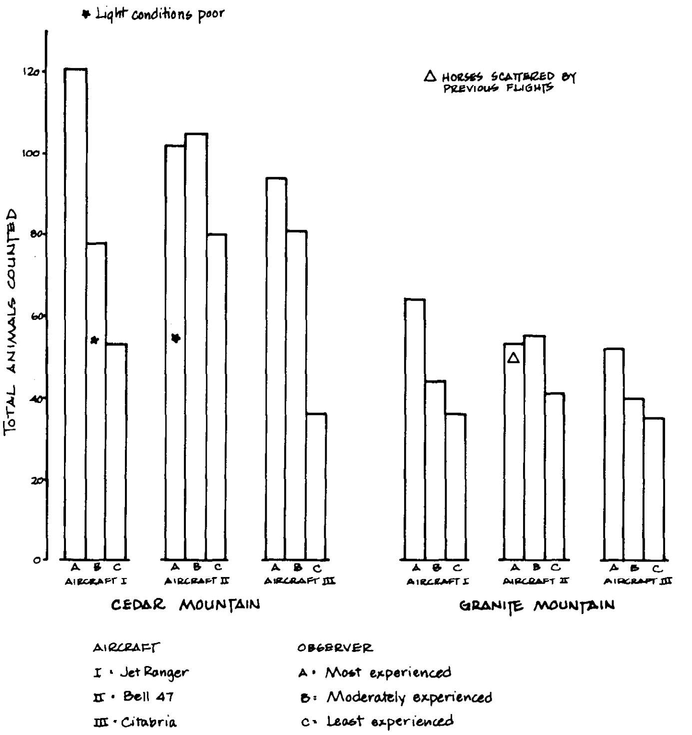


Fig. 2. *Total animals counted by experience of observer, aircraft type, and mountain range.*

of the 18 census flights. These factors represent realistic conditions frequently encountered in aerial surveys.

Methods

The censusing was done with three different aircraft and three observers with a variety of experience. The aircraft consisted of two helicopters: (1) a Bell Jet-Ranger, and (2) a Bell 47 utilizing the same pilot, and (3) a fixed-wing, aerobatic Citabria with a different pilot. The Jet-Ranger is a high powered turbine craft, as compared with the low-powered reciprocal engine in the Bell-47. The Bell-47's most favorable features are its lower hourly cost and the excellent visibility. The fixed-wing Citabria has the lowest hourly cost, but lacks the maneuverability and visibility offered by rotary-wing craft. The three observers were classified according to their prior experience in aerial censusing of wild horses. Observer A had 900 hours of census experience; B, 150 hours of census experience; and C, no census experience. Also, observer A had extensive recent ground and air experience in the survey area; B had a few hours past ground and aerial census experience in these areas; and C had no experience in the areas.

Each observer separately censused the two mountains in each of the aircraft. The pilots were instructed to maneuver the aircraft only when directed by the observer and to make no indication of horse sightings. Airspeed and altitude were left to the discretion of each observer as a function of experience; however, they generally remained similar for all observers. The number of animals was written down following each pass over a group or band. To compare counts between differing levels of experience, no specific surveying techniques or results were discussed prior to or during the censusing period. This was an attempt to keep each observer's findings from biasing another. Due to various constraints, the time of day of comparable flights was not made uniform, though a maximum time limitation was placed on the observer for any specific count. Each observer felt that the allotted time was more than sufficient to census the areas adequately and usually utilized less than the maximum time allowed. Each observer concluded each flight with the feeling that he had counted most of the animals within the area.

Results

The combined total horse count for both mountains ranged from a minimum of 71 by the least experienced observer (C) in the fixed wing aircraft (3) to a maximum of 185 by the most experienced (A) in the Jet Ranger (1). This amounts to a 160% discrepancy between the minimum and maximum number of animals counted.

The histograms (Fig. 2 & 3) illustrate the marked differences between observers (experience) and aircraft. The average band size viewed by observers A and B was 5.2 animals, while the average size for observer C was 6.3. This may indicate that observer C viewed the larger bands, but missed small bands, or that he was unable to discern individual bands. The virtual inability of observer C to distinguish age classes using aircraft 1 is thought to be due to the fact that this was his first aerial census (Fig. 3).

Gilbert and Grieb (1957) state that the study area for deer populations should support at least 100 animals, or aerial census results will be obtained that will be unsatisfactory for statistical analysis. The counts on Granite Mountain involved considerably less than 100 animals. Because of this factor, differences between observers and aircraft on Granite Mountain did not lend themselves to statistical analysis.

A comparison of the total counts (Fig. 2) on both Cedar and Granite Mountains among observers, by aircraft, showed increasing numbers with more experience, except for aircraft 2. On these mountain ranges, the differences between observers A and B did not follow the pattern of the other flights. In the Cedar Mountains, the observers felt that the differences in results when utilizing aircraft 2 were due to excellent light conditions on the day that observer B flew, and overcast poor light conditions during the flight of observer A. On Granite Mountain, observer A felt that the animals were scattered into the adjacent flats by previous helicopter and fixed-wing flights, whereas observer B had the first flight of the day when the animals were relatively grouped.

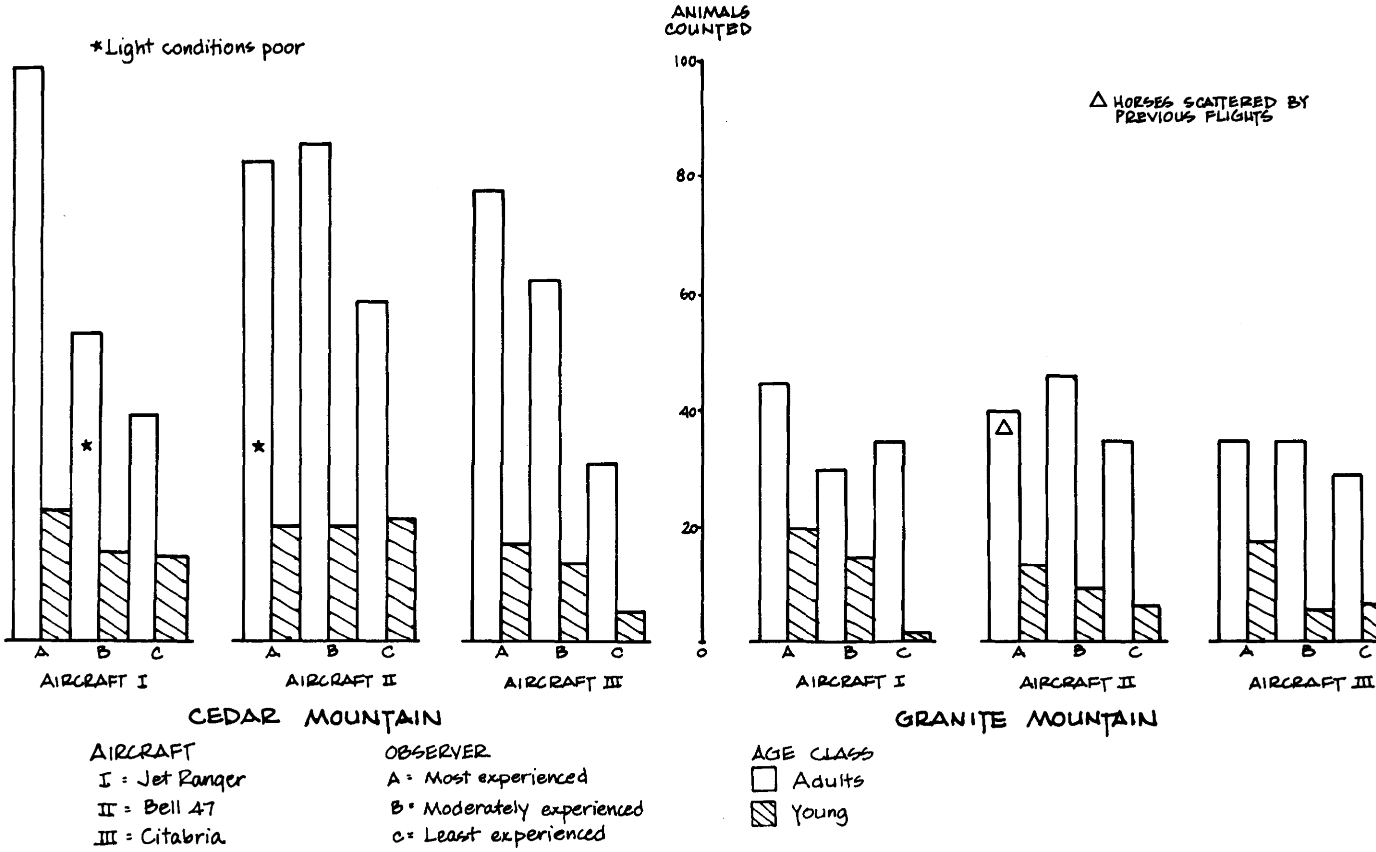


Fig. 3. *Age class distribution of horse populations by experience of observer, aircraft type, and mountain range.*

An analysis of variance was initially performed on the total animals derived from both mountains. The considered factors were (a) experience, (b) aircraft type, and (c) mountain. When analyzing the counts by analysis of variance, a lack of replication severely limited the degrees of freedom that could be used. Several sources of variation (aircraft, aircraft × experience, mountain × aircraft × experience) were pooled to produce an estimate of the error term. Visually (Figs. 2 and 3), the difference among factors looks significant, and statistically the comparison between mountains was significant at the 1% level, with experience being significant at the 5% level. The large significance of the mountain factor and the lack of replications appeared to be masking the difference between aircraft. Because of this, and the larger population of Cedar Mountain, it was determined that statistical analysis be limited to the Cedar Mountain only.

An analysis of variance was next performed on the total animals counted on the Cedar Mountain. From these data, a comparison of computed versus table F values (Table 1) demonstrated that the differences among aircraft were not significant at the 5% level while the differences among observer experience were significant at the 5% level.

Table 1. Analysis of variance for total wild horses counted on the Cedar Mountain.

Source of variation	Sum of squares	Degree of freedom	Mean square	Computed F values	Table F values 0.05	Table F values 0.01
Aircraft type	522.9	2	261.4	2.15	6.94	18.00
Observer experience	2928.2	2	1464.1	12.04	6.94	18.00
Error	486.4	4	121.6	–	–	–
Total	3937.6	8	–	–	–	–

To obtain a pictorial representation of the differences among observer experience and aircraft type, an analysis of means following Ott (1975) was performed on the data. As shown in Figure 4, the points representing the means of the counts obtained from each type of aircraft are contained within the .05 limits, thereby indicating their lack of significance at the 5% level. However, the spread of the means of the aircraft counts points towards a very positive difference between types of

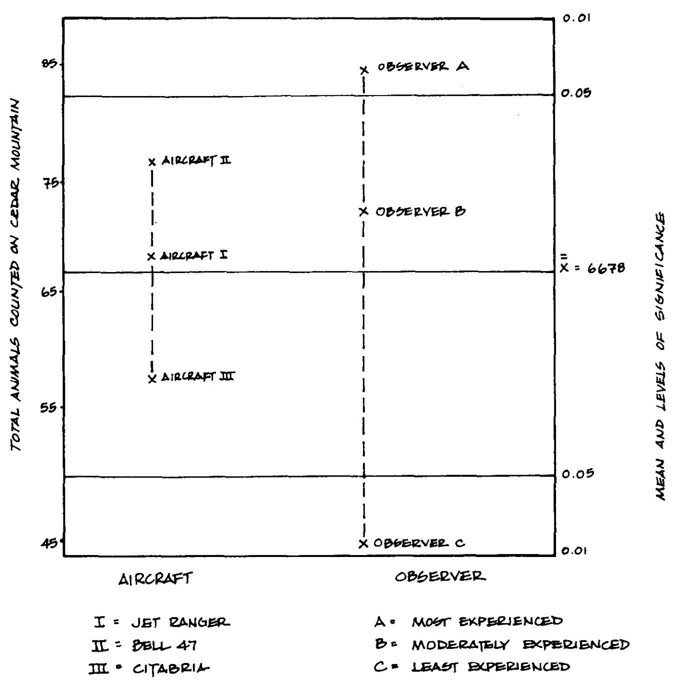


Fig. 4. *Analysis of means.*

aircraft used. This can logically be attributed to the physical characteristics of each aircraft. Although not demonstrated statistically, it is felt that the analysis of means (Fig. 4) indicates the selection of aircraft will have a considerable affect on relative population counts.

The histograms (Figs. 2 & 3) illustrate the fact that the differences between experience were least when utilizing aircraft 2. This is thought to be a function of the slower speed and greater visibility of this aircraft. For these reasons the Bell 47 helicopter is considered to be the aircraft of choice, among those considered, in the aerial census of wild horses. Cost and horsepower limitations will be important considerations in selecting one of the types of aircraft.

Conclusions

Statistically, experience was the most significant factor analyzed in this study. The study illustrates that under similar conditions aerial counts on a wild horse population could increase significantly if successive counts are performed by more experienced personnel. To a degree this is an unavoidable variable, since experience will increase every time an aerial census is conducted. Therefore, the factor of experience alone could easily account for a significant portion of the large increases in numbers of wild horses that have been noted by aerial census. The results indicate that for the most accurate counts of relative wild horse numbers, only personnel with census experience should be used. Also, better counts will be obtained from those familiar with the area on the ground and from the air.

As a general conclusion, the authors believe the wide variability in animals counted, demonstrated by this study, places considerable uncertainty on rate of increase projections which are based upon a comparison of two or more aerial censuses. At best, aerial census will provide minimally acceptable estimates of wild horse population densities and broad overviews of population trend. Since population increase is a function of fecundity and survival, these factors should be important considerations in rate of increase projections.

Literature Cited

Bergerud, A.T. 1963. Aerial winter census of caribou, J. Wildl. Manage. 27:438-449.

Caughley, G. 1974. Bias in aerial survey. J. Wildl. Manage. 38:921-933.

Caughley, G. 1977. Analysis of Vertebrate Populations. John Wiley & Sons, N.Y.

Fuller, W.A. 1950. Aerial census of bison in Wood Buffalo Park. J. Wildl. Manage. 14:445-451.

Gilbert, P.F., and J.R. Grieb. 1957. Comparison of air and ground deer counts in Colorado. J. Wildl. Manage. 21:33-37.

Golley, F.B., and H. Buechner. 1968. A practical guide to the study of the productivity of large herbivores. IBP Handbook No. 7 Blackwell Scientific Publications. Oxford and Edinburgh.

Heady, H.F., and J. Bartolome. 1977. The Vale rangeland rehabilitation program: The desert repaired in southeastern Oregon. U.S.D.A., PNWF&-RES, Forest Serv. Res. Bull. PNW-70.

LeResche, R.E., and R.A. Rausch. 1974. Accuracy and precision of aerial moose counting. J. Wildl. Manage. 38:175-182.

Ott, E.R. 1975. Process Quality Control. McGraw-Hill. N.Y.

U.S. Department of Interior. Draft Challis environmental impact statement. Bureau of Land Management.

U.S. Department of Interior. Susanville District wild horse and burro statistics. Bureau of Land Management (Unpublished).

Election Results

The 2,007 ballots cast in the 1978 election were counted on December 8. Selected by the membership to serve the Society during the next 3 years were:

President Elect ...... **Harold F. Heady**
Directors .... **S. Clark Martin**
Jack R. Miller

The new officers will be installed at the forthcoming Annual Meeting in Casper, at which time Daniel Merkel, the current president elect, will succeed to the presidency. Harold Heady will serve as president in 1980, and the two newly elected directors will serve for the 3-year term 1979-1981.

Retiring next month from the Board of Directors are Past President Thadis W. Box and Directors Edward A. McKinnon and Jeff Powell. The very significant service rendered to the Society by these men is greatly appreciated.

Dr. Harold F. Heady is at present assistant vice president for Agriculture and University Services and associate director of the Agricultural Experiment Station, University of California.

Dr. S. Clark Martin is principal range scientist with the Rocky Mountain Forest and Range Experiment Station, U.S. Forest Service, Tempe, Arizona. Jack R. Miller, is a range and wildlife specialist for the U.S. Forest Service, Missoula, Montana.

Members voted to amend Article 1, Section 6 of the Bylaws to read: Family (membership dues)—As shall be established from time to time by the Board of Directors.

Office staff at the SRM headquarters in Denver counted the ballots. Ballots and tally sheets are kept on file in the Society office for 1 year.

Occurrence of C_3 and C_4 Photosynthetic Pathways in North American Grasses

S.S. WALLER AND J.K. LEWIS

Abstract

A literature survey was made for the occurrence of C_3 and C_4 photosynthetic pathways in the United States Gramineae. Distinctive characteristics of the two photosynthetic pathways are discussed. Leaf anatomy, CO_2 compensation point, net enhancement of photosynthesis in oxygen-deficient atmosphere, ^{13}C discrimination, and initial product labeling were criteria selected to evaluate data for 6 subfamilies including 25 tribes, 138 genera, and 632 species. The Arundinoideae, Bambusoideae, Oryzoideae, and Pooideae (Festucoideae) are composed of species with C_3 pathways. All tribes within the Eragrostoideae have C_4 pathways with the exception of Unioleae. Within the Panicoideae, the Andropogoneae and all of the Paniceae, excepting the genera *Sacciolepus, Isachne, Oplismenus, Amphicarpum,* and *Panicum,* have C_4 pathways. The subgenus *Dichanthelium* within *Panicum* is C_3 while the *Eupanicum* subgenus contains plants with both C_3 and C_4 photosynthetic pathways.

Plant productivity is dependent on several environmental and biological factors. The most important single factor is photosynthesis. A pathway for carbon dioxide (CO_2) fixation was described by Calvin and Bassham (1962) in which CO_2 was incorporated into a 6-carbon compound and rapidly converted to a 3-carbon compound, 3-phosphoglyceric acid (3PGA). Previous to discoveries of Kortschalk et al. (1965) and Hatch and Slack (1966), the Calvin cycle (C_3, reductive pentose pathway) was considered the major photosynthetic mechanism for carbon (C) fixation. However, Hatch and Slack (1966) described CO_2 fixation in which labeled CO_2 was first incorporated in 4-carbon compounds (malic, aspartic, or oxaloacetic acid) prior to transfer to sugars by way of 3-phosphoglycerate. The proposed mechanism involved the operation of two interconnected metabolic cycles. Downton (1970) described carbon fixation into C_4-dicarboxylic acids in mesophyll cells and subsequent incorporation into the Calvin cycle located in the bundle sheath cells. Plants (C_4 plants) possessing the 4-carbon pathway (also called C_4, dicarboxylic acid, Kranz type, low CO_2 compensation, tropical, Hatch and Slack, or β carboxylation pathway) were of tropical origin and more efficient. They produced two- to threefold more dry matter than plants possessing the 3-carbon pathway (C_3 plants), especially in relatively sunny, warm, dry climates (Black 1971).

Distinctive characteristics associated with the C_4 pathway prompted intensive research in photosynthetic processes of flowering plants. The most important photosynthetic pathways are the C_3 and C_4; however, a crassulacean acid pathway (CAM) has been reported in some succulents (Ranson and Thomas 1961; Ting 1971).

The first listing of C_4 plants was prepared in 1970 (Downton 1971). By 1974, the C_4 photosynthetic pathway had been identified in 13 families (Aizoaceae, Amaranthaceae, Boraginaceae, Caryophyllaceae, Chenopodiaceae, Compositae, Convolvulaceae, Cyperaceae, Euphorbiaceae, Gramineae, Nyctaginaceae, Portulacaceae and Zygophyllaceae) and 117 genera of the Angiospermae (Downton 1975). Bjorkman (1976) identified three additional families: Acanthaceae, Capparidaceae, and Scrophulariaceae. Many publications have been concerned with identification of the C_4 pathway in individual species.

Knowledge about the photosynthetic pathway allows interpretation of several important ecological characteristics. Black et al. (1969) proposed that competitive ability of plants primarily depended on net capacity of CO_2 assimilation, resulting in increased foliage extension and size. Other factors being equal, plants with higher apparent photosynthetic rates (C_4 plants: species having the C_4 pathway, Calvin pathway and Kranz anatomy) have a competitive advantage over those with lower rates (C_3 plants: species having only the Calvin pathway). Such advantage can help explain aspects of structure and function in terrestrial ecosystems and the importance of warm-season and cool-season plant classification in range management.

The present literature review was undertaken to compile a listing of photosynthetic pathways and related attributes of United States grasses to serve as a reference for range scientists.

Methods of Determining the Photosynthetic Pathway

Plants possessing the C_4 photosynthetic pathway are very different from C_3 plants in a variety of characteristics (Black 1971). The net photosynthetic rate is two- to threefold greater; CO_2 compensation points are lower; photosynthesis is not suppressed by oxygen concentration between 1 and 100%; CO_2 is not evolved during illumination; bundle sheath cells contain chloroplasts and starch; discrimination against ^{13}C compounds is lower; and CO_2 fixation initially yields 4-C acids as opposed to 3-C acids found in the C_3 photosynthetic pathway. Since these distinguishing characteristics are coexistent, various characters have been used as criteria for determining the photosynthetic process. Five characteristics have been widely used to classify the photosynthetic pathway and are discussed below.

Photosynthetic Products

Initial product labeling with ^{14}C is the only direct method for photosynthetic pathway determination. Hatch et al. (1967) reported that in C_4 plants as much as 93% of fixed radioactivity appeared in oxaloacetic, malic, and aspartic acids following

Authors were assistant and associate professor, Animal Science Department, South Dakota State University, Brookings 57007. Senior author is presently Associate Professor, Department of Agronomy, University of Nebraska, Lincoln, Nebr. 68583.

This report was approved for publication by the Director, Agricultural Experiment Station, South Dakota State University, Brookings, as Journal series No. 1533.

The authors extend appreciation to Dr. D. Kenefick and Dr. C. Chen, South Dakota State University, for their helpful suggestions in manuscript preparation. We also appreciated the aid of Dr. S. Hatch, New Mexico State University, in reviewing the taxonomic classification. We would also like to thank Mrs. Susanne Gardner for typing the manuscript.

Manuscript received January 10, 1978.

exposure to $^{14}CO_2$ for approximately 1 second. In contrast, early products of the C_3 process were 3-PGA and hexose phosphates.

CO_2 Compensation and Photorespiration

Carbon dioxide compensation point (the point at which photosynthetic CO_2 uptake equals respiratory CO_2 evolution when measured in a closed chamber) is an easily obtainable characteristic. During photosynthesis a light-induced release of CO_2 can occur and is referred to as photorespiration as contrasted to CO_2 released by mitochondria or dark respiration. Plants with the C_4 pathway have a photosynthetic CO_2 compensation in the range of 0-10 ppm, indicating a lack of significant net photorespiration (Downton and Tregunna 1968). Photorespiration does occur as a normal product of the Calvin cycle within the bundle sheath cells of C_4 plants. However, since the mesophyll layer surrounds the bundle sheath, the C_4 pathway would rapidly refix any photorespiratory CO_2 and prevent leakage to the atmosphere (Bowes and Ogren 1972). A much higher CO_2 compensation point (37-70 ppm) is characteristic of C_3 plants (Black 1971). Carbon dioxide compensation points provide a convenient means of identifying the type of photosynthetic pathway. The low CO_2 compensation point of C_4 plants indicates an ability to utilize more external CO_2 as compared to C_3 plants.

Oxygen Suppression

Oxygen differentially affects CO_2 exchange in C_3 and C_4 plant species, primarily because of differences in photorespiration. In soybean (*Glycine max*), and probably other C_3 species as well, the total O_2 inhibition consists of two discernible effects. Oxygen substitutes for CO_2 in the carboxylase reaction to yield P-glycolate, a C_3 photorespiratory intermediate. As a result of this subsitution, O_2 competitively inhibits the carboxylase with respect to CO_2 (Ogren 1976). During photorespiration glycolate is oxidized, releasing CO_2. Consequently, oxygen depletion will reduce glycolate oxidation thereby increasing photosynthetic CO_2 assimilation by 40 to 50% in species possessing the C_3 pathway, while having no effect on C_4 plants (Downes and Hesketh 1968). The refixation of photorespiratory CO_2 allows C_4 plants to utilize all of the fixed CO_2, thus increasing photosynthetic efficiency.

Chollet (1976) postulated that the enzyme complement of the C_4 pathway increased CO_2 concentration at the site of the C_3 carboxylase, reducing the competitive inhibition of O_2 and minimizing photorespiration. The CO_2 concentration at the site of the C_3 carboxylase coupled with a specialized leaf anatomy, allowing recapture of photorespiratory CO_2, was apparently responsible for the lack of photorespiration and absence of the inhibitory effect of 21% O_2 on net photosynthesis in C_4 plants.

Leaf Anatomy

Leaf anatomy provides an easily distinguished difference between C_3 and C_4 plants. Plants with the C_3 photosynthetic capabilities lack well-defined parenchymatic bundle sheaths and starch grains are found mainly within the mesophyll (Bisalputra et al. 1969) (Fig. 1). Plants with the C_4 photosynthetic pathway generally have well-developed parenchymatic bundle sheaths containing high concentrations of chloroplasts and starch. Bundle sheath cells utilize the C_3 photosynthetic process; however, they are surrounded by mesophyll cells containing chloroplasts utilizing the C_4 photosynthetic process which

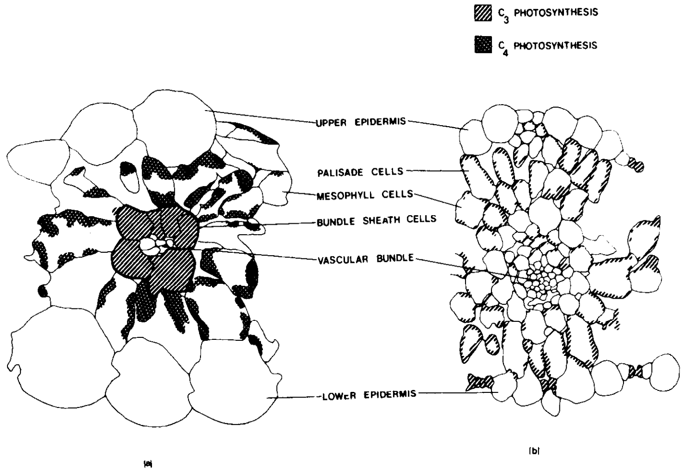


Fig. 1. *Comparison of leaf anatomy between plants having C_4 photosynthesis (a) and C_3 photosynthesis (b). The C_4 plant exhibits prominent bundle sheath cells and concentrated photosynthetic activity near the vascular bundles (Adopted from Black 1971).*

fix and then supply CO_2 for the C_3 pathway.

The unique leaf anatomy (Kranz type) of C_4 plants provides several advantages for efficient CO_2 fixation. Surrounding the C_3 bundle sheath cells with C_4 mesophyll cells minimizes the loss of CO_2 from C_3 photorespiration. The presence of two active photosynthetic carboxylases and their associated enzymes in the same leaf of a C_4 plant appears to result in a higher affinity for and more rapid uptake of CO_2. The close proximity of starch formation to the vascular bundles should make photosynthate translocation more efficient.

Carbon Isotope Discrimination

Carbon isotope ratio ($^{13}C/^{12}C$) determination in plant tissue is characteristically less than the carbon isotope ratio of atmospheric CO_2, indicating that plants preferentially assimilate the lighter of the two isotopes (Troughton et al. 1974). Carbon isotope values are defined as the difference in per mil of the $^{13}C/^{12}C$ ratio of the sample relative to a standard and reported as $^{13}C°/oo$ (Smith and Epstein 1971). Details of the procedure are described elsewhere (Park and Epstein 1960). Higher plants are placed into two categories, those with low $^{13}C°/oo$ values (-24 to $-34°/oo$) and those with high values(-6 to $-19°/oo$ (Smith and Epstein 1971). Grasses relatively enriched in ^{13}C have $^{13}C°/oo$ values in the -6 to $-19°/oo$ range and are reported to be C_4 while those with relatively low $^{13}C°/oo$ values are C_3 species (Bender 1971). Troughton et al. (1974) reported a mean $^{13}C°/oo$ value of -28.11 ± 2.55 for C_3 and -13.46 ± 1.55 for C_4 grasses. The distinctive difference apparently results from differences in affinity of the enzyme systems of the two pathways for the two isotopes of carbon (Whelan et al. 1973). Thus, the carbon isotope technique was cited as a reliable method of distinguishing between C_3 and C_4 plants (Bender 1971).

Other Characteristics Related to Photosynthetic Pathway

Several other physiological characteristics are closely related to photosynthetic pathway, but have not been widely used in plant classification. Light saturation differs in the two pathways. C_4 plants exhibit continued increase in CO_2 uptake as light intensity increases to nearly full sunlight (approximately 1.5 to 1.8 langleys), while C_3 plants are saturated at 0.2 to 0.4 langleys. Maximum CO_2 assimilation on a leaf area basis at normal atmospheric concentration of CO_2 ranges from 50 to 80 mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$ for C_4 plants, but only 15 to 35 mg CO_2

dm^{-2} hr^{-1} for C_3 (Black 1971). Consequently, C_4 plants are more efficient in energy conversion at high light intensities.

Optimum temperature for CO_2 uptake by C_4 plants was reported to be 30 to 40°C with uptake decreasing rapidly below 15 to 20°C. In contrast, temperature optima for C_3 plants ranged from 10 to 25°C with usually a sharp decrease above 25°C (Black 1971). Low night temperatures adversely affected chloroplast ultrastructure and chloroplast development in leaves of C_4 plants (Slack et al. 1974). The physiological response of the photosynthetic apparatus to temperature is the probable reason for the observed phenological development of cool-season plants such as western wheatgrass (*Agropyron smithii*) (C_3) and warm-season plants, such as blue grama (*Bouteloua gracilis*) (C_4) (Williams 1974).

Translocation capacity is larger in C_4 than C_3 plants because of a larger cross-sectional area of phloem (Gallaher et al. 1975). Species with the C_4 photosynthetic pathway have fewer cells between leaf vascular bundles than do C_3 species (Crookston and Moss 1974). The closeness of all leaf cells to vascular tissue in C_4 plants suggests greater efficiency in transporting photosynthate. Takeda and Fukuyama (1971) determined an interveinal distance of 25 to 70 μm (micrometers) for C_4 species and 75 to 130 μm for C_3 species.

Enzyme systems differ in plants with the two photosynthate pathways. Significant physical and kinetic differences were reported for phosphoenolpyruvate carboxylase taken from C_4 and C_3 species (Ting and Osmond 1973). However, carboxydismutase activity (ribulose-1, 5-diphosphate carboxylase) was found to be similar in both C_3 and C_4 plants. A low carbonic anhydrase activity appears distinctive of species with low compensation points and high rates of photosynthesis (C_4), while the inverse is true for C_3 plants (Chen et al. 1970; Triolo et al. 1974).

Photoperiod requirements generally differ in the two groups, but not directly. Since C_4 plants are well adapted to tropical regions, it is natural that most would be short-day or day-neutral with respect to flowering. However, C_4 plants growing at higher latitudes have become adapted to long days for flowering. Genetic plasticity therefore apparently exists for selection for adaptation to photoperiod (Evans 1975).

Bender and Smith (1973) have reported a relationship between type of nonstructural polysaccharide (starch or fructosan) accumulated in the lower internodes of grass shoots and carbon isotope determinations. They found that the type of nonstructural polysaccharide was not dependent on the type of photosynthetic pathway. However, data reported by Smith (1968) indicated C_4 plants accumulated starch while C_3 plants generally accumulated fructosans. Selected species of *Oryzopis, Phragmites, Stipa,* and *Panicum* were of the C_3 type but accumulated starch.

Water is a common limiting factor for plant growth throughout western rangelands. Plants which are efficient in water use would have a competitive advantage over less efficient plants during periods of moisture stress. C_4 plants required about half as much water as C_3 plants to produce one unit of dry matter (Black 1971). However, desert biome researchers in the Curlew Valley of northwestern Utah determined that *Atriplex confertifolia* (C_4) and *Ceratoides lanata* (C_3) were about equal in their annual water use while photosynthetic rates were similar (Cox 1977). High photosynthetic rates in C_4 plants did not result in increased transpiration rates compared to C_3 plants (El-Sharkawy and Hesketh 1965).

Taxonomic Classification

Photosynthetic pathway data for 632 species representing 138 genera and 25 tribes of the United States Gramineae were summarized (Table 1). Results were reported for tribes within each of subfamilies (Gould 1968) (Table 2).

Few intermediate values occurred between the identified C_3 and C_4 range of any characteristic utilized for photosynthetic pathway determination. Also, there was little variation within any characteristic from plant to plant within a species. Selected characteristics for photosynthetic pathway determination were consistently in agreement. Thus, in general, knowledge of any one characteristic could be used to predict the presence and level of associated characteristics.

All species studied in the subfamilies Arundinoideae, Bambusoideae, Oryzoideae, and Pooideae (Festucoideae) possessed C_3 characteristics. Within these subfamilies, there is a high probability that all species will possess the C_3 photosynthetic pathway.

Within the subfamilies Eragrostoideae and Panicoideae, both C_3 and C_4 photosynthetic pathways are present. Both subfamilies are predominantly C_4, while the exceptions apparently indicate a need for taxonomic reclassification rather than heterogeneity of photosynthetic pathway within a taxonomic division. In the Eragrostoideae, as defined by Gould (1968), the genus *Uniola* in the tribe Unioleae appears to possess the C_3 photosynthetic pathway as reflected by ^{13}C°/oo percentages. Consequently, *Uniola* was placed in the Oryzoideae by Smith and Brown (1973).

Within the subfamily Panicoideae, the genera *Oplismenus, Sacciolepis, Amphicarpum,* and *Isachne* are C_3. The genus *Panicum* contains species with both C_3 and C_4 pathways. The subgenus *Paurochaetium* C_4) was reclassified as *Sertaria* by Gould (1968). The subgenus *Dichanthelium* contained only C_3 species, while *Eupanicum* contained species with both C_3 and C_4 pathways. Further evaluation of the subgenus *Dichanthelium* has been reported by Brown and Smith (1975).

Adaptation and Competition

The function of the C_4 pathway is, in effect, to concentrate CO_2 in the bundle sheath cells, permitting the Calvin cycle to operate at more favorable concentrations of this rate-limiting substrate. This provides a more efficient mechanism for CO_2 fixation at low CO_2 concentrations in the intercellular spaces than does C_3 photosynthesis. Thus, the advantage of C_4 photosynthesis is maximal when photosynthesis is operating at high light intensities and temperature, and especially when stomatal conductance to gas exchange is low. In the case of low temperatures and light intensities the advantage would at most be marginal (Bjorkman 1976).

This adaptation correlates well with the historical concept of warm- and cool-season plants used by range scientists, verifying the ecological importance of such a classification. Brown (1978) reported that C_4 plants have a greater nitrogen (N) use efficiency compared to C_3 plants, which may give them an adaptive advantage, particularly on sites low in N. This is probably one of the factors responsible for the greater abundance of C_4 species in range soils lower in fertility (White 1961). It appears probable that the growing season of the species with the C_3 pathway would coincide with the cool, moist months, while the physiological traits of C_4 plants allow them to grow during the hotter, drier months. This would allow many species to occupy the same site with minimal interspecific competition (Williams and Markley 1973). The C_4 pathway is an important adaptive mechanism in hot environments, but it does not necessarily provide a significant advantage in cool, moist environments (Bjorkman et al. 1974).

Table 1. Identification of taxa within the United States Gramineae possessing the C_3 or C_4 photosynthetic pathway. Occurrence of distinct bundle sheath cells (BS: $-=C_3$, $+=C_4$); carbon dioxide compensation point (CO_2:H=C_3, L=C_4); net enhancement of photosynthesis in oxygen deficient atmosphere NE: $>+8=C_3$ $<+8=C_4$); $^{13}C/^{12}C$ ratio (^{13}C°/oo: <-22°oo$=C_3$ >-22°/oo$=C_4$); and occurrence of C_4 compounds as initial products in photosynthesis (C_4 cpd: $<2\%C_3$ $2\%C_4$) were characteristics used to evaluate photosynthetic pathway. Taxonomic classification follows that of Gould 1968, 1975)

Species	BS	CO_2	NE	^{13}C°/oo	C_4 cpd (%)	C_3	C_4
			Subfamily: Arundionoideae				
TRIBE: Arundineae							
[a]Arundo							
A. donax L.				<−22[21,23]		*	
[a]Cortaderia							
C. fulvida (J. Buchanan) Zotov				<−22[21,23]		*	
C. selloana (Schult.) Aschers. and Graebn.		H[12]		<−22[21,23]		*	
Phragmites							
P. communis Trin				<−22[1,21,23]		*	
(P. australis (Cav.) Trin. ex. Steud.)[b]				−27[21]		*	
[a]Molinia							
M. caerulea (L.) Moench				−27[21]		*	
TRIBE: Centotheceae							
Chasmanthium latifolium (Michx.) Yates							
(Uniola latifolia Michx.)[b]				−29[21]		*	
TRIBE: Danthonieae							
Danthonia							
D. montevidensis Hack. and Arech.		H[18]				*	
D. pilosa R. Br.		H[18]				*	
D. spicata (L.) Beauv. ex Roem. and Schult.				−26[21]		*	
[a]Schismus							
S. barbatus (L.) Thell.				−23[21]		*	
			Subfamily: Bambusoideae				
TRIBE: Bambuseae							
Arundinaria							
A. tecta (Walt.) Muhl.				−26[21]		*	
[a]Bambusa							
B. eutuloides McClure				−28[23]			
B. vulgaris Schrad. ex Wendl.				−30[21,22]	0[12,15]	*	
[a]Phyllostachys							
P. aurea A.				−28[21]		*	
P. bambusoides Sieb. and Zucc.				−31[23]		*	
TRIBE: Phareae							
Pharus							
P. latifolius L.				−30[21]		*	
			Subfamily: Eragrostoideae				
TRIBE: Aeluropodeae							
Distichlis							
D. spicata (L.) Greene	+[4]		<8[4]	>−20[1,20,21]			*[10]
D. stricta (Torr.) Rydb.				>−20[2]			
Monanthochloe							
M. littoralis Engelm.				>−20[20,21]			*
TRIBE: Aristideae							
Aristida							
A. adscensionis L.		L[3]	<8[3]				*[10,11]
A. armata Henrard				−14[23]			*
A. glauca (Nees) Walp.				−13[21]			*[1]
A. longiseta Steud.	+[16]						*[10,11]
A. purpurea Nutt.				−14[21]			*[11]
A. ternipes Cav.	+[16]						*[10,11]
A. uniplumis Lichtst in Roem. and Schult.		L[22]					*[10,11]
TRIBE: Chlorideae							
Bouteloua							
B. curtipendula (Michx.) Torr.		L[18]	+8[8]	>−20[1,21]			*[10,11]
B. filiformis (Fourn.) Griffiths.		L[18]		−13[21]			*[11]
B. gracilis (H.B.K.) Lag.		L[24]		−13[1]			*[11]
B. hirsuta Lag.		L[18]					*
Buchloe							
B. dactyloides (Nutt.) Engelm.		L[18,24]		>−20[1,21]			*[10,11]

Table 1 Continued

Species	BS	CO_2	NE	$^{13}C°/oo$	C_4cpd (%)	C_3	C_4
Chloris							
C. acicularis Lind. L. in Mitch.		L[18]					*
C. argentina (Hack.) Lillo. and Parodi		L[18]					*
C. canterai Arech.		L[18]					*
C. caribaea Spreng.		L[18]					*
C. cucullata Bisch.				−16[21]			*[11]
C. distichophylla Lag.		L[18]					*[11,6]
C. gayana Kunth	+[12]	L[5,12,18]	+3[5,8]	−15[23]	70[15] 90[9]		*[10,11]
C. inflata Link		L[18]					*
C. pectinata Benth.		L[18]					*
C. petraea Swartz		L[18]					*
C. pilosa Schum. and Thonn.		L[18]					*
C. polydactyla (L.) Sw.		L[18]					*
C. pycnothrix Trin.		L[18]					*
C. radiata (L.) Sw.		L[18]					*
C. submutica H.B.K.		L[18]					*
C. truncata R. Br.		L[18]					*
C. uliginosa Hack.		L[18]					*
C. ventricosa R. Br.				−16[23]			*
C. virgata Swartz				−14[23]			*
[a]Cynodon							
C. arcuatus F. and C. Presl		L[18]					*
C. dactylon (L.) Pers.		L[5,7,12,18]		>−20[1,20,21]			*[10,11,6]
Hilaria							
H. belangeri (Steud.) Nash				−14[21]			*[11]
H. mutica (Buckl.) Benth.	+[16]						*[10,11]
Schedonnardus							
S. paniculatus (Nutt.) Trel.	+[16]						*[10,11]
Spartina							
S. alterniflora Loisel.				−13[20,21]			*[11]
S. cynosuroides L.				−14[1]			*[11]
S. pectinata Link		L[18]		−13[1]			*[11]
Trichloris							
T. crinita (Lag.) Parodi		L[18]					*[10]
			Subfamily: Eragrostoideae				
TRIBE: Eragrosteae							
Blepharidachne Hack.	+[17]						
Blepharoneuron Nash	+[17]						*
Calamovilfa Hack.	+[17]						*
[a]Dactyloctenium							
D. aegyptium (L.) Beauv.		L[7]					*[10]
D. aegyptiacum Willd.		L[18]		−12[21]			*[11]
[a]Eleusine							
E. compressa Aschers. and Schweinf. ex Christensen.		L[18]					*
E. coracana (L.) Gaertn.		L[5,18]	+8[5,8]				*[10,11]
E. flagellifera Nees		L[18]					*
E. floccifolia Spreng.		L[18]					*
E. indica (L.) Gaertn.		L[7,18]					*[10,11]
E. jaegeri Pilger		L[18]					*
E. multiflora Hochst.		L[18]					*
E. tristachya (Lam.) Lam.		L[18]					*
Eragrostis							
E. acutiflora Nees		L[18]					*
E. acutiglumis Parodi		L[18]					*
E. airoides Nees		L[18]					*
E. atherstonei Stapf		L[18]					*
E. bahiensis Schrad.		L[18]					*
E. bicolor Nees		L[18]					*
E. brasiliensis Nees		L[18]					*
E. brownei (Kunth) Nees					97[15]		*[10,11]
E. chalcantha Trin.		L[18]					*
E. chariis (Schult.) Hitchc.		L[18]					*
E. chloromelas Steud.		L[7,18]	0[5,8]				*[10,11]
E. cilianensis (All.) Lutati		L[18]		>−20[1,23]			*[11]
E. collocarpa K. Schum. ex Engl.		L[18]					*
E. curvula (Schrad.) Nees	+[14]	L[18]					*[10,11,6]
E. denudata Hack. ex Schinz.		L[18]					*
E. dielsii Pilg. ex Diels and Pritz.		L[18]					*

Table 1 continued

Species	BS	CO_2	NE	^{13}C°/oo	C_4 cpd (%)	C_3	C_4
E. diffusa Buckl.		L[18]					*
E. ferruginea Beauv.		L[18]					*
E. flaccida Lindm.		L[18]					*
E. gummiflua Nees		L[18]					*
E. heteromera Stapf		L[18]					*
E. horizontalis Peter.		L[18]					*
E. intermedia Hitchc.	+[16]	L[18]		−16[21]			*[10,11]
E. lappula Nees		L[18]					*
E. lehmanniana Nees		L[18]					*
E. margaritacea Stapf		L[18]					*
E. mexicana (Hornem.) Link		L[12,18]					*[10,11]
E. nigra Nees. ex Steud.		L[18]					*
E. obtusa Munro		L[18]					*
E. oxylepis (Torr.) Torr.		L[18]					*
E. papposa Steud.		L[18]					*
E. patentissima Hack. ex Schinz.		L[18]					*
E. pilosa (L.) Beauv.		L[5,12]					*[10,11]
(E. parviflora Trin.)[b]	+[12]			−17[23]			*
E. plana Nees		L[18]					*
E. poaeoides Beauv. ex R. and S.		L[18]					*
E. polytricha Nees		L[18]					*
E. rigidior Pilger		L[18]	0[8]				*[10,11]
E. robusta Stent.		L[18]					*
E. rufescens R. and S.		L[18]					*
E. secundiflora Presl		L[18]					*
E. spectabilis (Pursh.) Steud.				−11[2]			*
E. starosselskyi Grossheim.		L[18]					*
E. stenophylla Hochst.		L[18]					*
E. superba Peyr.		L[18]					*
E. tremula Hochst.		L[18]					*
E. trichodes (Nutt.) Wood		L[18]					*
E. truncata Hack.		L[18]					*
E. unioloides (Retz.) Nees		L[18]					*
E. virescens Presl		L[18]					*
Gymnopogon							
G. ambiguus (Michx.) B.S.P.				−13[21]			*[11]
Leptochloa							
L. dubia (H.B.K.) Nees		L[7,18]					*[10,11]
L. fascicularis (Lam.) A. Gray		L[18]					*
L. fusca Kunth		L[7,18]					*[10,11,6]
L. monostachya Roem. and Schult.		L[7,18]					*[11,6]
Lycurus							
L. phleoides H.B.K.	+[17]			−14[21]			*
Muhlenbergia							
M. emersleyi Vasey				−11[21]			*[11]
M. lindheimeri Hitchc.				−12[21]		*[11]	*[11]
M. racemosa (Michx.) B.S.P.		L[17,18]					*[10,11]
M. schreberi Gmel.				−13[1]			*[11]
Sporobolus							
S. asper (Michx.) Kunth				−13[2]			*[11]
S. capensis Kunth		L[18]					*
S. contractus Hitchc.		L[18]					*
S. cryptandrus (Torr.) A. Gray.		L[17,18]					*[10,11]
S. elongatus R. Br.		L[18]		−13[23]			*
S. fimbriatus Nees		L[18]					*
S. helvola Th. Dur. and Schinz.		L[18]					*
S. heterolepsis A. Gray.				−13[2]			*
S. indicus (L.) R. Br.		L[18]					*
(S. jacquemontii Kunth)[b]		L[18]					*
(S. poiretii (R. and S.) Hitchc.)[b]		L[18]					*[11,6]
S. ioclados Nees		L[18]					*
S. phyllotrichus Hochst.		L[18]					*
S. pyramidatus (Lam.) Hitchc.		L[18]					*
S. spicatus Kunth	+[16]						*
S. usitatus Stent.		L[18]					*[10,11]
S. usitatus Stent.		L[18]					*
S. wrightii Munro. ex Scribn.				12[21]			*
Tridens							
T. albescens (Vasey) Woot. and Standl.	+[17]			−14[21]			*[11]
T. pilosus (Buckl.) Hitchc.				−13[21]			*[11]
Vaseyochloa							
V. multinervosa (Vasey) Hitchc.		L[17,18]		−15[21]			*[10,11]

Table 1 continued

Species	BS	CO_2	NE	^{13}C‰	C_4 cpd (%)	C_3	C_4
TRIBE: Orcuttieae							
Neostapfia							
N. colusana (Davy.) Davy.				−13[21]			*[11]
Orcuttia							
O. californica Vasey				−14[21]			*[11]
TRIBE: Pappophoreae							
Pappophorum							
P. bicolor Fourn.		L[17,18]		−13[21]			*[10,11]
TRIBE: Zoysieae							
[a]Tragus							
T. australianus S.T. Blake		L[8]	+2[8]				*[10,11]
[a]Zoysia							
Z. japonica Steud.				−15[21]			*[10,11]
Z. matrella (L.) Merr.				−12[21]			*[11]
Z. minima (Colenso) Zotov				−14[23]			*
TRIBE: Unioleae							
Uniola							
U. paniculata L.	+[14]			−28[20,21]		*	*[11,6]
Subfamily: Oryzoideae							
TRIBE: Oryzeae							
Ehrharta							
E. calycina J.E. Smith			+47[8]			*	
Hydrochloa							
H. carolinensis Beauv.				−27[21]		*	
Leersia							
L. hexandra Swartz					0[15]	*	
L. oryzoides (L.) Swartz		H[18]		−28[21]		*	
Luziola							
L. bahiensis (Steud.) Hitchc.				−28[21]		*	
[a]Oryza							
O. rufipogon Griff.			+55[8]			*	
O. sativa L.		H[5,12]	+45[8,5]	−26[21]		*	
Zizania							
Z. aquatica L.		H[18]		<−22[1,21]		*	
Z. texana Hitchc.				−27[21]		*	
Zizaniopsis							
Z. miliacea (Michx.) Doell and Aschers.				<−22[1,21]		*	
Subfamily: Panicoideae							
TRIBE: Andropogoneae							
Andropogon							
A. gayanus Kunth			−2[5,8]				*[10,11]
A. gerardi Vitman		L[18]		−13[2]			*
A. glomeratus (Walt.) B.S.P.				>−20[21]			*[11]
A. lateralis Nees		L[18]					*
A. papillosus Hochst. ex A. Rich.		L[18]					*
A. selloanus Hack.		L[18]					*
A. ternatus Nees		L[18]					*
A. virgatus Desv.		L[18]					*
A. virginicus L.		L[7]					*[10,11,6]
[a]Anthraxon							
A. hispidus (Thunb.) Makino		L[18]					*
Bothriochloa							
B. alta (Hitch.) Henrard		L[18]		−12[21]			*
B. barbinodis Herter		L[18]					*
B. decipiens (Hackel) C.E. Hubb.		L[18]					*
B. ewartiana (Domin) C.E. Hubb.		L[18]					*
B. glabra (Rox B.) A. Camus		L[19]					*
B. exaristata (Nash) Henr. (Andropogon hassleri Hack.)[b]		L[18]					*
B. insculpta (Hochst.) A. Camus		L[18]					*
B. intermedia (R. Br.) A. Camus		L[18]					*
B. ischaemum (L.) Keng		L[18]					*
B. laguroides (D.C.) Herter		L[18]					*
B. pertusa (Willd.) A. Camus		L[18]					*

Table 1 continued

Species	BS	CO	NE	^{13}C°/oo	C_4cpd (%)	C_3	C_4
B. saccharoides Swartz (Andropogon saccharoides Swartz)[b]				−12[21]			*[10]
B. springfieldii (Gould) Parodi		L[18]					*
Chrysopogon							
C. gryllus (L.) Trin.							*[11,6]
C. montanus Trin.		L[18]		−12[21]			*[11]
C. serrulatus Trin.		L[18]					*
[a]Coix							
C. lacryma jobi L.			0[8]				*[10,11]
[a]Cymbopogon							
C. citratus Stapf				−15[20,21]			*[11]
C. martini (Roxb.) W. Watson		L[18]					*
[a]Dichanthium							
D. annulatum Stapf		L[18]					*
D. aristatum (Poir.) C.E. Hubb.			0[8]				*[10]
D. sericeum A. Camus		L[18]					*
D. superciliatum A. Camus		L[18]					*
[a]Eremochloa							
E. ophiuroides (Munro) Hack.	+[16]			−11[21]			*[10,11,6]
Erianthus							
E. maximus Brongn.					84[15]		*[10,11]
Heteropogon							
H. contortus (L.) Beauv.		L[7,18]	0[8]				*[11,6]
[a]Hyparrhenia							
H. hirta (L.) Stapf		L[18]					*[10]
H. rufa (Nees) Stapf		L[18]					*
Imperata							
I. arundinacea Cyrilli							*[10,11]
I. chesemanii Hack.				−13[23]			*
I. cylindrica (L.) Beauv.				−12[23]			*
Manisuris							
M. altissima (Poir.) Hitchc.							*[11,6]
[a]Miscanthus							
M. sacchariflorus (Maxim.) Hack.							*[10]
[a]Saccharum							
S. officinarum L.		L[5,18]		>−20[21,15]	65,86[9,15]		*[10,11,6]
S. robustum Brandes and Fesw.							*[10,11]
S. sinense Roxb.					63[15]		*[10,11]
S. spontaneum L.					65[15]		*[10,11]
Schizachyrium							
S. cirratus Hack.		L[18]					*
S. condensatus H.B.K.		L[18]					*
S. hirtiflorus (Nees) Kunth		L[18]					*
S. scoparium Michx.							*
(Andropogon scoparius Michx.)[b]		L[7]		−14[2]			*[10,6]
Sorghastrum							
S. nutans (L.) Nash	+[16]	L[18]		−12[2]			*[10,11]
S. pellitum Parodi		L[18]					*[6,11]
[a]Sorghum							
S. arundinaceum Stapf		L[18]					*[11]
S. bicolor (L.) Moench		L[7,18]			94[9]		*[10,11,6]
S. caffrorum Beauv.		L[18]					*
S. caudatum Stapf		L[18]					*
S. controversum (Steud.) Snowden		L[18]					*
S. dochna (Forsk.) Snowden		L[18]					*
S. drummondii Nees		L[18]					*
S. gambicum Snowden		L[18]					*
S. halepense (L.) Pers.		L[7,18]		−12[23]	64[15]		*[10,11]
S. japonicum (Hackel) Roshev.		L[18]					*
S. nigricans Hort. ex R. and S.		L[18]					*
S. propinquum (Kunth) Hitchc.							*[10,11]
S. saccharatum Moench		L[18]					*
S. sudanense Stapf	+12[3]	L[3,12,18]	−10[8]		88[9]		*[10,11]
S. technicum (Koern.) Battand and Trab.		L[18]					*
S. verticilliflorum Stapf		L[18]					*[11]
S. virgatum (Hack.) Stapf		L[18]					*
S. vulgare Pers.		L[12]	+4[5,8]	−14[21]			*[10,11]
Tripsacum							
T. dactyloides L.		L[7]		−12[21]			*[10,11]
[a]Zea							
Z. mays L.	+[4,12,22]	L[7,22,13,12,18]	0-6,[4,5,8]	>20[21,22,23,20]	86[9,15,22]	*[10,11,6]	

Table 1 continued

Species	BS	CO_2	NE	^{13}C°/oo	C_4 cpd (%)	C_3	C_4
TRIBE: Paniceae							
Amphicarpum							
A. purshii Kunth				−27[21]		*	
Anthaenantia							
A. rufa (Ell.) Schult.				−12[21]			*[11]
[a]Anthephora							
A. cristata Hack. ex Wildem. and Th. Dur.	+16						*[10,11]
A. elongata Wildem.				−10[21]			*[11]
A. hermaphrodita O. Ktz							
(A. elegans Schreb.)[b]				−11[21]			*
A. pubescens Nees		L[17,18]		−12[21]			*[10,11]
Axonopus							
A. affinis Chase				−11[21]			*[11]
A. compressus (Swartz) Beauv.		L[22]					*[10]
Brachiaria							
B. erucaeformis (J.E. Smith) Griseb.		L[18]					*
B. laeta (Mez) A. Camus		L[18]					*
B. platyphylla (Griseb.) Nash				−13[21]			*[6]
(Paspalum platyphyllum (Griseb.)[b]		L[18]					*[11]
B. ramosa Stapf		L[18]					*
Cenchrus							
C. biflorus Roxb.		L[18]					*
C. calycalatus Cav.				−12[23]			*
C. ciliaris L.		L[18]		−12[21]			*[10,11,6]
C. echinatus L.		L[7]					*[10]
C. incertus M.A. Curtis				−12[21]			*[11]
C. myosuroides H.B.K.	+16	L[18]					*[10,11]
C. pauciflorus Benth.		L[18]					*
C. pilosus H.B.K.		L[18]					*
C. setigerus Vahl.		L[18]					*
Dichanthelium[c]							
(Panicum)[b]							
D. ciliatum Ell.				−26[21]		*	
D. clandestinum (L.) Gould		H5[17,18]		<−22[2,21]		*	
D. commutatum (Schult.) Gould		H[5]		−26[21]		*	
D. depauperatum (Muhl.) Gould				−25[21]		*	
D. lancearium Trin.				−27[21]		*	
D. lanuginosum (Ell.) Gould				−26[2]		*	
D. latifolium L.				−25[21]		*	
D. leibergii (Vasey) Scribn.				−26[1]		*	
D. lindheimeri (Nash) Gould		H[5]				*	
D. linearifolium (Scribn.) Gould				−26[21]			
D. meridionale Ashe.				−24[21]		*	
D. microcarpon Muhl. ex Ell.				−27[21]		*	
D. nodatum (Hitchc. and Chase) Gould				−28[2]		*	
D. oligosanthes (Schult.) Gould		H[17,18,19]				*	
D. pacificum Hitchc. and Chase	−[22]	H[18,22]		<−22[1,21]	0[22]		
D. praecocius Hitch. and Chase		H[17,18,19]				*	
D. scribnerianum (Nash) Fern.				−32[1]		*	
D. sphaerocarpon (Ell.) Gould				−28[2]		*	
D. webberianum Nash				−26[21]		*	
D. xalapense H.B.K.				−27[21]		*	
Digitaria							
D. adscendens (H.B.K.) Henrard				−12[21]			*[11]
D. argyrograpta Stapf		L[18]	0[8]				*[10,11]
D. biocornis R. and S. ex Loud.		L[18]					*
D. brownei Hughes		L[18]					*
D. californica (Benth.) Henr.							*[10]
(Trichachne californica (Benth.) Chase[b]		L[7,18]		−11[21]			*
D. decumbens Stent.							*[10,11]
D. diagonalis Stapf		L[18]					*
D. eriantha Steud.		L[18]					*
D. eriostachya Mez.		L[18]					*
D. gazensis Rendle		L[18]					*
D. glauca Stent.		L[18]					*
D. horizontalis Willd.		L[18]					*
D. iburua Stapf		L[18]					*
D. insularis (L.) Mez ex Ekmann							
(Trichachne insularis (L.) Nees)[b]		L[7]					*
D. ischaemum (Schreb.) Schreb. ex Muhl.		L[18]					*
D. kilimandscharica Mez.		L[18]					*

Table 1 continued

Species	BS	CO_2	NE	^{13}C°/oo	C_4^{cpd} (%)	C_3	C_4
D. milanjiana Stapf		L[18]					*
D. pentzii Stent.		L[7,18]					*[10,11]
D. phaeothrix Parodi		L[18]					*
D. sanguinalis (L.) Scop.		L[5, 12,18]		−15[23]			*[10,11,6]
D. seriata Stapf		L[18]					*
D. smutsii Stent.		L[18]	−1[8]				*[10,11]
D. swazilandensis Stent.		L[18]					*
D. valida Stent.		L[18]					*
Echinochloa							
E. colonum (L.) Link		L[4]					*[10,6,11]
E. crusgalli (L.) Beauv		L[5,7,12,13,18]		>-20[1,21,23]			*[10,6,11]
E. frumentacea (Roxb.) W.F. Wight		L[18]		−15[23]			*
E. haploclada Stapf		L[18]					*
E. holubii Stapf		L[18]					*
E. pyramidalis Hitchc. and Chase		L[18]					*
E. spiralis Vasinger		L[18]					*
E. stagnina Beauv.		L[5]	−3[5,8]				*[10]
Eriochloa							
E. lemmoni Vasey and Scribn. (E. gracilis (Fourn) Hitchc.)[b]							*[11,6]
E. michauxii (Poir) Hitchc. (Panicum molle Michx.)[b]		L[18]					*
[a]Isachne							
I. globosa Kuntze				−28[23]		*	
Leptoloma							
L. cognatum (Schult.) Chase				>−20[2,21]			*[11]
[a]Melinis							
M. minutiflora Beauv.			0[8]	−13[21]			*[10,11]
[a]Oplismenus							
O. burmanni (Retz.) Beauv.				−28[21]		*	
O. hirtellus (L.) Beauv.				−31[21]		*	
O. undulatifolius Beauv. (O. imbecillus Roem. and Schult.)[b]				−27[23]		*	
Panicum							
P. bisulcatum Thunb.		H[17,18,19]				*[6]	
P. gymnocarpon Ell.				−29[21]		*	
P. hemitomon Schult.		H[18]		−25[21]		*	
P. hians Ell.				−26[21]		*	
P. trichanthum Nees		H[18]				*	
P. verrucosum Muhl.				−26[21]		*	
P. wilcoxianum Vasey		H[17,18]		−26[21]		*	
P. amarulum Hitchc. and Chase		L[18]		−13[1]		*	*[11]
P. anceps Michx.		L[17,18,19]		−12[21]			*[11]
P. antidotale Retz.		L[17,18,19]		−14[21]	84[9]		*[10,11]
P. bergii Arech.		L[18]					*[11,6]
P. bulbosum H.B.K.		L[5]			87[9]		*[10',11]
P. capillare L.	+[12,22]	L[5,7,12,17,18,19,22]		−14[21]	89[9]		*[10,11,6]
P. coloratum Cav. (Walt.)		L[17,18,19]		−12[23]			*[10,11]
P. cymbiforme D.K. Hughes		L[17,18]					*[11,6]
P. decompositum R. Br.		L[17,18]					*[11,6]
P. deustum Thunb.		L[17,18]					*[11]
P. dichotomiflorum Michx.		L[17,18,19]		>20[1,21]			*[10,11]
P. effusum R. Br.		L[18]					*
P. filipes Scribn.	+[16]						*[10,11]
P. geminatum Forsk.				−11[21]			*[11]
P. hallii Vasey		L[17,18,19]		−13[21]	93[9]		*[10,11]
P. havardii Vasey		L[18]			96[9]		*
P. laevifolium Hack.		L[17,18,19]			97[9]		*[10,11]
P. lanipes Mez.		L[18]					*
P. larcomianum D.K. Hughes		L[18]					*
P. longijubatum Stapf		L[18]					*
P. makarikariense (Van Rensb.) Gooss		L[17,18]					*[11]
P. maximum Jacq.		L[7,17,18,19]		−13[21]	99[9]		*[10,11,6]
P. miliaceum L.		L[5,12,17,18,19]			96[9]		*[10,11,6]
P. milioides Nees ex Trin.	−[14]	L[18]				*[6]	*[10]
P. obtusum H.B.K.		L[17,18,19]		−13[21]	90[9]		*[10,11]
P. philadelphicum Bernh. ex Trin.							*[10,11]
(P. minus Nash)[b]		L[17,18,19]			93[9]		*[10,11]
P. plenum Hitchc. and Chase		L[17,18,19]		−12[21]	85[9]		
P. polygonatum Schrad.		L[17,18]					*[10,11]
P. prolutum F. Muell.		L[17,18,19]			93[9]		*[10,11]

Table 1 continued

Species	BS	CO_2	NE	^{13}C°/oo	C_4 cpd (%)	C_3	C_4
P. purpurascens Raddi				—11[21]			*[11]
P. queenslandicum Domin.		L[18]					*
P. reptans. L.				−11[21]			*[11]
P. stapfianum Fourc.		L[18]					*[10,11]
P. tenerum Beyr.				−11[21]			*[11]
P. texanum Buckl.		L[17,18]			97[9]		*[10,11,6]
P. trachyrahachis Benth.		L[18]					*
P. turgidum Forsk.		L[17,18,19]			94[9]		*[10,11,6]
P. urvilleanum Kunth				−12[21]			*[11]
P. virgatum L.		L[7,17,18,19]		>−20[1,21]	97[9]		*[10,11]
P. whitei J.M. Black		L[18]					*
Paspalidium							
P. geminiflorum Steud. (Paspalum geminiflorum Steud.)[b]		L[18]					*
Paspalum							
P. almum Chase		L[18]					*
P. boscianum Fluegge		L[18]					*
P. brunneum Mez.		L[18]					*
P. ciliatifolium Michx.		L[18]					*
P. conjugatum Bergius		L[18]					*[11]
P. dilatatum Poir.		L[7,12,18]		−13[23]	66[15]		*[10,11]
P. distichum L.	+[4]	L[5,12,18]	−8[4]	−14[23]			*[10,11]
P. hartwegianum Fourn.	+[16]						*[10,11]
P. intermedium Munro ex Morong		L[18]					*
P. juegensii Hack.		L[18]					*
P. mandiocanum Trin.		L[18]					*
P. nicorae Parodi		L[18]					*
P. notatum Fluegge		L[5,7,18]	+2[5,8]	−12[23]			*[10,11,6]
P. paniculatum L.		L[18]					*
P. paspaliodes Scribn.				−13[23]			*
P. paucispicatum Vasey		L[18]					*
P. plicatulum Michx.		L[18]					*
P. polystachyum Kuntze		L[18]					*
P. pubiflorum Rupr. ex Fourn.		L[18]		−13[21]			*[11]
P. pumilum Nees		L[18]		−12[23]			*
P. quadrifarium Lam.		L[18]					*
P. rojasii Hack.		L[18]					*
P. scrobiculatum L.		L[18]					*
P. umbrosum Trin.		L[18]					*
P. urvillei Steud.		L[18]		−11[21]			*[11]
P. virgatum L.		L[18]					*
P. yaguaronense Henr.		L[18]					*
[a]Pennisetum							
P. ciliare (L.) Link		L[18]		−11[21]			*[11]
P. flaccidum Griseb. in Goett.		L[18]					*
P. glaucum (L.) R. Br.		L[12,18]	−3[8]				*[10,11]
P. macrourum Trin.		L[18]		−12[23]			*
P. massaicum Stapf		L[18]					*
P. orientale Rich.		L[18]					*
P. pedicellatum Trin.		L[18]	0[8]				*[10,11]
P. polystachyum Schult.		L[18]					*
P. purpureum Schum.		L[7]					*[10,7,11]
P. spicatum R. & S.		L[18]					*
P. typhoideum Rich.		L[18]					*
Reimarochloa							
R. acuta Hitchc.				−12[21]			*[11]
[a]Rhynchelytrum							
R. repends (Willd.) C.F. Hubbard (R. roseum (Nees) Stapf and Hubb.)[b]				−13[21]			*[11]
Sacciolepis							
S. striata (L.) Nash				−27[21]		*	
Setaria							
S. adhaerens (Forsk.) Chiov.		L[18]					*
S. almaspicata de Wit.		L[18]					*
S. argentina Herrm.		L[18]					*
S. faberri Herrm		L[18]					*[11]
S. firmulum Hitchc. and Chase (Panicum firmulum Hitchc. and Chase)[b]		L[18]					*
S. glauca (L.) Beauv.		L[5,13,18]					*[11]
S. holstii Herrm.		L[18]					*
S. italica (L.) Beauv.		L[7,12,18]	0[8]	−14[23]			*[10,6]

Table 1 continued

Species	BS	CO_2	NE	$^{13}C°/oo$	C_4 cpd (%)	C_3	C_4
S. lutescens (Weigel) Hubb.	+[12]	L[12,18]					*[10,11,6]
S. neglecta de Wit.		L[18]					*
S. pallidifusca Stapf and C.E. Hubb.		L[18]					*
S. palmifolia (Koen.) Stapf		L[18]					*
S. phanerococca Stapf		L[18]					*
S. reverchoni Vasey				−12[21]			*
(Panicum reverchoni Vasey)[b]		L[17,18]					*[11]
S. scheelei (Steud.) Hitchc.				−13[21]			*
S. sphacelata (Schum.) Stapf and C.E. Hubb.		L[18]	0[8]	−14[23]			*[10,11,6]
S. verticillata (L.) Beauv.		L[18]					*
S. viridis (L.) Beauv.		L[7,18]		−13[23]			*[10,11]
Stenotaphrum							
S. secundatum (Walt.) Kuntze				−16[20,21]			*[11,6]
Subfamily: Pooideae							
TRIBE: Aveneae							
Agrostis							
A. alba L.		H[5,12,18]	+42[8]	−28[2]		*	
A. castellana Boiss and Reut.			+45[8]			*	
A. hiemalis (Walt.) B.S.P.		H[18]		−28[21]		*	
A. perennans (Walt.) Tuckerm.				−30[1]		*	
S. scabra Willd.				−29[1]		*	
A. tenuis (Sibth.)				−28[21]		*	
Alopecurus							
A. pratensis L.		H[18]		<−22[2,23]		*	
Ammophila							
A. breviligulata Fern.				−28[1]		*	
[a]Anthoxanthum							
A. odoratum L.		H[12]		−28[21]		*	
[a]Arrhenatherum							
A. elatius (L.) Presl		H[12,18]		<−22[2,23]		*	
[a]Avena							
A. abyssinica Hochst. ex A. Rich		H[18]				*	
A. alba Vahl.			+50[8]			*	
A. barbata Brot.		H[18]				*	
A. clauda Dur. in Duch.		H[18]				*	
A. fatua L.		H[18]				*	
A. longiglumis Dur. in Duch.		H[18]				*	
A. pilosa Bieb.		H[18]				*	
A. sativa L.		H[5,12,18]		−24[21]	2[15]	*	
A. semipervirens Will.			+51[8]			*	
A. sterilis L.		H[18]				*	
A. strigosa Schreb.		H[18]				*	
A. ventricosa Balansa		H[18]				*	
Beckmannia							
B. syzigachne (Steud.) Fernald.		H[12]		−25[21]		*	
Calamagrostis							
C. canadensis (Michx.) Beauv.		H[18]		<−22[2,21]		*	
Cinna							
C. latifolia (Trevir.) Griseb.		H[12]		−25[21]		*	
Deschampsia							
D. caespitosa (L.) Beauv.		H[18]				*	
D. chapmani Petrie				−27[23]		*	
D. flexuosa (L.) Trin.				−24[21]		*	
Helictotrichon							
H. hookeri (Scribn.) Henr.		H[18]				*	
Hierochloe							
H. odarata (L.) Beauv.				−23[21]		*	
H. redolens Roem. and Schult.				−29[23]		*	
[a]Holcus							
H. lanatus L.				−31[23]		*	
Koeleria							
K. cristata (L.) Pers.		H[18]				*	
K. phleoides (Vill.) Pers.		H[18]				*	
K. setacea D.C.		H[18]				*	
K. valesiaca Gaud.		H[18]				*	
Limnodea							
L. arkansana (Nutt.) L.H. Dewey				−28[21]		*	
Milium							
M. effusum L.				<−22[21,23]		*	

Table 1 continued

Species	BS	CO_2	NE	^{13}C°/oo	C_4 cpd (%)	C_3	C_4
Phalaris							
P. californica Hook and Arn.							
(P. amethystina Trin.)			+60[8]			*	
P. arundinacea L.		H[5,7,12,18]	+45[5,8]	<−22[2,21]		*	
P. brachystachys Link				−25[21]		*	
P. canariensis L.		H[7]		<−22[23,21]		*	
P. minor Retz.				−28[23]			
P. tuberosa L.			+39[8]			*	
Phleum							
P. alpinum L.			+40[8]			*	
P. nodosum L.			+45[8]			*	
P. phleoides Simenkai				−30[23]		*	
P. pratense L.		H[18]		−27[2]		*	
Polypogon							
P. monspeliensis (L.) Desf.				−28[23]		*	
Sphenopholis							
S. obtusata (Michx.) Scribn.				−29[21]		*	
Trisetum							
T. flavescens (L.) Beauv.		H[18]				*	
TRIBE: Brachyelytreae							
Brachyelytrum							
B. erectum (Schreb.) Beauv.				−27[21]		*	
TRIBE: Diarrheneae							
Diarrhena							
D. americana Beauv.				−30[21]		*	
TRIBE: Meliceae							
Glyceria							
G. grandis S. Wats.				−24[21]		*	
G. striata (Lam.) Hitchc.				−25[21]		*	
Melica						*	
M. altissima L.				−28[23]		*	
M. mutica Walt.		H[7]		−26[21]		*	
Schizachne						*	
S. purpurascens (Torr.) Swallen				−28[21]			
TRIBE: Monermeae							
[a]Parapholis							
P. incurva (L.) C.E. Hubb.				−26[21]		*	
P. pannonica Kunth				−25[21]		*	
TRIBE: Nardeae							
[a]Nardus							
N. stricta L.				−26[21]		*	
TRIBE: Poeae							
[a]Brachypodium							
B. phoenicoides Roem. and Schult.				−26[23]		*	
[a]Briza							
B. maxima L.				−29[23]		*	
B. minor L.				−30[23]		*	
B. rotundata Steud.				−27[21]		*	
Bromus							
B. albidus M.B.							
(B. biebersteinii R. and S.)[b]		H[18]				*	
B. coloratus Steud.			+40[8]			*	
B. commutatus Schrad.				−28[21]		*	
B. diandrus Roth.							
(B. rigidus Roth.)[b]		H[18]				*	
B. hankeanus (Presl) Kunth			+49[8]			*	
B. inermis Leyss.		H[12,18]		<22[2,21]		*	
B. kalmii A. Gray				−30[1]		*	
B. purgans L.				−25[21]		*	
B. tectorum L.		H[12,18]		<−22[23]		*	
B. unioloides (Willd.) H.B.K.							
(B. catharticus Vahl.)[b]		H[18]		<−22[1,23]		*	
[a]Dactylis							
D. aschersoniana Graebn.			+25[8]			*	
D. glomerata L.	+[14]	H[5,12,18]	+46[5,8]	<−22[2,21]		*[6]	
Festuca							
F. ampla Hack			+53[8]			*	

Table 1 continued

Species	BS	CO_2	NE	^{13}C°/oo	C_4 cpd (%)	C_3	C_4
F. arundinacea Schreb.		H[7]		<−22[2,23]		*[6]	
F. pratensis Huds.						*	
(F. elatior C.)[b]		H[12,18]		−29[2]		*	
F. rubra L.				−27[1,2]		*	
[a]Lolium							
L. gaudinii Parl.			+49[8]			*	
L. multiflorum Lam.		H[7,18]	+50[5,8]			*	
L. perenne L.		H[18]		−29[2]		*	
L. persicum Boiss. and Hohen.		H[18]				*	
L. rigidum Gaud.		H[18]				*	
L. strictum Presl		H[18]				*	
L. temulentum L.		H[18]				*	
[a]Lamarckia							
L. aurea (L.) Moench				−30[23]		*	
Poa							
P. ampla Merr.			+40[8]			*	
P. annua L.		H[18]				*	
P. compressa L.		H[12]		−22[2,21]		*	
P. pratensis L.		H[18]	+37[5,8]	−27[2]		*	
P. trivialis L.		H[18]				*	
P. secunda Presl				−28[20,21]		*	
Puccinellia							
P. distans (L.) Pal.				−28[23]		*	
Vulpia							
V. myuros (L.) K.C. Gremlin							
(F. megalura Nutt.)[b]		H[18]				*	
TRIBE: Stipeae							
Oryzopsis							
O. hol iformis (MB) Rich.			+45[8]			*	
O. hymenoides (Roem. and Schult.) Ricker				−28[1]		*	
O. miliacea (L.) Benth. and Hook. ex Aschers. and Schweinf.				−30[23]		*	
O. racemosa (J.E. Smith) Ricker		H[12]				*	
Stipa							
S. columbiana Macoun				−24[20,21]		*	
S. comata Trin. and Rupr.				−25[1]		*	
S. leucotricha Trin. and Rupr.				−27[21]		*	
S. nitida Spraque and Summerh.			+40[8]			*	
S. robusta (Vasey) Scribn.				−25[21]			
S. Spartea Trin.				−28[1]			
S. tenuissima Trin.				−25[21]		*	
S. viridula Trin.				−27[2]		*	
TRIBE: Triticeae							
[a]Aegilops							
A. bicornis Jakub et. Sp.		H[13]				*	
A. biuncinalis Vis.		H[13]				*	
A. caudata L.		H[13,18]				*	
A. columnaris Zhukov		H[13,18]				*	
A. comosa Sibth. et. Sm.		H[13]				*	
A. crassa Boiss		H[13,18]				*	
A. cylindrica Host.		H[13,18]	+42[8]			*	
A. heldreichii Holzm.		H[18]				*	
A. ligustica (Savign.) Coss		H[18]				*	
A. longissima Schw. et. Musch.		H[13]				*	
A. ovata L.		H[13]				*	
A. perigrina (Hack.) Eig.			+40[8]			*	
A. sharonensis Eig.		H[13]				*	
A. speltoides Tausch		H[18]				*	
A. squarrosa L.		H[13,18]		−34[23]		*	
A. triaristata Willd.		H[13,18]				*	
A. triuncialis L.		H[13,18]				*	
A. umbellulata Zhukov.		H[13,18]				*	
A. uniaristata Vis.		H[13]				*	
A. variabilis Eig.		H[13]				*	
A. ventricosa Tausch		H[13]				*	
Agropyron							
A. glaucum R. and S.		H[18]				*	
A. inerme (Scribn. and Smith) Rydb.		H[18]				*	
A. intermedium (Host) Beauv.		H[18]		<−22[1,21,23]		*	
A. junceum (L.) Beauv.		H[18]				*	
A. kosanini Nabelek		H[18]				*	
A. latiglume (Scribn. and Smith) Rydb.		H[18]				*	
A. leptourum (Nevski) Grossheim		H[18]				*	

Table 1 (continued

Species	BS	CO_2	NE	^{13}C°/oo	C_4 cpd (%)	C_3	C_4
A. littorale Dum.		H[18]				*	
A. loliodes (Karel. and Kir.)		H[18]				*	
A. obtusiusculum Lange P. Candargy		H[18]				*	
A. orientale R. and S.		H[18]				*	
A. panormitanum Parl. ex Boiss.		H[18]					
A. pectiniforme R. and S.		H[18]				*	
A. pseudorepens Scribn. and Smith		H[18]				*	
A. pungens (Pers.) R. and S.		H[18]				*	
A. repens (L.) Beauv.		H[8]		<−22[2,21]		*	
A. rigidum Beauv.		H[18]				*	
A. scabriglume (Hack.) Parodi		H[18]				*	
A. semicostatum (Steud.) Ness ex Boiss		H[18]				*	
A. sibiricum (Willd.) Beauv.		H[18,24]		−28[2]		*	
A. Smithii		H[18,24]		−28[2]		*	
A. spicatum (Pursh) Scribn. and Smith		H[18]		−27[21]		*	
A. striatum (Steud.) P. Candargy		H[18]				*	
A. subulatum R. and S.		H[18]				*	
A. tenerum Vasey		H[18]				*	
A. trachycaulum (Link) Steud.				−28[2]		*	
A. trichophorum (Link) Richt.		H[18]				*	
A. violaceum Vasey		H[18]				*	
Elymus							
E. agropyroides Presl		H[18]				*	
E. angustus Trin. ex Ledeb.		H[18]				*	
E. antarcticus Hook.		H[18]				*	
E. arenarius L.		H[18]				*	
E. canadensis L.		H[18]		−27[2]		*	
E. carolinianus Walt.		H[18]				*	
E. cinereus Scribn. and Merr.		H[18]				*	
E. crinitus Schreb.		H[18]				*	
E. dahuricus Turcz.		H[18]				*	
E. glaucus Buckl.		H[18]				*	
E. innovatus Beal		H[18]				*	
E. junceus Fisch.		H[18]		−26[2]		*	
E. mollis Trin.	−[4]		7+[8,4]	−28[1]		*	
E. paboanus Claus		H[18]				*	
E. virginicus L.		H[18]		−27[21]		*	
Hordeum							
H. bogdani Wilensky		H[18]				*	
H. brevisubulatum Link		H[18]				*	
H. bulbosum L.		H[18]	+47[8]			*	
H. chilense Roem. and Schult.			+34[8]			*	
H. comosum Presl		H[18]				*	
H. compressum Griseb.		H[18]				*	
H. hystrix Roth.		H[18]				*	
H. jubatum L.		H[18]		−29[2]		*	
H. marinum Huds.		H[18]				*	
H. pusillum Nutt.				−27[21]		*	
H. spontaneum Koch		H[18]				*	
H. stebbinsii Covas		H[18]				*	
H. vulgare L.		H[5,12,13,18]				*	
[a]Secale							
S. ancestrale Zhuk.			+48[8]			*	
S. cereale L.		H[18]	+37[8]			*	
S. montanum Guss.		H[18]				*	
S. vavilovii Grossheim		H[18]				*	
Sitanion							
S. hystrix (Nutt.) J.G. Smith							
[a]Triticum							
T. aestivum L.	−[22]	H[5,22,3,18,13]	+23[8], +50[5]	<−22[20,22,23]		*[6]	
(T. sativum Lam.)[b]		H[12]			0[15]	*	
(T. vulgare Vill.)[b]		H[18]				*	
T. baeoticum Boiss. et. Schiem.		H[13]				*	
T. compactum Host.		H[13]				*	
T. dicoccoides Korn.		H[13]				*	
T. dicoccum Schrank		H[18]				*	
T. durum Desf.		H[18]	+50[8]			*	
T. monococcum L.		H[18,13]				*	
T. persicum Vav.		H[13]				*	
T. polonicum L.		H[13]				*	
T. spelta L.		H[13]				*	
T. sphaerococcum Perc.		H[13]				*	
T. timopheevi Zhukov		H[13]				*	

Table 1 continued

Species	BS	CO_2	NE	$^{13}C°/oo$	C_4cpd (%)	C_3	C_4
T. turanicum Jakubz.		H[13]				*	
T. turgidum L.		H[13]				*	
T. vavilovii Tuman		H[13]				*	

[a]= genera represented by introduced or adventive species only
[b]= indicates synonym of preceding taxa
[c]=Recent interpretations have elevated the subgenus *Dichanthelium* to the generic level. This change was made for all species in the *Dichanthelium* subgenus, regardless of the publication of a current authority.

[1]Bender (1971)
[2]Bender and Smith (1973)
[3]Bisalputra et al. (1969)
[4]Bjorkman and Gauhl (1969)
[5]Black et al. (1969)
[6]Brown and Gracen (1972)
[7]Chen et al. (1970)
[8]Downes and Hesketh (1968)
[9]Downton (1970)
[10]Downton (1971)
[11]Downton (1975)
[12]Downton and Tregunna (1968)
[13]Dvorak and Natr (1971)
[14]Gracen et al. (1972)
[15]Hatch et al. (1967)
[16]Johnson (1964)
[17]Krenzer and Moss (1969)
[18]Krenzer et al. (1975)
[19]Moss et al. (1969)
[20]Smith and Epstein (1971)
[21]Smith and Brown (1973)
[22]Tregunna et al. (1970)
[23]Troughton et al. (1974)
[24]Williams and Markley (1973)

Caswell et al. (1973) proposed that C_4 plants are generally inferior food sources for herbivores, primarily insects, and are often avoided by them relative to C_3 plants. Caswell and Reed (1975) determined that the grasshopper (*Melanoplus confusus*) was capable of digesting C_3 grass material, but was unable to totally digest the thick-walled bundle sheath cells of C_4 grasses. Further research with 10 species of grasshoppers indicated that the large quantities of nutritional material in the bundle sheath cell of C_4 plants was at least partially unavailable (Caswell and Reed 1976). Plants with the C_4 photosynthetic pathway are also generally lower in total digestible nutrients for cattle and sheep than C_3 plants at the same stage of maturity (Crampton and Harris 1969). Akin and Burdick (1977) reported that the large amount of potential nutrients in the parenchyma bundle sheath of selected warm-season (C_4) grasses may not be readily available because of slow degradation of the sheath cell wall by rumen bacteria. They hypothesized that the "sheath barrier" to utilization of starch and other nutrients in these cells may be a factor responsible for the lower nutritive value to ruminants of some warm-season grasses compared to cool-season (C_3) species. However, many factors interact to determine both herbivore preference and digestibility (Stoddart et al. 1975). Rogler (1944) reported that warm-season grasses were, in general, more highly relished by steers than cool-season grasses. Tomanek et al. (1958) determined that big bluestem (C_4) (*Andropogon gerardii*) and little bluestem (C_4) (*Schizachyrium scoparium*) had a significant positive preference by grazing cattle wherever they occurred, while preference for western wheatgrass (C_3) (*Agropyron smithii*) varied with site. This indicates that a generalization concerning lower palatability of C_4 species compared to C_3 may not apply to all herbivores.

Table 2. A summary of C_3 and C_4 photosynthetic pathway in the United States. Taxonomic classification follows that of Gould (1968).

Subfamily	Tribe	Number Genera	Number Species	C_3	C_4
Arundinoideae	Arundineae	4	5	*[1]	
	Centotheceae	1	1	*	
	Danthonieae	2	4	*	
Bambusoideae	Bambuseae	3	5	*	
	Phareae	1	1	*	
Eragrostoideae	Aeluropodeae	2	3		*
	Aristideae	1	7		*
	Chlorideae	13	49		*
	Eragrosteae	9	72		*
	Orcuttieae	2	2		*
	Pappophoreae	1	1		*
	Zoysieae	1	3		*
	Unioleae	1	1	*	
Oryzoideae	Oryzeae	7	10	*	
Panicoideae	Andropogoneae	20	73		*
	Paniceae	23	189	*	*
Pooideae	Aveneae	21	51	*	
	Brachyelytreae	1	1	*	
	Diarrheneae	1	1	*	
	Meliceae	3	5	*	
	Monermeae	1	2	*	
	Nardeae	1	1	*	
	Poeae	10	36	*	
	Stipeae	2	12	*	
	Triticeae	7	97	*	
		138	632		

[1]* indicates presence of either C_3 or C_4 photosynthetic pathway.

Significance of the Photosynthetic Pathway for Range

Knowledge of the photosynthetic pathway is an important tool in plant classification and will be useful to plant breeders in developing improved species and varieties of forage (Downton and Tregunna 1968). However, the greatest value of this knowledge in range management will be the better understanding of the reasons for the patterning of range vegetation along environmental gradients, including those produced by man. Better understanding of the structure and function of range ecosystems should lead to wiser management decisions for optimum utilization of the most extensive of our terrestrial ecosystems.

Literature Cited

Akin, D.E., and D. Burdick. 1977. Rumen microbial degradation of starch-containing bundle sheath cells in warm-season grasses. Crop Sci. 17:529-533.

Bender, M.M. 1971. Variations in the $^{13}C/^{12}C$ ratios of plants in relations to the pathway of photosynthetic carbon dioxide fixation. Phytochemistry 10:1239-1244.

Bender, M.M., and D. Smith. 1973. Classification of starch-and fructosan-accumulating grasses as C-3 or C-4 species by carbon isotope analysis. J. Brit. Grassl. Soc. 28:97-100.

Bisalputra, T., W.J.S. Downton, and E.B. Tregunna. 1969. The distribution and ultrastructure of chloroplasts in leaves differing in photosynthetic carbon metabolism. I. Wheat, *Sorghum*, and *Aristida* (Gramineae). Can. J. Bot. 47:15-21.

Bjorkman, O. 1976. Adaptive and genetic aspects of C_4 photosynthesis. p. 287-309. *In:* R.H. Burris, and C.C. Black. (Eds.) CO_2 metabolism and plant productivity. University Park Press, Baltimore, Md.

Bjorkman, O., and E. Gauhl. 1969. Carboxydismutase activity in plants with and without β-Carboxylation photosynthesis. Planta 88:197-203.

Bjorkman, O., B. Mahall, M. Nobs, W. Ward, F. Nicholson, and H. Mooney. 1974. An analysis of the temperature dependence of growth under controlled conditions. p. 757-767. *In:* S.A. McGough, (Ed.). Carnegie Institution of Washington, Yearbook 73. J.D. Lucas Printing Co., Baltimore, Md.

Black, C.C. 1971. Ecological implications of dividing plants into groups with distinct photosynthetic production capacities. p. 87-114. *In:* J.B. Cragg, (Ed.) Advances in Ecological Research. Academic Press, New York, N.Y.

Black, C.C., T.M. Chen, and R.H. Brown. 1969. Biochemical basis for plant competition. Weed Sci. 17:338-344.

Bowes, G., and W.L. Ogren. 1972. Oxygen inhibition and other properties of soybean ribulose 1, 5-diphosphate carboxylase. J. Bio. Chem. 247:2171-2176.

Brown, R.H. 1978. A difference in N use efficiency in C_3 and C_4 plants and its implications in adaptation and evolution. Crop Sci. 18:93-98.

Brown, R.H., and V.E. Gracen. 1972. Distribution of the postillumination CO_2 burst among grasses. Crop Sci. 12:30-33.

Brown, W.V., and B.N. Smith. 1975. The genus *Dichanthelium* Gramineae). Bull. Torrey Bot. Club 102:10-13.

Calvin, M., and J.A. Bassham. 1962. The Photosynthesis of Carbon Compounds. W.A. Benjamin, New York, N.Y. 127 p.

Caswell, H., and F.C. Reed. 1975. Indigestibility of C_4 bundle sheath cells by the grasshopper, *Melanoplus confusus*. Ann. Entomol. Soc. Amer. 68:686-688.

Caswell, H., and F.C. Reed. 1976. Plant-herbivore interactions: the indigestibility of C_4 bundle sheath cells by grasshoppers. Oecologia (BERL) 26:151-156.

Caswell, H., F.C. Reed, S.N. Stephenson, and P. Werner. 1973. Photosynthetic pathways and selective herbivory: a hypothesis. Amer. Natur. 107:-465-480.

Chen, T.M., R.H. Brown, and C.C. Black. 1970. CO_2 compensation concentration, rate of photosynthesis, and carbonic anhydrase activity of plants. Weed Sci. 18:399-403.

Chollet, R. 1976. C_4 control of photorespiration: studies with isolated mesophyll cells and bundle sheath strands. p. 327-341. *In:* R.H. Burris and C.C. Black, (Eds.) CO_2 Metabolism and Plant Productivity. University Park Press, Baltimore, Md.

Cox, L.M. 1977. Asking questions of desert shrubs. Utah Sci. 38:71-74.

Crampton, E.W., and L.E. Harris. 1969. Applied Animal Nutrition. W.H. Freeman and Co. San Francisco, Calif. 753 p.

Crookston, R.K., and D.N. Moss, 1974. Interveinal distance for carbohydrate transport in leaves of C_3 and C_4 grasses. Crop Sci. 14:123-125.

Downes, R.W., and J.D. Hesketh. 1968. Enhanced photosynthesis at low oxygen concentrations: differential response of temperate and tropical grasses. Planta 78:79-84.

Downton, W.J.S. 1970. Preferential C_4 -dicarboxylic acid synthesis, the postillumination CO_2 burst, carboxyl transfer step, and grana configurations in plants with C_4 —photosynthesis. Can. J. Bot. 48:1795-1800.

Downton, W.J.S. 1971. Check list of C_4 species, p. 554-558. *In:* M.D. Hatch, C.B. Osmond, and R.O. Slayter, (Eds.). Photosynthesis and Respiration. Wiley Interscience, New York, N.Y.

Downton, W.J.S. 1975. The occurrence of C_4 photosynthesis among plants. Photosynthetica 9:96-105.

Downton, W.J.S., and E.B. Tregunna. 1968. Carbon dioxide compensation—its relation to photosynthetic carboxylation reactions, systematics of the Gramineae, and leaf anatomy. Can. J. Bot. 46:207-215.

Dvorak, J., and L. Natr. 1971. Carbon dioxide compensation points of *Triticum* and *Aegilops* species. Photosynthetica 5:1-5.

El-Sharkaway, M., and J.D. Hesketh. 1965. Photosynthesis among species in relation to characteristics of leaf anatomy and CO_2 diffusion resistances. Crop Sci. 5:517-521.

Evans, L.T. 1975. Photoperiodism and photosynthetic pathways. Can. J. Bot. 53:590-591.

Gallaher, R.N., D.A. Ashley, and R.H. Brown. 1975. ^{14}C photosynthate translocation in C_3 and C_4 plants as related to leaf anatomy. Crop Sci. 15:55-59.

Gould, F.W. 1968. Grass Systematics. McGraw-Hill Book Co., New York, N.Y. 382 p.

Gould, F.W. 1975. The Grasses of Texas. Texas A&M University Press, College Station, Tex. 653 p.

Gracen, V.E. Jr., J.H. Hilliard, R.H. Brown, and S.H. West. 1972. Peripheral reticulum in chloroplasts of plants differing in CO_2 fixation pathways and photorespiration. Planta 107:189-204.

Hatch, M.D., and C.R. Slack. 1966. Photosynthesis by sugar-cane leaves. A new carboxylation reaction and the pathway of sugar formation. Biochem. J. 101:103-111.

Hatch, M.D., C.R. Slack, and H.S. Johnson. 1967. Further studies on a new pathway of photosynthetic carbon dioxide fixation in sugar-cane and its occurrence in other plant species. Biochem. J. 102:417-422.

Johnson, M.C. Sr. 1964. An electron microscope study of the photosynthetic apparatus in plants with special reference to Gramineae. PhD Thesis, Univ. of Texas, Austin. 264 p.

Kortschalk, H.P., C.E. Hartt, and G.O. Burr. 1965. Carbon dioxide fixation in sugar-cane leaves. Plant Physiol. 40:209-213.

Krenzer, E.G. Jr., and D.N. Moss. 1969. Carbon dioxide compensation in grasses. Crop Sci. 9:619-621.

Krenzer, E.G. Jr., D.N. Moss, and R.K. Crookston. 1975. Carbon dioxide compensation points of flowering plants. Plant Physiol. 56:194-206.

Moss, D.N., E.G. Krenzer, and W.A. Brun. 1969. Carbon dioxide compensation points in related plant species. Science 164:187-189.

Ogren, W.L. 1976. Search for higher plants with modifications of the reductive pentose phosphate pathway of CO_2 assimilation. p. 19-29. *In:* R.H. Burris and C.C. Black, (Eds.) CO_2 Metabolism and Plant Productivity. University Park Press, Baltimore, Md.

Park, R., and S. Epstein. 1960. Carbon isotope fractionation during photosynthesis. Geochim. Cosmochim. Acta. 21:110-126.

Ranson, S.C., and M. Thomas. 1961. Crassulacean acid metabolism. Annu. Rev. Plant Physiol. 11:81-110.

Rogler, G.A. 1944. Relative palatabilities of grasses under cultivation on the Northern Great Plains. J. Amer. Soc. Agron. 36:487-496.

Slack, C.R., P.G. Roughan, and H.C.M. Bassett. 1974. Selective inhibition of mesophyll chloroplast development in some C_4—pathway species by low night temperature. Planta 118:57-73.

Smith, B.N., and S. Epstein. 1971. Two categories of $^{13}C/^{12}C$ ratios for higher plants. Plant Physiol. 47:380-384.

Smith, B.N., and W.V. Brown. 1973. The Kranz syndrome in the Gramineae as indicated by carbon isotopic ratios. Amer. J. Bot. 60:505-513.

Smith, D. 1968. Classification of several native North American grasses as starch or fructosan accumulators in relation to taxonomy. J. Brit. Grassl. Soc. 23:306-309.

Stoddart, L.A., A.D. Smith, and T.W. Box. 1975. Range management. McGraw Hill Book Co., Inc., New York, N.Y. 532 p.

Takeda, T., and M. Fukuyama. 1971. Studies on the photosynthesis of the Gramineae. I. Differences in photosynthesis among subfamilies and their relations with the systematics of the Gramineae (in Japanese, English summary). Crop Sci. Soc. Japan, Proc. 40:12-19.

Ting, I.P. 1971. Non autotrophic CO_2 fixation and crassulacean acid metabolism. p. 169-185. *In:* M.D. Hatch, C.B. Osmond, and R.O. Slayter (Eds.), Photosynthesis and Photorespiration. Wiley Interscience, New York, N.Y.

Ting, I.P., and C.B. Osmond. 1973. Photosynthetic phosphoenol-pyruvate carboxylases, characteristics of alloenzymes from leaves of C_3 and C_4 plants. Plant Physiol. 51:439-447.

Tomanek, G.W., E.P. Martin, and F.W. Albertson. 1958. Grazing preference comparisons of six native grasses in the Mixed Prairie. J. Range Manage. 11:191-193.

Tregunna, E.B., B.N. Smith, J.A. Berry, and W.J.S. Downton. 1970. Some methods for studying the photosynthetic taxonomy of the angiosperms. Can. J. Bot. 48:1209-1214.

Triolo, L., D. Bagnara, L. Anselmi, and C. Bassanelli. 1974. Carbonic anahydrase activity and localization in some plant species. Physiol. Plant. 31:86-89.

Troughton, J.H., K.A. Card, and C.H. Hendy. 1974. Photosynthetic pathways and carbon isotope discrimination by plants. p. 768-780. *In:* S.A. McGough, (Ed.). Carnegie Institution of Washington, Yearbook 73. J.D. Lucas Printing Co., Baltimore, Md.

Whelan, T., W.M. Sackett, and C.R. Benedict. 1973. Enzymatic fractionation of carbon isotopes by phosphoenolpyruvate carboxylase from C_4 plants. Plant Physiol. 51:1051-1054.

White, E.M. 1961. A possible relationship of little bluestem distribution to soils. J. Range Manage. 14:243-247.

Williams, G.J. III. 1974. Photosynthetic adaptation to temperature in C_3 and C_4 grasses. Plant Physiol. 54:709-711.

Williams, J. III., and J.L. Markley. 1973. The photosynthetic pathway type of North American shortgrass prairie species and some ecological implications. Photosynthetica 7:262-270.

Brush Control on Sandy Rangelands in Central Alberta

ARTHUR W. BAILEY AND HOWARD G. ANDERSON

Abstract

Balsam poplar, aspen, and willows that had invaded subirrigated sandy rangeland were treated with (1) prescribed spring burning, (2) the herbicide 2,4-D ester, and (3) prescribed burning followed by 2,4-D ester. After 5 years, burning and spraying had reduced brush the most. Brush reinvasion was occurring rapidly on all treated areas. Stand openings of about one quarter hectare in an 8 meter high poplar forest resulting from these treatments did persist for at least 5 years. Treatments were effective enough to lower the forest cover and in some cases increase forage production. Repeated burning and spraying substantially reduced the density of reinvading woody suckers.

The presence of woody plants on rangeland has long been of concern to the land managers interested in increasing forage production. Woody species encroachment has been attributed to fire control, overgrazing, and farm abandonment (Friesen et al. 1965) although climatic cycles have also been influential (Bailey and Wroe 1974). Forage production could be increased if woody vegetation was reduced. The depressing effect of woody plants on grasses has been demonstrated (Bailey and Wroe 1974; Whysong and Bailey 1975).

Methods of brush control have focused upon mechanical means, prescribed burning and herbicides, or some combination of these. Mechanical removal of aspen forest and replacement by forages has not been always successful in arresting aspen suckering (Pringle et al. 1973). Burning of aspen cover is not always successful because of the discontinuous coverage of fuels and the difficulty in obtaining suitable burning conditions (Perala 1974). A single fire also fails to control aspen suckering (Horton and Hopkins 1966). However under appropriate conditions, and in conjunction with spraying, prescribed burning may be an effective range improvement tool. Foliar applications of herbicides have been used with some success on aspen in western Canada (Bailey 1972; Bowes 1976) indicating the usefulness of continued research in this area.

The experiments reported here were designed to determine the magnitude and duration of the effects of prescribed burning, herbicide treatment, and a combination of the two on species composition, density of woody stems, and herbage production of a mix poplar-willow (*Populus-Salix*) forest which had encroached on subirrigated sandy ranges dominated by a baltic rush-Kentucky bluegrass (*Juncus balticus*[1]-*Poa pratensis*) grassland.

Methods

The study area was located on the eastern shoreline of Beaverhill Lake, approximately 80 km east of Edmonton, Alta. The lake level has receded considerably during the past 60 years exposing new soil. Baltic rush and Kentucky bluegrass colonized the uplands but were invaded by balsam poplar (*Populus balsamifera*), aspen poplar (*P. tremuloides*), and willows (*Salix*) spp.). Average maximum heights in 1976 were 8 m for poplars and 2 m for willows. Grassland openings were dominated by baltic rush and Kentucky bluegrass. The substratum consists of approximately 4 dm of sand overlying a heavy clay subsoil. The water table occurs at approximately 8 dm. The surface configuration of the land is marked by a series of berms and bars with relief differences of less than 1 m. Drainage and sand texture differences are apparent due to the micro-relief.

An experiment was established in 1971 in a 15-year-old stand of aspen and balsam poplar. Understory vegetation included the willows *Salix bebbiana, S. discolor, S. petiolaris, S. serissima,* baltic rush, Kentucky bluegrass and slender wheatgrass (*Agropyron trachycaulum*). The common forbs were wild strawberry (*Fragaria virginiana*) and many flowered aster (*Aster hesperius*). Four treatments were established within each of four replicates: (1) control, (2) burn, (3) spray, and (4) a burn and spray combination. Prescribed burning was conducted on May 18, 1971. About ¼ hectare was burned in each replicate. All spraying was carried out on July 5, 1971. The ester of 2,4-D was applied at 2.2 kg/ha (2 lb/acre) in 1:14 diesel: water ratio at 157 l/ha (14 gal/acre). Within each treatment eight permanent plots were randomly located. Data was collected three times from 128 plots.

Canopy coverage (7-part scale) of each species (Daubenmire 1968) and density of live, injured, and dead woody stems by d.b.h. (diameter breast high 1.4 m above ground) class were recorded in August of 1971, 1972, and 1976. Sizes of quadrats were 0.1 m^2 for canopy cover and 0.84 m^2 for density of woody stems. Herbage production was assessed by clipping vegetation from 0.28 m^2 quadrats in August 1972.

Woody density data were sorted into the following species groups: aspen poplar, balsam poplar, willows. Two size categories were used for each: (1) those less than 1 m high were classed as suckers regardless of origin; and (b) those greater than 1 m were classed as stems. Data were basically examined by analysis of variance. A randomized complete block design facilitated a two-way analysis of variance. Duncan's new multiple range test ($P<0.05$) was used to compare means of canopy coverage, woody density and herbage production.

A preliminary unreplicated experiment was initiated May 11, 1968, by burning a 2-ha area. The burned area was sprayed August 7, 1968, with a mixture of 1.7 kg/ha (1.5 lb/acre) 2,4-D ester and 0.14 kg/ha (2 oz/acre) picloram (Tordon 22 k) in 78 l/ha (7 gal/acre) of water. The area was reburned in May, 1971, accidentally burn-

Authors are professor and research associate, Department of Plant Science, University of Alberta, Edmonton, Alberta.
This research was supported by an Alberta Agricultural Research Trust grant and a National Research Council of Canada grant to the senior author.
Manuscript received July 19, 1977.

[1] Nomenclature follows Moss (1959).

ing the control area as well as the treatment area. The original treatment area was resprayed on July 6, 1971, with 2.2 kg/ha (2 lb/acre) 2,4-D ester in a 1:14 diesel:water mixture at 157 l/ha (14 gal/acre). Data were collected in 1968, 1971, and 1976 using the procedures already described for the main experiment.

Results

Canopy cover of aspen and willows was reduced by the brush control treatments (Table 1). After 5 years, the burning and spraying treatment was most consistent in reducing the cover of woody species. This method did not cause long-term detrimental effects to herbaceous vegetation. Wild strawberry expanded under this treatment. Short-term changes in herbaceous vegetation did occur. Kentucky bluegrass and wild strawberry were reduced by burning 1 year after treatment.

One year after treatment, rush, grass, and forb production was higher on burned areas (1,150 kg/ha) than on control areas (470 kg/ha). There was no change in forage production on other treated areas. The fire consumed about 2,300 kg/ha of litter. Litter production averaged 3,050 kg/ha in unburned areas and 750 kg/ha in burned areas.

The effect of spraying on live stems was not obvious until 1 year after treatment (Table 2). Suckers started to emerge in 1972 but the residual effect of the herbicide was evident for willows. Five years after treatment, only willows had lower stem densities in sprayed areas.

The effect of burning was apparent several months after treatment. Burning alone resulted in a mortality of about 79, 83, and 96% for balsam, aspen, and willow stems, respectively. Suckering occurred soon after the fire. By August 1971, there were about as many balsam, aspen, and willow suckers on the burned areas as there were suckers and stems on the control area. Suckering continued in 1972 for all species. Most balsam suckers grew in 1972 rather than 1971. Fewer aspen and willow suckers established in 1972. Five years after treatment, there were more balsam stems and the same number of aspen and willow stems in burned and control areas.

Burning followed 6 weeks later by spraying was generally the most effective treatment by the end of the 1972 growing season. By 1972, the mortality of live stems was about 96, 88, and 94% for balsam, aspen and willows, respectively. There were fewer balsam and willow suckers in 1972 in burned and sprayed areas than in burned only areas. After 5 years only willows had fewer stems than control areas.

Burning followed by spraying was most effective in causing a shift in distribution of the tree size classes 5 years after treatments (Table 3). All treatments stimulated suckering but a follow-up treatment reduced suckers and small stems.

A preliminary experiment without replication was initiated in 1968. Most woody stems were killed (Fig. 1) but a new forest could develop from the woody sprouts (Fig. 2). Repeated treatments did reduce density of willow stems (Table 4). The mean density of

Table 1. Canopy cover (%) of common species 5 years after brush control treatments.

Treatment	Balsam	Aspen	Willows	Baltic rush	Kentucky bluegrass	Wild strawberry
Control	30a[1]	48a	27a	35b	21a	0.4b
Sprayed	31a	15b	7b	45ab	20a	2ab
Burned	28a	5c	9ab	60a	11a	2ab
Burned and sprayed	18a	10bc	3b	43ab	18a	4a

[1] Means followed by the same letter in vertical sequence within 1 species are not significantly different ($P<0.05$).

Table 2. Density of woody stems and woody suckers (No./10m²) in four treatments the year of treatment (1971), 1 year (1972) and 5 years (1976) afterward.

Year and treatment	Balsam Suckers[1]	Balsam Stems[2]	Aspen Suckers	Aspen Stems	Willows Suckers	Willows Stems	All species Suckers	All species Stems	All species Dead[4]
1971:									
Control	9cd[3]	19b-f	6c	18ab	52cd	46bd	68efg	83cd	20e
Sprayed	11cd	16c-f	12bc	14abc	52cd	34cd	75ef	64de	23e
Burned	26cd	4def	20abc	3d	113b	2e	161bc	9f	62cd
Burned and Sprayed	17cd	3ef	33ab	4cd	135ab	2e	186b	8f	73c
1972:									
Control	14cd	25abc	10b	16ab	64c	66b	88de	110c	73c
Sprayed	33bc	6def	14abc	9bcd	35c-f	17de	81ef	32ef	129ab
Burned	92a	3def	33ab	3cd	159a	25cde	289a	34ef	117b
Burned and sprayed	49b	1f	36a	2d	49cde	4e	134cd	7f	161a
1976:									
Control	2d	20bcd	2c	18ab	9f	113a	12h	157b	36cde
Sprayed	6d	15cf	10bc	18ab	13ef	46bc	24gh	85cd	26de
Burned	3d	39a	13abc	20a	20def	131a	37e-h	198a	22e
Burned and sprayed	5d	34ab	11bc	18ab	18def	35cd	34fgh	89cd	24de

[1] Less than 1 m high, commonly shoots of the current year.
[2] All stems one or more years old greater than 1 m high.
[3] Means followed by the same letter in vertical sequence are not significantly different ($P<0.05$).
[4] Includes stems and suckers.

balsam and aspen stems averaged one-half of the 1968 control. More suckers were continuing to sprout in the treated areas in 1976 than were present in the 1968 control.

Discussion

Brush control treatments used have been effective in temporarily checking the forest advance. Forage production was increased in some areas and it was demonstrated that the forb wild strawberry can expand after treatment with 2,4-D ester as reported by Hilton and Bailey (1974). Burning followed by spraying of woody sucker regrowth with 2,4-D ester showed promise of being an effective means of brush control. However, spraying should not be done just 6 weeks after burning. Not a long enough period of time has passed to permit sprouting of most suckers. Sprouting was observed to continue after the spraying of July 5, 1971, in both 1971 to 1972. Balsam poplar suckers resprouted more slowly than aspen or willow, essentially avoiding the herbicide. Spraying should have been done the second year to kill the sprouts which established in 1971 and 1972.

The reinvasion of balsam and aspen poplar on treated plots was probably greater than under field scale opertions. Both poplar species grew as a clone. Many stems are connected together by the root system. Brush control treatments applied to ¼- to ½-hectare areas can be very effective but they do not last because of rapid lateral reinvasion. Only the willows grew as distinct individuals. The brush control treatment that included herbicide laster longer on willows than on either poplar species.

Minor site differences apparently caused differential tree survival and differential reinvasion of woody suckers. Berms and bars occurred throughout the four blocks. Balsam and aspen poplar were dense on old berms or bars that varied from 2 dm to 1 m in elevation above the surrounding landscape. Soils of berms and bars were droughty because they had nearly pure sand and were deeper to clay. There was very little understory fuel. More trees survived the fire because of the scanty fuels. Most woody suckers sprouted after the herbicide application.

Repeated brush control treatments caused a gradual decline in density of woody stems. However, all brush species studied were alive and reestablishing 5 years after the second treatment.

Grazing ranged from none to light on the study area. The leaves and suckers of aspen and willow are readily eaten by cattle (Hilton and Bailey 1974). Controlled moderate to heavy grazing would probably injure the woody suckers more than the herbaceous

Table 3. Diameter size class distribution of live woody stems (No./10m²) 5 years after treatment.

Treatment	Suckers	Stem diameter class (cm) 1	4	6	9+	Total
Control	12	157	3	2	1	174
Sprayed	24	85	3	1	1	114
Burned	38	198	1	1	1	237
Burned and sprayed	34	89	2	0	0	125

Fig. 1 *A poplar-willow forest burned and sprayed twice and photographed one year after second set of treatments.*

Fig. 2 *Willow and poplar suckers one year after treatment. There is sufficient density to quickly reduce forage production under a new forest canopy.*

Table 4. Density of woody plants (No./10m²) over an 8-year period on control and burned plus sprayed treatment areas.

Species	Size class	Control 1968	Burned + 1968	Sprayed 1976
		n=30	n=30	n=30
Balsam	Suckers	2c[2]	64a	12b
	Live stems[1]	29a	2b	17a
Aspen	Suckers	4c	62a	28ab
	Live stems	37a	1b	20a
Willows	Suckers	10c	294a	162b
	Live stems	141a	1c	23b
All species	Suckers	15c	423a	203b
	Live stems	216a	3c	62b
	Dead stems	0c	193a	7b

[1] Includes all stems at least 1 m high.
[2] Means followed by the same letter in horizontal sequence are not significantly diffeent ($P<0.05$).

understory. This would permit more effective competition by grasses for light, moisture and nutrients. Bailey and Gupta (1973) have demonstrated that grass can effectively compete with brush. Forage production was not high enough on this sandy, impoverished site for the grass to provide much competition to brush (Fig. 1). However, forage competition with brush was likely very important in the studies of Bailey (1972) and Bowes (1975) in reducing brush density and growth rate.

Curtis and Partch (1948) demonstrated that Kentucky bluegrass was reduced more by May burning in Wisconsin than by March or October burning. On our sandy lakeshore, fall burning may be a better time since Kentucky bluegrass is the most desirable forage species.

The experiment has provided preliminary results on the effectiveness and duration of brush control treatments on sandy, subirrigated rangeland. Burning killed most woody stems and stimulated profuse suckering. If burning was followed by a herbicide application, many suckers were killed. For species having sprouts arising from roots, killing of the suckers should result in decreased food reserves in the root system. The effects of fire on aspen regeneration are not conclusive as some studies have shown an increase in stem density (Perala 1974) while others have shown a decrese (Buckman and Blankenship 1965). However, burning is a desirable option because of its low cost and its ability to kill woody stems. Where this is the case it is suggested that most effective results would be achieved by burning at about 4-year intervals. Reburning has a number of problems including the low quantities of fuels in poplar stands and high fuel moisture levels (Perala 1974). However, good burning conditions are needed only once every 4 years, a situation that is realistically attainable.

Literature Cited

Bailey, Arthur W. 1972. Forage and woody sprout establishment on cleared, unbroken land in central Alberta. J. Range Manage. 25: 119-112.

Bailey, Arthur W., and R.K. Gupta. 1973. Grass-woody plant relationships. Can. J. Plant Sci. 53: 671-676.

Bailey, Arthur W., and R.A. Wroe. 1974. Aspen invasion in a portion of the Alberta Parklands. J. Range Manage. 27: 263-266.

Bowes, G.G. 1975. Control of aspen and prickly rose in recently developed pastures in Saskatchewan. J. Range Manage. 28: 227-229.

Bowes, Garry. 1976. Control of aspen poplar, and prickly rose by picloram alone and in mixtures with 2,4-D. J. Range Manage. 29: 148-150.

Buckman, Robert E., and Lytle H. Blankenship. 1965. Repeated spring prescribed burning reduces abundance and vigor of aspen root suckering. J. Forest. 63: 23-25.

Curtis, J.T., and M.L. Partch. 1948. Effect of fire on the competition between blue grass and certain prairie plants. Amer. Midl. Natur. 39: 437-443.

Daubenmire, R. 1968. Plant communities. Harper & Row. New York. 300p.

Friesen, H.A., et al. 1965. Brush control in western Canada. Can. Dep. Agr. Pub. 1240. 26p.

Hilton, J.E., and A.W. Bailey. 1974. Forage production and utilization in a sprayed aspen forst in Alberta. J. Range Manage. 27: 375-380.

Horton, K.W., and E.J. Hopkins. 1966. Influence of fire on aspen suckering. Can. Dep. Forest Pub. 1095. 19p.

Moss, E.H. 1959. Flora of Alberta. Univ. Toronto Press, Toronto. 546p.

Perala, Donald A. 1974. Repeated prescribed burning in aspen. U.S. Dep. Agr. Forest Serv., North Central Forest Res. Sta., Res. Note NC-171. St. Paul, Minn. 4p.

Pringle, W.L., C.R. Elliott, and J.L. Dobb. 1973. Aspen regrowth in pastures of the Peace River region. J. Range Manage. 26: 260-262.

Whysong, Gary L., and Arthur W. Bailey. 1975. Production and nitrogen content of herbage in a silverberry (*Elaeagnus commutata*) community compared to adjacent grassland and forest communities. Can. J. Plant Sci. 55: 801-808.

Influence of Soil, Vegetation, and Grazing Management on Infiltration Rate and Sediment Production of Edwards Plateau Rangeland

W. ALLAN McGINTY, FRED E. SMEINS AND LEO B. MERRILL

Abstract

Terminal infiltration rates for one pasture in a 4-pasture deferred-rotation grazing system and a 27-year exclosure were found to be similar (10.40 and 10.24 cm/hr, respectively). A heavily, continuously grazed pasture exhibited less than one-half the infiltration rate (4.41 cm/hr) of the rotation pasture and exclosure. Grazed pastures were stocked at approximately the same rate (5.0 ha/AU/yr). The continuously grazed pasture also had greater sediment loss (211 kg/ha) than the rotation pasture and exclosure (134 and 160 kg/ha, respectively). Infiltration rate and sediment production were significantly influenced by plant biomass, bulk density, depression storage, and soil depth.

Soil and vegetation influences on infiltration and sediment production of rangeland have been documented (Coleman 1953; Branson et al. 1972). Grazing influences infiltration and erosion primarily through its impact on soil and vegetation. Overgrazing generally decreases infiltration (Rhoades et al. 1964; Rauzi and Hanson 1966; Lusby 1970) and causes an increase in erosion (Dunford 1949; Johnston 1962).

Although effects of different intensities and durations of continuous grazing on infiltration and sediment production have been studied, there is a lack of information on the effects of rotational grazing on the hydrologic condition of rangeland. There have been few infiltration studies of any type in Texas, and no published data exists for the Edwards Plateau relative to the influence of soil or grazing management on infiltration and sediment production. The purpose of this study was to evaluate edaphic variables, vegetation and grazing management as they influence infiltration rate and sediment production of Edwards Plateau rangeland.

Study Area

The study was conducted on the 1,430-ha Texas A&M University Agricultural Research Station, which is located 56 km south of Sonora, Texas, within the Edwards Plateau Land Resource Area (Godfrey et al. 1970). Mean July temperature is 30°C; mean January temperature is 9°C (Hardy et al. 1962). Mean annual rainfall at the Station is 57.2 cm. May and September are the wettest months and average 7.8 and 7.6 cm, respectively (Long 1962).

Authors are, respectively, graduate research assistant and associate professor, Department of Range Science, Texas A&M University, College Station; and professor, Texas A&M University Agricultural Research Station, Sonora.

This report is published with approval of the Director, Texas Agricultural Experiment Station, as TA-14,485.

The authors wish to acknowledge the Office of Water Research and Technology (Project C-6310) for financial support, Dr. W.H. Blackburn for assistance in construction and use of the drip infiltrometer, and personnel of the Sonora Research Station for their field assistance.

Manuscript received June 3, 1978.

Dominant soils are Tarrant stony clays (Lithic Haplustolls) which are grayish brown and 15 to 30 cm deep. They contain large amounts of limestone fragments, stones and gravel, and are underlain by a hard limestone substratum that is usually fractured and porous. These soils occupy level divides and sloping areas adjacent to small streams (Carter et al. 1938). Slopes vary from 0 to 8%. Tarrant silty clays also occur; they are deeper soils and have fewer limestone fragments and stones.

The area is characterized by mid and short grasses with varying densities of woody plants scattered singly or in clumps throughout the grassland. Dominant herbaceous plants include common curlymesquite (*Hilaria belangeri*), threeawn (*Aristida* spp.) and sideoats grama (*Bouteloua curtipendula*). Important woody plants include vasey shin oak (*Quercus pungens* var. *vaseyana*), live oak (*Quercus virginiana*), honey mesquite (*Prosopis glandulosa* var. *glandulosa*), ashe juniper (*Juniperus ashei*), and redberry juniper (*Juniperus pinchoti*) (Smeins et al. 1975).

Methods

Two grazed pastures (each 32 ha) and an ungrazed exclosure (16 ha) were selected for study. One pasture has been heavily stocked (4.6 to 5.4 ha/AU) and continuously grazed (heavy continuous pasture) for the past 27 years with a 60-20-20 AU ratio of cattle, sheep, and goats, respectively. Herbaceous vegetation was dominated by common curlymesquite with lesser amounts of threeawns and red grama (*Bouteloua trifida*). Total standing herbaceous biomass averaged 1,270 kg/ha and litter 1,188 kg/ha in June, 1976. Soil depth varied from 3 to 60 cm and slope ranged from 0 to 4%.

Another pasture, under the Merrill four pasture, three herd, deferred-rotation system (4-pasture system) (Merrill 1954) since 1969, was stocked at 5.2 ha/AU with a 60-20-20 AU ratio of cattle, sheep, and goats, respectively. It was grazed continuously from 1949 to 1969 with cattle and goats at a moderate rate of 16.2 ha/AU. Herbaceous vegetation was dominated by common curlymesquite with lesser amounts of threeawns, sideoats grama, and cane bluestem (*Bothriochloa barbinodes*). Total standing herbaceous biomass averaged 2,200 kg/ha and litter 2,700 kg/ha in June, 1976. Soil depth and slope were similar to the heavy continuous pasture.

The exclosure has been protected from livestock grazing for the past 28 years, but wildlife, primarily white-tailed deer (*Odocoileus virginianus*), had access to the area. Dominant grasses were common curlymesquite, cane bluestem, sideoats grama, and threeawns. Total standing herbaceous biomass averaged 2,000 kg/ha and litter 3,000 kg/ha in July, 1976. Soil depth and slope were similar to those of the other two pastures.

Soil depth was variable within each of the pastures. Thus, sites were selected within each pasture that represented shallow, intermediate, and deep soils. Means and standard deviations of soil depths in these sites were 20±8.9 cm, 31.5±9.3 cm, and 47.3±13.4 cm, respectively. During August, 1975, six soil samples were randomly collected from the upper 5 cm of each site using a 156-cc core. Bulk density, particle density, pore space (Vormocil 1965), soil texture (Day 1956), and aggregate stability (Ashcroft 1954) were analyzed for these samples. Soil organic matter was determined by the Wakley-Black and loss on ignition (24 hr at 430°C) methods (Broadbent 1965; Davies 1974).

Infiltration rate, sediment production, vegetation biomass, and soil moisture were examined on 14 randomly selected, variable-sized plots (Blackburn et al. 1974) within each site in each pasture during the summer of 1976. A meter-square grid, divided into 0.01 m^2 segments, was placed over each plot to determine its area. Areas varied from 0.35 to 0.45 m^2.

Infiltration rates were determined with a mobile drip infiltrometer (Blackburn et al. 1974). An application rate of 15.25 cm/hr was used to insure that infiltration rate was exceeded on all plots. Plots were initially sprinkled to constitute a dry run (soil moisture at antecedent levels). After each dry run the plots were covered with plastic and 24 hr later were resprinkled with soil moisture at field capacity to constitute a wet run. Infiltration rates were measured as the difference between application rate and measured runoff rate. Runoff was pumped from the plots into 19 liter plastic bottles and measured gravimetrically at 5-min intervals. Infiltration runs lasted for 1 hr on all dry runs to insure comparable soil moisture among all plots for the wet runs. Wet runs lasted for 1 hr, or until terminal infiltration rate was reached.

Before each infiltration run a soil sample of the upper 5 cm was taken outside each plot frame and the soil was oven-dried at 105°C for 24 hr for soil moisture determinations.

During each wet and dry infiltration trial, a 900-ml sample of the runoff was taken to determine sediment production. Samples were transported to the laboratory in nalgene containers, filtered through #41 Whatman filter paper, and oven dried at 105°C for 24 hr.

After wet runs a 0.25 m^2 quadrat was placed on each plot, and standing biomass was clipped at ground level and litter collected from the soil surface. Plant material was oven dried at 105°C for 24 hr. A steel probe was driven to bedrock at random locations within each plot to determine an average soil depth. Ocular estimates were made of percentage rock cover (Daubenmire 1959), slope, and micro-depression numbers, size, and depth.

All data were analyzed using the Statistical Analysis System (Barr and Goodnight 1972). All variables were tested for skewness and kurtosis. Soil organic matter values were transformed to square roots and sediment values to logarithms. Stepwise multiple-regressions were used to determine variables associated with terminal infiltration rates and sediment production.

Results

Soil and Vegetation

All soils were sandy clay loams. Particle density means were similar at approximately 2.50 g/cc. Bulk density of soils from the heavy continuous pasture and the 4-pasture system were similar, but the exclosure had lower bulk densities. There was a trend of decreased pore space with increased grazing pressure. Percent organic matter of the two grazed pastures was lower than that of the exclosure; but all soils had relatively high organic matter, and comparable values were obtained with chemical and ashing methods of analysis. Soil aggregates were very stable and all samples rated 1 (Ashcroft 1954). Soil moistures for the grazed pastures were similar, while high values for the exclosures were due to over 25 cm of precipitation just prior to infiltration trials. Three categories of phytomass were approximately twice as great in the 4-pasture system and the exclosure as compared to the heavy continuous pasture (Table 1).

Table 1. Soil and Vegetation variables for the three study pastures.

Variable	Pasture		
	Heavy continous	4-pasture	Exclosure
Bulk density (g/cc)	1.28±.12[1]	1.23±.09	1.16±.07
Pore space (%)	48.6±4.7	50.9±3.5	53.7±2.9
Organic matter (%)	5.32±.65	5.26±1.02	5.76±.41
Soil moisture (dry) (%)	19.7±6.5	18.6±6.9	42.6±5.9
Soil moisture (wet) (%)	31.9±3.8	33.3±3.4	47.4±6.0
Standing phytomass (kg/ha)	1270±508	2257±1235	1907±811
Litter phytomass (kg/ha)	1188±594	2758±1601	3031±2338
Total phytomass (kg/ha)	2458±869	5016±2507	4939±2618

[1] Mean and standard deviation.

Infiltration

Infiltration data are presented for only wet runs (field capacity). Dry run (antecedent moisture) infiltration curves were similar to wet runs; however, terminal infiltration rates were 1 to 4 cm/hr greater for dry runs. Most plots reached terminal infiltration midway through the 1-hr test (Fig. 1). Infiltration was similar for sites in the 4-pasture system and the exclosure while sites in the heavy continuous pasture were always lower than on corresponding sites in other pastures. When infiltration rate was averaged by site, deep sites had the highest values, followed by intermediate and shallow sites (Fig. 2). Infiltration rates averaged by pasture showed the exclosure and 4-pasture system to have almost identical curves and terminal infiltration values, while both had greater than twice the terminal infiltration rate of the heavy continuous pasture (Fig. 3).

Stepwise multiple-regressions were used to determine variables associated with terminal infiltration rates by sites and pastures and combined across all pastures and sites. Variables that were significant in at least one equation included: % soil moisture wet (SMw), kg/ha litter phytomass (LP), kg/ha total standing phytomass (TP), cm soil depth (SD), % rock cover (RC), number of depressions (ND), and g/cc bulk density (BD). Regression equations and results are presented for only wet runs, except in the combined analysis, since similar variables and R^2 values were obtained for equations of both dry and wet runs.

By site, litter phytomass, bulk density, and number of depressions were important variables in the infiltration regression equations (Table 2). On shallow sites with low vegetation production, variation in soil characteristics accounted for a greater proportion of the variation in infiltration, while on deeper soils phytomass exerted more influence over infiltration rate.

By pasture, litter phytomass and bulk density showed the greatest degree of association with infiltration rate in the heavy continuous pasture (R^2=0.37). Number of depressions was the most important variable for wet runs in the 4-pasture system, with total phytomass and rock cover also appearing in the equation (R^2=0.48). Soil depth in the exclosure had the greatest influence on infiltration, followed by litter and number of depressions (R^2=0.52)(Table 2).

Stepwise multiple regressions were used in a combined analysis to determine correlated factors with infiltration across

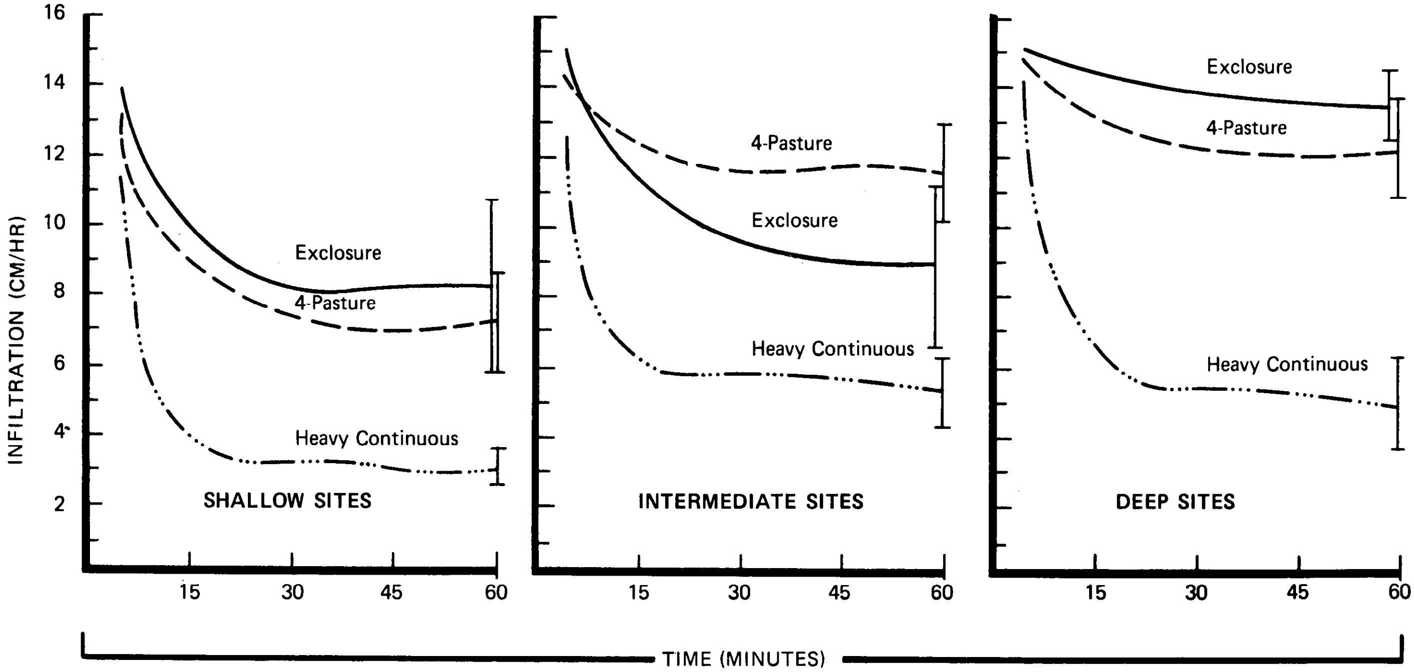


Fig. 1. *Infiltration rates at field capacity soil moisture for three pastures (heavy continuous, 4-pasture system, and exclosure) on shallow, intermediate and deep sites. Vertical lines at the end of each curve represent 95% confidence intervals for mean terminal infiltration rates.*

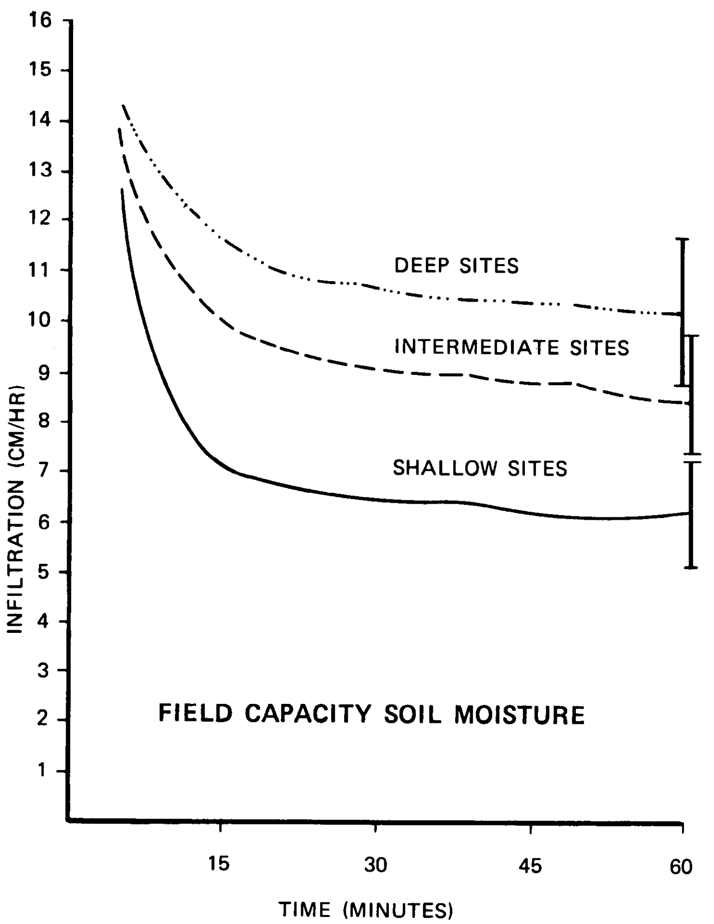


Fig. 2. *Infiltration rates at field capacity soil moisture for shallow, intermediate, and deep sites. Vertical lines at the end of each curve represent 95% confidence intervals for mean terminal infiltration rates.*

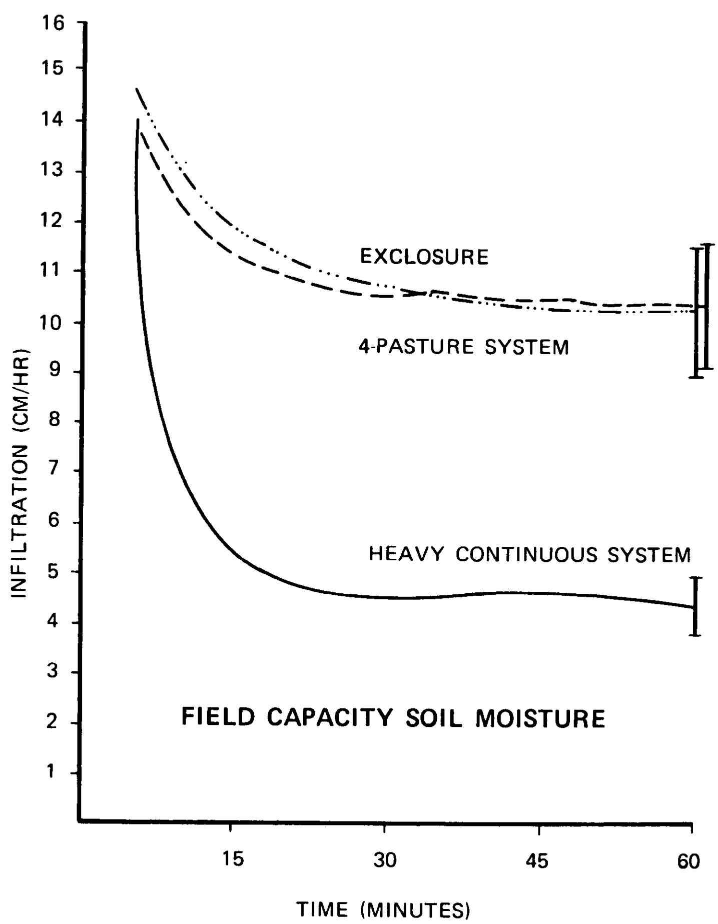


Fig. 3. *Infiltration rates at field capacity soil moisture for three pastures (heavy continuous, 4-pasture system, and exclosure). Vertical lines at the end of each curve represent 95% confidence intervals for mean terminal infiltration rates.*

Table 2. Multiple-regression equations for infiltration rate and sediment production at field capacity soil moisture by site and pasture.

Dependent Variable	Site or pasture	Regression equation[1]	R^2
		Site Equations	
Infiltration	Shallow	IW=38.978−25.723 (BD)−0.403 (RC)+0.0006 (LP)	0.54
Infiltration	Intermediate	IW=59.108+0.001 (LP)+1.084 (ND)−40.188 (BD)− 0.191 (SMw)	0.72
Infiltration	Deep	IW=3.656+0.001 (LP) + 1.726 (ND)	0.60
Sediment	Shallow	SW=2.468−0.00007 (TP)	0.09
Sediment	Intermediate	SW=2.976-0.0001 (TP) − 0.013 (SD)	0.36
Sediment	Deep	SW=3.025−0.019 (SD) − 0.223 (ND)	0.40
		Pasture Equations	
Infiltration	Heavy continuous	IW=16.545+0.0016 (LP) − 10.986 (BD)	0.37
Infiltration	4-pasture	IW=7.643+0.921 (ND) + 0.0004 (TP) − 0.626 (RC)	0.48
Infiltration	Exclosure	IW=2.978+0.078(SD)+0.0006(LP)+1.415(ND)	0.52
Sediment	Heavy continuous	SW=2.448−0.0001 (LP)	0.13
Sediment	4-pasture	SW=2.997−0.026 (SD) − 0.0008 (LP)	0.49
Sediment	Exclosure	SW=4.204−0.025 (SD)−0.029 (SMw)	0.44

[1] Variables corresponding to abbreviations in regression equations for independent variables are defined in the text. All variables in regression equations are significant at the 90% confidence level.

Table 3. Multiple-regression equations for infiltration rate and sediment production combined across pastures and sites at antecedent and field capacity soil moisture.

Dependent variable	Regression equation[1]	R^2
Infiltration (antecedent)	ID=31.842+0.006 (TP)−21.387 (BD)+1.283(ND)	0.58
Infiltration (field capacity)	IW=23.053+0.0001(TP)+1.661(ND)−16.517(BD)	0.62
Sediment (antecedent)	SD=2.833−0.0001(LP)−0.232(ND)−0.101(SD)	0.46
Sediment (field capacity)	SW=2.852−0.012(SD)−0.0007(TP)−0.107(ND)	0.42

[1] Variables corresponding to abbreviations in regression equations for independent variables are defined in the text. All variables in regression equations are significant at the 90% confidence level.

all pastures and sites. The equation accounted for 58% of the variation for dry runs with total phytomass and bulk density as the most important variables. Total phytomass, number of depressions, and bulk density accounted for 62% of the variation in infiltration rate during wet runs (Table 3).

Sediment Production

Sediment production values are described for only the wet runs; similar results were obtained for dry runs. Sediment production for the three pastures was similar for shallow and intermediate sites (Table 4). On deep sites, the exclosure and 4-pasture system were similar, although both produced approximately one-fourth as much sediment as the heavy continuous pasture. The exclosure and 4-pasture system tended to produce less sediment as soil depth increased. High sediment loss from deep sites in the heavy continuous pasture was probably due to low vegetation cover compared to deep sites in the other pastures.

Table 4. Sediment production (kg/ha) at field capacity soil moisture for shallow, intermediate, and deep sites within three pastures (heavy continuous, 4-pasture system and exclosure).

Site	Heavy continuous	4-pasture	Exclosure	Mean
Shallow	236±125[1]	184±191	274±211	231±179
Intermediate	180±135	171±110	147±149	166±130
Deep	219±141	49±65	59±79	109±126
Mean	211±132	134±143	160±177	

[1] Mean and standard deviation.

The heavy continuous pasture had the greatest sediment production followed by the exclosure and the 4-pasture system. Shallow sites had the greatest sediment loss, while deep sites had less than half as much sediment production (Table 4).

Stepwise multiple-regression equations were generated to define variables which related to sediment production within sites (Table 2). Only wet runs are presented except for the combined analysis. The only variable related to sediment production on shallow sites for wet runs was total phytomass (R^2=0.09). On intermediate sites total phytomass and soil depth were important variables (R^2=0.36), while on deep sites soil depth and number of depressions accounted for 40% of the variation.

When stepwise multiple regressions were calculated for each pasture, litter phytomass was the most important variable for the heavy continuous pasture (R^2=0.13)(Table 2). In the 4-pasture system, soil depth was highly associated with sediment production with litter phytomass of less importance (R^2=0.49). In the exclosure soil depth was the most important variable, followed by field capacity soil moisture (R^2=0.44).

In the combined analysis for dry runs, the regression equation accounted for 46% of the variation in sediment production with litter the most important variable, followed by number of depressions and soil depth. For wet runs, soil depth was the most important and total phytomass and depression numbers of lesser importance. These factors accounted for 42% of the variation in wet run sediment production (Table 3).

Discussion

Grazing management affects water intake and sediment production by altering soil and vegetation variables. Rangeland under heavy, continuous grazing had lower infiltration rates and higher sediment loss than rangeland under the 4-pasture deferred-rotation grazing system or the livestock exclosure. Infiltration rate and sediment production differences between pastures were generally related to differences in plant biomass, bulk density, depression storage, and soil depth. Decreased infiltration and increased erosion have been shown to be related to increased grazing intensity, particularly under continuous grazing (Dunford 1949; Johnston 1962; Rauzi and Hanson 1966). The impact of deferred-rotation grazing has not, however, been adequately evaluated.

Prior to establishment of the three study pastures in 1948, they had been subjected to longterm heavy, continuous grazing. At the time of this study, 27 years later, the exclosure and the deferred-rotation pasture had improved greatly in range condition (Smeins et al. 1975; Reardon and Merrill 1976). The two pastures also had similar and favorable hydrologic properties (Fig. 3 and Table 4). Improvement of range condition and hydrologic properties in the 4-pasture system cannot be attributed solely to the deferred-rotation grazing system. From 1948 to 1969 the pasture had been under continuous, moderate grazing and some improvement took place under those conditions. This study has shown that the deferred-rotation system maintained and possibly continued to improve range and hydrologic conditions. This relationship is true even though the stocking rate of the 4-pasture deferred-rotation pasture (5.2 ha/AU) and the heavy, continuous pasture (4.6-5.4 ha/AU) are nearly equal. Thus, it appears that deferred-rotational grazing can contribute to the maintenance, and possibily the improvement, of range condition and hydrologic conditions compared to heavy continuous grazing on Edwards Plateau rangeland.

Literature Cited

Ashcroft, G.L. 1954. Soil additives and their effect on the yield of various crops and the physical properties of an agricultural soil. MS Thesis. Utah State Univ. Logan. 88 p.

Barr, A.J., and J.H. Goodnight. 1972. A Users Guide to the Statistical Analysis System. N. Carolina State Univ. Press. Raleigh. 259 p.

Blackburn, W.H., R.O. Meeuwig, and C.M. Skau. 1974. A mobile infiltrometer for use on rangeland. J. Range Manage. 27:322-323.

Branson, F.A., F.G. Gifford, and J.R. Owen. 1972. Rangeland Hydrology. Soc. for Range Manage. 84 p.

Broadbent, F.E. 1965. Organic matter, p. 1397-1400. *In:* C.A. Black, Ed. Methods of Soil Analysis. Amer. Soc. Agron., Inc., Madison, Wisc. 1,572 p.

Carter, W.T., E.E. Templin, and I.C. Mowerg. 1938. Soil survey report of the Texas Range Station. Unpub. Rep.

Coleman, E.A. 1953. Vegetation and Watershed Management. Ronald Press Co. New York, N.Y. 412 p.

Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Sci. 33:43-64.

Davies, B.E. 1974. Loss-on ignition as an estimate of soil organic matter. Soil Sci. Soc. Amer. Proc. 38:150-151.

Day, P.R. 1956. Report of the committee on physical analysis. Soil Sci. Soc. Amer. Proc. 21:662.

Dunford, E.G. 1949. Relation of grazing to runoff and erosion on bunchgrass ranges. U.S. Forest Serv. Rocky Mt. Forest and Range Exp. Sta. Res. Note 7. 2 p.

Godfrey, C.L., C.R. Carter, and G.S. McKee. 1970. Land resource areas of Texas. Tex. Agr. Ext. Serv., Tex. Agr. Exp. Sta. Bull. 1070. 10 p.

Hardy, W.T., L.B. Merrill, C.W. Livingston, J.W. Menzies, and P.L. Huss. 1962. Agricultural Research in Texas. Tex. Agr. Prog. 8:17-20.

Johnston, A.F. 1962. Effects of grazing intensity and cover on the water-intake rate of fescue grassland. J. Range Manage. 15:79-82.

Long, A.T. 1962. Ground water geology of Edwards County. Tex. Water Develop. Board Bull. 6208. 128 p.

Lusby, G.C. 1970. Hydrologic and biotic effects of grazing vs. nongrazing near Grand Junction, Colorado. J. Range Manage. 23:256-260.

Merrill, L.B. 1954. A variation of deferred rotation grazing for use under Southwest range conditions. J. Range Manage. 7:152-154.

Rauzi, F., and C.L. Hanson. 1966. Water intake and runoff as affected by intensity of grazing. J. Range Manage. 19:351-355.

Reardon, P.O., and L.B. Merrill. 1976. Vegetative response under various grazing management systems in the Edwards Plateau. J. Range Manage. 29:195-198.

Rhoades, E.E., L.F. Locke, H.M. Taylor, and E.H. McIlvain. 1964. Water intake on a sandy range as affected by 20 years of differential cattle stocking rates. J. Range Manage. 17:185-189.

Smeins, F.E., T.W. Taylor, and L.B. Merrill. 1975. Vegetation of a 25-year exclosure on the Edwards Plateau, Texas. J. Range Manage. 29:24-29.

Vormocil, J.A. 1965. Pore space. p. 299-300. *In:* C.A. Black, Ed. Methods of Soil Analysis. Amer. Soc. Agron., Inc., Madison, Wisc. 1,572 p.

Grazing System Identification

JOHN R. LACEY AND H. WALT VAN POOLLEN

Abstract

Grazing system terminology is a problem in the range management field. The proposed dichotomous key standardizes terminology and facilitates communication.

Grazing systems have been clearly defined as the manipulation of animals to accomplish a desired result (Range Term Glossary Committee 1964, and Soil Conservation Society 1976). Unfortunately, "grazing system" terminology has not been consistently defined. The "confusing terminology" (Shiflet and Heady 1971) disrupts communication between rangemen in the field.

The purpose of this paper is to stress the need for standardizing grazing system terminology and to present an approach which can be used to consistently classify grazing systems.

Problems

The problems created by including many range management practices in grazing system terminology are evident when grazing literature is reviewed (Hickey 1969). In the early 1900's, deferred grazing was defined as "grazing after seed maturity" (Jardine and Anderson), but Dyksterhuis (1949) modified the definition to the "practice of taking all the livestock out of one pasture for certain months." However, Shiflet and Heady (1971) concluded that deferred rotation grazing is discontinuing grazing on various parts of a range in succeeding years. Then, the Range Term Glossary Committee (1974) felt they had developed a precise meaning when they wrote "deferred-rotation is any grazing system having a stocking density greater than one and less than two which provides for a systematic rotation of the deferment among pastures."

With the above definitions, it is not surprising that there are inconsistencies among authors. For example, Schmutz's (1973) 3-pasture deferred-rotation alternately rests or "defers" grazing on the pasture during critical growing periods. Each pasture is grazed 4 months of the year. Schmutz's system is patterned after Martin's (1973) 3-pasture system. Both utilize one herd; however, Martin's provides 12 months, instead of 16 months of nonuse. Merrill's (1954) deferred rotation system differs. It utilizes three herds, and each pasture is grazed 12 months, then rested 4 months.

In the early 1900's, the life cycle of forage plants was tied to grazing management (Sampson 1913). These principles were formulated into the rest-rotation grazing system by Hormay and associates (Hormay and Evanko 1958; and Hormay and Talbot 1961). Rest-rotation is a grazing system in which at least one range unit is left ungrazed for 1 year, and then this rest is rotated among units in succeeding years (Range Term Glossary Committee 1964, Soil Conservation Society 1976; and Gifford and Hawkins 1976).

Rest-rotation systems have been extended to areas where they do not apply. Land management agencies are implementing rest-rotation grazing systems in regions with yearlong grazing seasons, although Hormay and associates (Hormay and Evanko 1958; and Hormay and Talbot 1961) designed the system for bunch grass ranges with a 3- to 6-month grazing season. This has created a terminology problem. Depending on locale, rest-rotation grazing may imply growing season or yearlong nonuse.

Both authors are employed as range conservationists by the Bureau of Land Management in Socorro, New Mexico.
Manuscript received March 10, 1978.

Some authors have used the rest-rotation terminology to describe different systems. Gibbens and Fisser (1975) discussed results of a system where some pastures were not used from May through October, but were winter-grazed by sheep. Their system was termed a rest-rotation system; however, it did not include a period of yearlong nonuse. The rest-rotation system described by Edwards (1972) contained yearlong nonuse. It also contained a management technique which separates it from other rest-rotation systems. Rather than systematically rotating rest among pastures, rest was scheduled on the basis of need. Pastures in poor condition received more rest than did the pastures that were in higher condition classes.

Proposed Solution

This paper is not intended to "correct" anyone. Each of the authors cited fully understands his system. However, the above review does illustrate the need for a certain degree of standardization in grazing system terminology. The standardization would minimize misunderstanding and facilitate communication. We feel that a dichotomous key[1] can be used to consistently classify grazing systems. For example, when use and nonuse periods in Schmutz's (1973) deferred-rotation grazing system are analyzed, the 16-month periods of nonuse become evident (Fig. 1).

Thus, according to the key, (Table 1), the system is identified as a rest-rotation grazing system.

[1] This concept came from James K. Lewis, South Dakota State University.

Table 1. Dichotomous key for classifying grazing systems.

1. Grazing a unit[1] for an entire year
    2. No rotation among pastures .... yearlong
    2. One or more pastures rested yearlong
        3. Scheduled, systematic rotation .... rest-rotation
        3. Flexible selection of pasture to rest .... selected-rotation
    2. One or more pastures rested less than yearlong
        3. All pastures grazed once or twice per year
            4. Scheduled grazing
                5. Systematic rotation during growing season . deferred-rotation
                5. Systematic rotation during non-growing season .... rotational-deferment
            4. Flexible rotation without regard to season ... intermittent-rotation
        3. All pastures grazed 3 or more times per year .. short duration-rotation
1. Grazing a unit less than a full year
    2. No rotation among pastures .... continuous-seasonal
    2. One or more pastures rested seasonlong
        3. Scheduled, systematic rotation .... rest-seasonal
        3. Flexible selection on unit to rest .... selected-seasonal
    2. One or more pastures rested less than seasonlong
        3. All pastures grazed once or twice per season
            4. Scheduled grazing
                5. Systematic rotation during growing season .... deferred-seasonal
                5. Systematic rotation during nongrowing season ... rotational-seasonal
            4. Flexible rotation .... intermittent-seasonal
        3. All pastures grazed more than twice per season .... short duration-seasonal

[1] An entire ranch or grazing allotment.

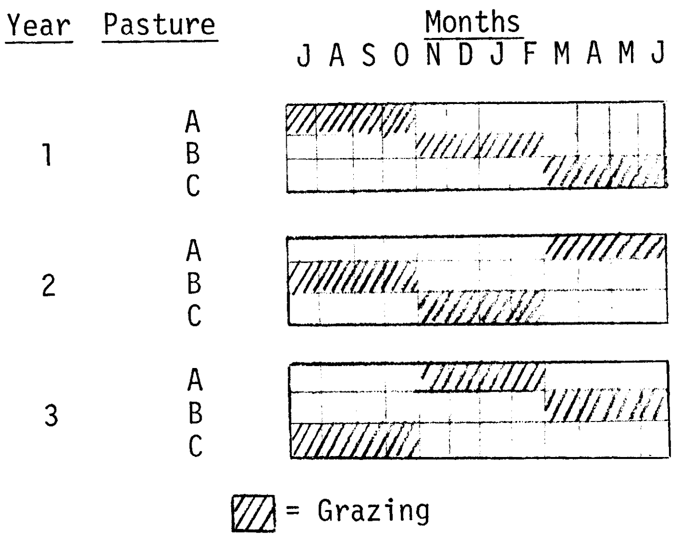


Fig. 1. *Grazing scheme outlined by Schmutz (1973.)*

It is interesting to classify other grazing systems that are described in literature. The "rest-rotation" system described by Gibbens and Fisser (1975) becomes a deferred-rotation. The system described by Edwards (1972) becomes a selected-rotation. The best-pasture system advocated in the Southwest (Herbel and Nelson 1969) is identified as an intermittent-rotation. When Merrill's (1954) "deferred-rotation" system is classified in the key, it remains identified as a deferred-rotation.

A fine distinction seperates deferred-rotation grazing from rotational deferment systems in the key. A grazing system is classified as a deferred rotation if livestock are rotated into a fresh pasture during the major growing season. If livestock are rotated during the nongrowing season, the system is classified as a rotational-deferment.

Conclusion

In summary, dichotomous keys can be used to consistently classify grazing systems. Keys may be designed to apply to large geographical areas, such as the Southwest, or modified to fit the specific needs of an area. Yet, if more keys are developed for localized situations, the confusion will probably be perpetuated. Thus a universal key is needed if the multiplicity of terms and confused terminology are to ultimately disappear. This would be accomplished with the proposed key.

Literature Cited

Dyksterhuis, E.J. 1949. Deferred and rotation grazing. The Cattleman 35: 21, 60.

Edwards, P.J. 1972. A system of veld classification and management planning. Dep. Agr. Tech. Serv. Pretoria, Republic of South Africa. 12 p.

Gibbens, R.P., and H.G. Fisser. 1975. Influence of grazing management systems on vegetation in the Red Desert region of Wyoming. Wyo. Agr. Exp. Sta. Sci. Monog. 29. 23 p.

Gifford, Gerald F., and Richard H. Hawkins. 1976. Grazing systems and watershed management: a look at the record. J. of Soil and Water Conserv. 31 (6):281-283.

Herbel, C.H., and A.B. Nelson. 1969. Grazing management on semidesert ranges in southern New Mexico. Jornada Exp. Range Rep. No. 1, 13 p.

Hickey, Wayne C., Jr. 1969. A discussion of grazing management systems and some pertinent literature, abstracts and excerpts, 1895-1966. U.S. Dep. Agr., Forest Serv. Regional Office, Denver, Colo. 1.1 unnumbered.

Hormay, A.L., and A.B. Evanko. 1958. Rest-rotation grazing—a new management system for bunchgrass ranges. California Forest and Range Exp. Sta. Misc. Pap. 27. 11p.

Hormay, A.L., and M.W. Talbot. 1961. Rest-rotation grazing—a new management system for perennial bunchgrass ranges. U.S. Dep. Agr., Prod. Res. Rep. 51. 43 p.

Jardine, J.T., and M. Anderson. 1919. Range management on the national forest. U.S. Dep. Agr. Bull. 790. 98 p.

Martin, S. Clark. 1973. Responses of semidesert grasses to seasonal rest. J. Range Manage. 26:165-170.

Merrill, L.B. 1954. A variation of deferred-rotation grazing for use under Southwest range conditions. J. Range Manage. 7:152-154.

Range Term Glossary Committee. 1964. A Glossary of Terms Used in Range Management. American Society of Range Management. Portland, Ore. 32 p.

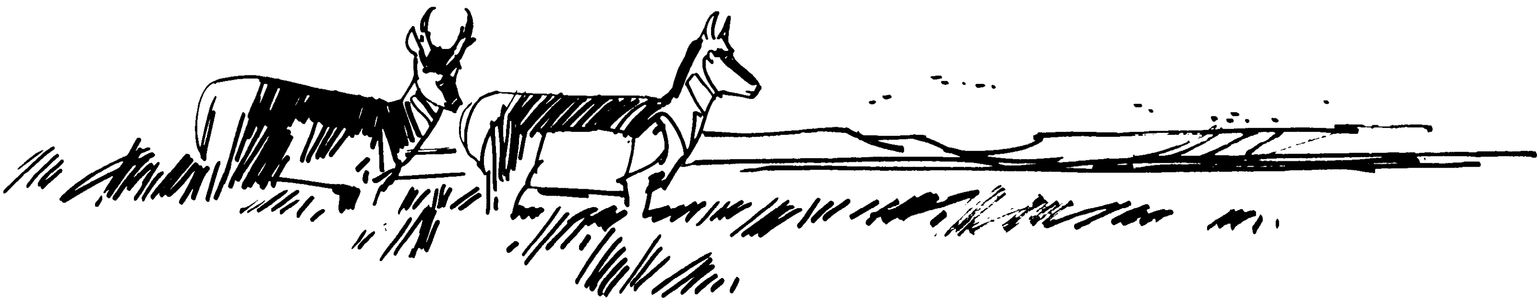
Range Term Glossary Committee. 1974. *A Glossary of Terms Used in Range Management*. Society for Range Management. Denver, Colorado. 36 p.

Sampson, Arthur W. 1913. Range improvement by deferred and rotation grazing. U.S. Dep. Agr., Bull. 34. 16 p.

Schmutz, Ervin M. 1973. A deferred-rotation grazing system for Southwestern ranges. Prog. Agr. Arizona. 25:12-13.

Shiflet, Thomas N., and Harold F. Heady. 1971. Specialized grazing systems: their place in range management. U.S. Dep. Agr., Soil Conserv. Serv. SCS-TP-152. 13p.

Soil Conservation Society. 1976. Resource Conservation Glossary. Soil Conservation Society of America. Ankey, Iowa. 61 p.



Forage Selection by Mule Deer on Winter Range Grazed by Sheep in Spring

MICHAEL A. SMITH, JOHN C. MALECHEK, AND KENNETH O. FULGHAM

Abstract

Late spring grazing by sheep altered the amount of several forage categories available to deer the subsequent autumn and winter. Total herbaceous plant material was much reduced by spring-time sheep grazing, but regrowth following fall precipitation increased the proportion of green herbaceous material available. Current year's growth of bitterbrush was also increased relative to the nongrazed situation due to the release of moisture and nutrients accompanying the removal of herbaceous plants by sheep. Subsequently winter diets of mule deer on the sheep-grazed area were higher in herbaceous components but lower in shrub components than on the adjacent area where sheep had not been previously grazed. Implications of these findings are that quality of deer diets was not detrimentally affected where sheep had grazed during the preceding spring and a much greater animal yield is possible through dual use.

A deficit of winter forage apparently limits mule deer (*Odocoileus hemionus hemionus*) population over much of their range (Aldous 1945; Doman and Rasmussen 1944). This can be viewed in terms of both extent of winter rangeland and quantity of forage (principally shrubs) produced there. The Utah Division of Wildlife Resources estimates that there are approximately 7,424,000 ha of mule deer winter range in Utah, including some 1,149,000 ha dominated by the sagebrush complex, primarily big sagebrush (*Artemisia tridentata*). However, big sagebrush is viewed as only moderate quality winter forage for deer because of its low acceptability (Smith and Hubbard 1954). This is a particular problem where sagebrush exists in stands devoid of more palatable shrub species. Winter deer losses in Utah appear to be inversely related to the amount of palatable browse species available (Robinette et al. 1952).

The grazing of deer winter ranges by domestic livestock is common throughout the Intermountain West. Such ranges are grazed in spring when forage is typically in short supply for the livestock industry. Hence, the generally low state of productivity of these ranges is viewed as a limitation to livestock production (Cook and Harris 1968) as well as to deer production.

Recent research indicates that with properly designed grazing strategies, livestock-big game competition can probably be minimized (Jensen et al. 1972; Jensen et al. 1976). Moreover, these same studies suggest that livestock may be used to manipulate vegetation on deer winter ranges to effectively increase quantities of browse available to wintering deer. However, the specific responses of mule deer to such grazing systems have not been well established. Thus, the study reported in this paper was designed to determine: (1) the plant species present and available to wintering mule deer following spring-time sheep grazing and (2) the relative proportions of the various plant species in the diets of mule deer during the winter following the spring sheep grazing treatment.

Methods

The study was conducted at Hardware Ranch, Cache County, Utah, on an area similar in physiography and vegetation to much of the northern Utah and southern Idaho deer winter range. The area has southerly and southeasterly slopes supporting a mixed shrub-forb-grass plant community codominated by antelope bitterbrush (*Purshia tridentata*) and big sagebrush (*Artemisia tridentata* subsp. *tridentata*). Two additional sagebrush species (*A. tridentata* subsp. *vaseyana*) and low sagebrush (*A. arbuscula*) occur in limited abundance as do snowberry (*Symphoricarpos oreophilus*), Saskatoon serviceberry (*Amelanchier alnifolia*), and Douglas rabbitbrush (*Chrysothamnus viscidiflorus*). Herbaceous species of most importance are bluegrasses (*Poa pratensis* and *P. secunda*), Junegrass (*Koeleria cristata*), beardless bluebunch wheatgrass (*Agropyron inerme*), and the forbs Pacific aster (*Aster chilensis* var. *adscendens*), and mulesear wyethia (*Wyethia amplexicaulis*).

Annual precipitation of the area varies from 46 to 66 cm, with roughly 60% falling as snow. Mid-winter snow accumulations of 40 to 50 cm are not uncommon; but a sustained snow cover is generally not present on the area until late December, and spring thaw bares patches of ground as early as mid-March.

The Hardware Ranch, situated at an elevation of approximately 1,760 m, is generally considered at the upper end of the altitudinal gradient occupied by wintering mule deer in northern Utah. The mid-winter snowpack effectively excludes the area from winter-long occupancy by deer during years of above-average snow fall. However, substantial early winter and late winter grazing use by deer occurs every year. Elk (*Cervus canadensis*) winter on the ranch, but a large-scale hay feeding program generally keeps heavy elk concentrations localized on meadows and peripheral foothills. The ranch had not received livestock grazing for approximately 25 years preceding this study.

Two adjacent 2.4-ha pastures were fenced on an area previously selected for uniformity of topography and vegetative cover. In late May and early June (1974) one pasture (designated sheep-deer) received 150 sheep-days per ha[1] of grazing use over a 20-day period. Previous research on comparable pastures in the vicinity of the study site (Jensen et al. 1976) indicated that this time and intensity of grazing by sheep would achieve approximately 70% mean utilization of the current year's forage crop. *Artemisia* species were not included as part of the available forage for sheep, due to their low acceptability in

Authors were research assistant, associate professor, and research assistant, respectively, Department of Range Science, Utah State University, Logan 84322.

Smith and Fulgham are now, respectively, assistant professor of animal science, Angelo State University, San Angelo, Texas 76901, and assistant professor of animal and range sciences, New Mexico State University, Las Cruces 88003.

This report is Journal Paper No. 2249 of the Utah Agricultural Experiment Station, the supporting institution for this research. Authors also acknowledge the Utah Division of Wildlife Resources (UDWR) for providing the study site, the experimental animals, and logistic support. Charles H. Jensen, game biologist, UDWR, assisted in site selection and study design. Dr. Charles Romesburg and Mr. Kim Marshall, US/IBP Desert Biome Project, were both especially helpful in the data analysis phase of the project.

Manuscript received November 14, 1977.

[1] Forage consumed by the average 57-kg ewe and her 15-kg lamb was considered as one sheep-day of grazing use. Similarly, the quantity consumed by the average 57-kg adult doe was considered as one deer day of grazing use. Fawns (average weight=23 kg) were calculated as 0.4 deer units.

spring. A flock of 20 range ewes and their lambs were obtained on loan from a local rancher and were used for the sheep grazing treatment. The other pasture (designated deer-only) was not grazed by sheep.

The following winter (1974-1975), five deer (two adult does and three fawns, born the previous June) were placed in each pasture for two 6-week periods. The first (early winter period) extended from early November to mid-December, and the second (late winter period) from mid-March to late April. Total cumulative deer grazing use was 100 deer-days per ha, an amount considered typical of northern Utah winter ranges.

The deer used in this experiment were hand reared on goat's milk on a feeding schedule similar to that of Reichert (1972). Frequent handling was emphasized during the fawns' first 2 months of life so that they imprinted on their handlers. Highly tractable animals were essential for making feeding observations in the experimental pastures, and the rearing process employed resulted in such animals. Any of the deer could be touched and handled by observers in the field situation.

Vegetation in the experimental pastures was sampled before and after deer grazing by using an electronically powered inclined point frame. The basic sampling unit, one frame of 20 pins, was observed on permanently located 1.0-m^2 quadrats during each sampling period. Forty-three and 62 randomly located quadrats were sampled in the deer-only and sheep-deer pastures, respectively. Point frame sampling (Warren-Wilson 1963), utilizing an angle of inclination of 32.5° from horizontal, identified species available and provided an index to abundance in both pastures before and after grazing by deer. Abundance is expressed here in terms of the mean number of contacts by the inclined point on each plant species and part (i.e., leaves and stems) as the pin traveled through successive 20-cm segments of the 120-cm vertical distance from the bar of the point frame to the soil surface. The vegetation abundance values reported for a species are means of all plant parts averaged over as many of the successive 20-cm strata as the species occupied or as the mean sum of two plant parts (leaves and stems) in the case of current annual growth (CAG), old, live, or dead parts. "All parts" is not a summation of the individual plant part categories but is a value obtained by averaging across part categories (such as stem, current, alive; stem, old, alive; or leaf, current, dead) applicable to a particular species. Values are not directly comparable between species because each species has a unique combination of plant parts and space occupied. CAG is defined as stems and leaves of grasses, forbs, or shrubs that were produced during a particular year's growing season. Old parts included all leaves and stems that had prevailed for one or more years, and in the case of shrubs, this category included all of the contacts on the plant trunk and smaller branches, except current year's twigs. Dead parts were attached to the parent plant. Litter was defined as all unattached ground cover of plant origin.

Dietary composition sampling consisted of ocular observations on four deer (two adults and two fawns) in each pasture. The fifth deer was maintained in each pasture to achieve the specified level of grazing use and was excluded from dietary observations. Each of the four were observed for one 30-minute period of actual grazing time daily for 4 consecutive days during the middle 4 weeks of the two grazing periods. Each deer was observed at a different time on successive days during a 4-day period. An observer counted the number of mouthfuls of each plant species and part consumed during the 30 minutes of daily grazing, and immediately following the observation, he hand-plucked representative mouthfuls of each species selected during that sampling interval for an estimate of mouthful weight. A mouthful was defined as the amount of forage for a particular species taken into the mouth between acts of swallowing. The slight, but obvious, contraction of throat muscles was the observer's visual cue to swallowing. Size of mouthfuls varied widely among different plant species but appeared to be relatively uniform for a particular species. Observations were conducted simultaneously by a separate observer in each pasture. Plucked samples were oven dried and weighed. The percent contribution of each species to the total mass of plant material consumed during a 30-minute grazing-period was calculated and served as the experimental unit for statistical analysis. Calculations consisted of multiplying the number of mouthfuls of each species consumed during a 30-minute daily sampling period for individual deer times the oven dry weight of the hand-plucked mouthful estimate. This gave the weight of forage of each species consumed during the sampling period. The weight of each species consumed divided by the sum of weights for all species yielded the proportion of the diet belonging to each species consumed during the 30-minute daily sampling period for each of the four deer sampled in each pasture. These procedures are adaptation of the methods of Reppert (1960) and Neff (1974). Neff (1974) discussed at some length the confidence to be placed in hand-plucked samples of deer diet components and the use of hand-reared deer. This method is similar to that described by Free et al. (1971) except that the mouthful is a composite of several bites, the number depending on the individual deer and the plant species. The strong tendency of deer to graze on one plant species at a time facilitated using this adaptation of the bite-count method.

Data were analyzed statistically by analysis of variance, using least squares procedures (Draper and Smith 1966). The components of the fixed model for diets were treatments (sheep-deer and deer-only), winter periods (early and late), and weeks (four within each period). Fixed model components for vegetation analysis were treatments (sheep-deer and deer-only) and time of measurement (before and after deer grazing). The vegetation experimental unit was number of pin hits on a plant part category of a species.

Results

Vegetation

Big sagebrush, bitterbrush, and bluegrasses (the aggregate of *Poa pratensis* and *P. secunda*) were the most abundant plant species growing on the study area (Jensen unpubl. data). Although we attempted to select the two pastures for uniformity of vegetal cover as well as physiographic features, appreciable differences were subsequently found in abundance of several shrub species. Considering that data in Table 1 are treatment means reflecting the combined effects of possible site differences, spring-time sheep grazing, and two winter periods of deer grazing, direct attribution of differences in shrub abundance to specific sources of variation is not uniformly possible. However, several strong inferences are possible. For example, big sagebrush was 77% more abundant in the sheep-deer pasture than in the deer-only pasture, while all bitterbrush was 59%

Table 1. Forage available to deer in two grazing regimes. Tabular values are mean numbers of point contacts per quadrat, averaged over October (before deer grazing) and May (after deer grazing) inventories.

Plant species and parts	Grazing regime: Sheep and deer	Grazing regime: Deer only	Standard error
Big sagebrush			
All parts[1]	0.19a[3]	0.11b[3]	0.01
Bitterbrush			
All parts[1]	0.10a	0.18b	0.01
Current year's parts[2]	0.05	0.05	0.01
Old live parts[2]	0.21a	0.35b	0.03
Bluegrasses			
All parts[1]	0.09a	0.24b	0.03
Live parts[2]	0.12	0.15	0.03
Standing dead parts[2]	0.11a	0.41b	0.04
Litter	9.71	9.32	0.50

[1] Values are quadrat means for each plant part occurring in all strata considered
[2] Values are quadrat means of the sum of leaves and stems in all strata considered.
[3] For a particular plant species or plant part means followed by different letter suffixes are significantly ($P<0.01$) different.

more abundant in the deer-only pasture. Although no specific observations were made on diet selection by sheep during the spring grazing treatment, big sagebrush was not consumed by sheep in a previous study (Iskander 1973) on an adjacent site. Neither did deer consume big sagebrush in the present study. Thus, pretreatment differences between pastures were undoubtedly the major contributor to differences noted for that species. Both sheep and deer consumed bitterbrush, but the remarkably larger quantity of old live parts in the deer-only pasture (Table 1) suggests that pretreatment differences between pastures also played an important role for that species. Spring-time sheep grazing may have had the effect of increasing the proportion of CAG on bitterbrush, however. CAG on bitterbrush was 24% of old live parts in the sheep-deer pastures and only 14% in the deer-only pasture (Table 1). The uniformity of climatic and soil conditions on the two pastures seems to eliminate other possible causes for this difference. This supports earlier findings by Jensen et al. (1972) and Smith and Doell (1968) who suggested that regulated livestock grazing during spring can have favorable effects on subsequent shrub production, primarily through suppression of competition from herbaceous understory plants. The least favorable interpretation is the habitat quality for deer is not diminished by regulated sheep grazing and that a greater proportion of the total plant community can be utilized. Jensen et al. (1976) found that heavy intense sheep grazing as used in this study may favor an increase in shrubs.

The removal of herbaceous plant material by sheep was indicated by the lesser amounts of bluegrasses present in the sheep-deer pasture. All bluegrass material was only 39% as abundant in the sheep-deer pasture as in the deer-only pasture (Table 1). Although live parts were about equally abundant in both pastures, dead leaves and stems were only 28% as abundant in the sheep-deer pasture as in the deer-only pasture. The ratio of live bluegrass parts to dead parts was 106% in the sheep-deer pastures and 37% in the deer-only pasture (Table 1). Grass plants in the sheep-deer pasture were characterized by short, dense tufts of new leaf material in comparison to those in the deer-only pasture that had few, but long and flexuous leaves dispersed through a sward of standing dead herbaceous material approximately 5-20 cm deep.

Temporal changes in plant material that occurred during the two deer-grazing periods (Table 2) were due to consumption and trampling by deer, breakage of snow cover, and beginning of spring growth. Lack of control area, free from deer or other grazing effects, precluded quantification of grazing removal of plant material. However, the disappearance of 75% of bitterbrush CAG during the course of the winter (Table 2) should be largely attributable to deer grazing. Old live bitterbrush parts were 25% less abundant at the end of the winter due to deer use and breakage while grasses were 83% less abundant than prior to deer grazing. The effect of the snowpack in layering herbaceous material is evident in the reduction of bluegrass dead parts from 0.52 to 0.0 contacts per quadrat over the winter period (Table 2).

Table 2. Temporal changes in the forage resource during winter. The interval between measurements included six weeks of early winter deer grazing, 12 weeks of no grazing but heavy snow cover, and six additional weeks of late winter deer grazing. Tabular values are mean numbers of point contacts per quadrat, averaged over both grazing regimes.

Species	Time of measurement: October 1974 (before deer grazing)	May 1975 (after deer grazing)	Standard error
Big sagebrush			
All parts[1]	0.16	0.14	0.01
Bitterbrush			
All parts[1]	0.17a[2]	0.11b[3]	0.01
Current parts[2]	0.08a	0.02b	0.01
Old live parts[2]	0.32	0.24	0.01
Bluegrass			
All parts[1]	0.29a	0.05b	0.02
Live parts[2]	0.18a	0.09b	0.03
Standing dead parts[2]	0.52a	0.00b	0.04
Litter	9.93	9.09	0.50

[1] Values are quadrat means for each plant part occurring in all strata considered.
[2] Values are quadrat means of sum of leaves and stems in all strata considered.
[3] For a particular plant species or plant part, means followed by different letter suffixes are significantly ($P<0.01$) different.

Diets

Treatment Effects

With the notable exception of big sagebrush and Oregon grape (*Mahonia repens*), plant species most common on the study area comprised the largest proportions of mule deer's diets in winter (Table 3). Big sagebrush, highly abundant in

Table 3. Diets (% botanical composition) selected by mule deer during two grazing seasons on a pasture grazed by sheep in spring and on a pasture grazed only by deer.

Species	Early winter: Sheep and deer	Early winter: Deer only	Late winter: Sheep and deer	Late winter: Deer only	Treatment means: Sheep and deer	Treatment means: Deer only
All shrubs	43.1a[1]	52.0b[1]	65.5	65.6	54.3	58.8
All bitterbrush	27.8a	42.0b	49.5	55.5	38.7a[2]	48.8b[2]
Current bitterbrush	27.8	33.1	32.9a[1]	26.7b[1]	30.4	29.9
Old bitterbrush	0.6a	8.9b	16.6a	28.8b	8.3a	18.9b
Oregon grape	9.0	8.0	9.3a	5.4b	9.2a	6.7b
Low sagebrush	2.7	1.1	5.5a	2.2b	4.1a	1.7b
Miscellaneous shrubs	3.5a	0.9b	1.2a	2.5b	2.3	1.7
All herbaceous	56.9a	48.0b	34.4	34.4	45.7	41.2
Green grasses	39.2a	32.4b	26.5	25.0	32.9	28.7
All forbs	17.7	15.6	7.9	9.4	12.8	12.5
Pacific aster	4.8	5.9	0.8	1.2	2.8	3.5
Mulesear wyethia	6.3	4.7	0.4a	4.3b	3.3	4.5
Miscellaneous forbs	6.7	5.2	6.7	3.9	6.7a	4.5b

[1] Within a particular grazing season, treatment means followed by different letter suffixes are significantly ($P<0.10$) different.
[2] Treatment means differing significantly ($P<0.10$) between grazing treatments are noted by different letter suffixes.

both pastures, received no measurable dietary use, whereas the infrequently occurring Oregon grape, not found in any vegetation sample quadrat, was consumed in significant amounts. Smith (1950) found big sagebrush to be only moderately acceptable to deer, yet he maintained that it is an important forage species in the Intermountain region, particularly on ranges where other browse species are absent or have been fully utilized. The lack of use of big sagebrush as food in the present study is probably explained by the relative abundance of other, more palatable forage species. However, dietary selection of plant species having high concentrations of secondary compounds (e.g., terpenes in sagebrush) is a complex and poorly understood process. For example, Smith and Hubbard (1954) observed yearly variation in consumption of big sagebrush by penned deer ranging from complete rejection one year to moderate consumption the next.

We cannot completely discount that our deer were reared under artificial circumstances and were not exposed to a wide array of native plant species prior to the grazing trials. Early experience or food imprinting has been found important in such monogastric species as wild and domesticated rats (Galef and Clark, 1971). Arnold and Maller (1977) recently demonstrated the importance of nutritional experience upon subsequent food selection in adult sheep. Unfortunately, our experimental design did not provide opportunities for evaluating the importance of such relationships in deer.

Bitterbrush and grasses (principally Kentucky and Sandberg bluegrass) were consistently greatest in dietary importance, comprising in aggregate at least 67% of the diets. Other plant species and species categories, including Oregon grape, low sagebrush, miscellaneous shrubs, Pacific aster, mulesear wyethia, and miscellaneous forbs were variably important (Table 3). The relationship of all bitterbrush and low sagebrush consumption between the two grazing regimes was similar to the relationship of amounts available. The deer-only pasture had more bitterbrush and less low sagebrush available than did the sheep-deer pasture.

The major dietary difference between grazing regimes involved the greater quantity of grasses and markedly more herbaceous species consumed by deer during early winter in the sheep-deer pasture than in the deer-only pasture (Table 3) even though equal amounts of bitterbrush CAG were available in both pastures. These differences are probably attributable to the smaller quantity of standing dead grass material in the sheep-deer pasture (Table 1). Heavy spring grazing by sheep had effectively utilized or layered the grass sward that would have otherwise accumulated during the early summer growing season. Thus, the absence of standing dead herbaceous material in the sheep-deer pasture had the important effect of making forbs, low growing shrubs (e.g., Oregon grape), and the new green leaf material resulting from autumn regrowth of the cool-seasonal bluegrasses more accessible to deer in early winter. Arnold (1964) suggested that tall grasses reduced consumption of low growing clover by sheep in Phalaris-annual grass-clover pasture. Other directly pertinent work recently reported by McLean and Willms (1977) showed that fall grazing by cattle removed mature stalks of bluebunch wheatgrass making new grass more accessible to deer in spring. Thus livestock grazing can delay the time when deer must depend on shrubs as the source of forage.

The greater quantity of old (from previous growing seasons) bitter-brush consumed in the deer-only pasture (Table 3) probably reflects the smaller proportion of bitterbrush CAG to old bitterbrush in that pasture (Table 1). The cumulative effect of these dietary differences would appear to be an increase in the nutritive quality of mule deer's diet in the sheep-deer pasture over those in the deer-only pasture. Short et al. (1972) have demonstrated the higher nutritional quality (digestibility, protein content) of current year's twigs as compared to 1-year-old and older twig material. However, preliminary data on the nutritional quality of diets consumed by deer in the two pastures (Fulgham et al. 1977) indicate that the relationships were complex. Dietary crude protein averaged about 2% higher in the deer-only pasture during the early winter period, while digestible energy content and in vitro digestibility of diets were numerically, although not significantly, higher in the sheep-deer pasture.

In the late winter, consumption of herbaceous species was less influenced by previous sheep grazing than by phenological changes. An exception was mulesear wyethia, which did not begin growth while deer were in the pastures during the late winter grazing period. However, appreciable quantities of the forb's large dry leaves had remained on the ground from the previous year's growing season in the deer-only pasture. Deer consumed these dead leaves soon after snow-melt. Both availability and consumption of mulesear wyethia were lower in the sheep-deer pasture during late winter (Table 3) because of prior use of the species by sheep. Consumption of all herbaceous species, in aggregate, did not differ between pastures.

Shrub content of diets in late winter was similar in both pastures but individual species categories were different (Table 3). More old bitterbrush was selected in the deer-only pasture. This difference probably indicates the combined effects of declining availability of bitterbrush CAG due to greater consumption in the early winter and the greater percentage of old bitterbrush there initially (Table 1). Bitterbrush CAG consumption was slightly greater in late winter in the sheep-deer pasture. Oregon grape and low sagebrush were also used to greater extent in the sheep-deer pasture. These dietary differences suggest, as did those for early winter, that dietary quality for mule deer was probably greater in the sheep-deer pasture than that in the deer-only pasture. Preliminary nutritional data (Fulgham et al. 1977) conditionally confirm this hypothesis. Averaged over the late winter period, dietary crude protein, digestible energy, and in vitro digestibility were all slightly higher in the sheep-deer pasture.

Temporal Effects

Reduction in forage availability due to deer use and snow cover, and changes in plant phenology seemed to account for the general trends in plant species present in mule deer diets through the winter. Considering the two treatments as a whole, shrubs were generally more important than other species in late winter primarily because snow cover (about 25 cm and 20 cm during weeks 1 and 2, respectively) limited availability of herbaceous species during the first half of the period (Table 4). Forbs and grasses declined from an average of 53% in early winter to 34% in late winter, while shrub use increased from 48% in early winter to 66% in late winter. During the early winter when snow cover was not a factor, shrubs (principally bitterbrush) in diets increased from about 40% in weeks 1 and 2 to approximately 55% in weeks 3 and 4, while dietary forbs declined from 22% and 27% in weeks 1 and 2, respectively, to 7% in week 4. This shift apparently resulted from a reduction in forb availability due to consumption. Green grasses consistently comprised about one-third of the diet throughout the early winter period (Table 4).

Table 4. Diets (% botanical composition) selected by mule deer during early and late winter grazing periods.

Species	Early winter weeks 1	2	3	4	Late winter weeks 1	2	3	4	Means Early winter	Means Late winter
All shrubs	39.5a[1]	39.4a	57.4b	53.8b	78.2a[1]	69.8b	72.0ab	42.4	47.5a[2]	65.6b[2]
All bitterbrush	30.1	29.7	38.7	41.2	61.5a	59.5a	57.0a	32.1b	34.9a	52.5b
Current bitterbrush	30.1a	29.7a	38.7b	23.4a	38.1a	38.3a	31.9a	10.9b	30.5	29.8
Old bitterbrush	0.0a	0.0a	0.0a	17.8b	23.4	21.2	25.1	21.9	4.4a	22.7b
Oregon grape	7.1	5.6	12.2	9.1	11.0a	8.3a	7.7a	2.3b	8.5	7.4
Low sagebrush	0.0a	1.1a	4.7b	2.0a	0.8a	1.2a	5.5b	7.9b	1.9a	3.9b
Miscellaneous shrubs	2.4	3.0	1.9	1.5	4.8a	0.7b	1.8b	0.0b	2.2	1.8
All herbaceous	60.5a	60.6a	42.6b	46.2b	21.8a	30.2b	27.9ab	57.6c	52.5a	34.4b
Green grasses	38.8	32.9	32.2	39.2	19.9a	24.0a	20.9a	38.1b	35.8a	25.8b
All forbs	21.6a	27.7b	10.3c	7.0c	1.9a	6.2b	7.0b	17.4c	16.7a	8.6b
Pacific aster	10.8a	7.7b	1.4c	1.5c	0.0a	0.0a	0.5a	3.4b	5.3a	1.0b
Mulesear wyethia	4.7a	11.1b	3.5ac	2.5c	1.3a	5.3b	2.2a	0.5a	5.5a	2.3b
Miscellaneous forbs	6.1ab	8.9a	5.4b	3.0b	0.6a	0.9a	4.4b	15.4c	5.8	5.3

[1] Within a particular grazing season, weekly means for a dietary component are significantly ($P<0.05$) different if followed by different letter suffixes.
[2] Seasonal means differing significantly ($P<0.05$) are denoted by different letter suffixes.

In late winter, snow melt was essentially complete by week 3 in the sheep-deer pasture and by week 4 in the deer-only pasture. Corresponding to the departure of the snow cover and the beginning of growth in cool season grasses and forbs, dietary shrubs declined from 78% in week 1 to 42% in week 4, while use of herbaceous species increased from 21% in week 1 to 58% in week 4 (Table 4). Continuation of observations into subsequent weeks would likely have shown even greater selection of green grass and emergent forbs.

Three dietary components, all bitterbrush, old bitterbrush, and all forbs, did not follow the same trends in both pastures, as indicated by significant season × week interactions in the analysis of variance. Bitterbrush consumption in early winter began at much lower levels in the sheep-deer pasture than in the deer-only pasture (Fig. 1a), probably due to the greater accessibility of the apparently preferred grass regrowth in the former. Consumption of old bitterbrush began during week 4 of early winter in the deer-only pasture, while no old bitterbrush was consumed in the sheep-deer pasture until late winter (Fig. 1b). This dietary component remained consistently lower in the sheep-deer pasture throughout late winter, varying from 5% to 35% lower, apparently in response to the greater proportion of bitterbrush CAG to old bitterbrush present where sheep had grazed in spring. The relatively high and similar consumption of all bitterbrush (about 60% of diets) in both pastures during the first 2 weeks of late winter (Fig. 1a) corresponded to a period when snow cover severely limited the availability of all herbaceous species. Animals in both pastures shifted away from bitterbrush and toward herbaceous species, particularly forbs, during the latter weeks of late winter. However, this shift occurred approximately 1 week earlier in the sheep-deer pasture (Fig. 1a). As mentioned above, snow cover persisted approximately 1 week longer in the deer-only pasture than in the sheep-deer pasture. A possible explanation of this difference is that the relatively deep layer of standing dead herbaceous material in the deer-only pasture presented an insulating effect, thus delaying soil warming (Geiger 1965). The major divergence in dietary forb use in the two pastures occurred during week 2 of late winter when animals in the deer-only pasture consumed appreciable quantities (10% of the diet) of the dry leaves of mulesear wyethia (Fig. 1c). This species had been partially consumed by sheep in the other pasture and was unavailable there because of snow cover. In the deer-only pasture, deer use in early winter had not reduced the stature of

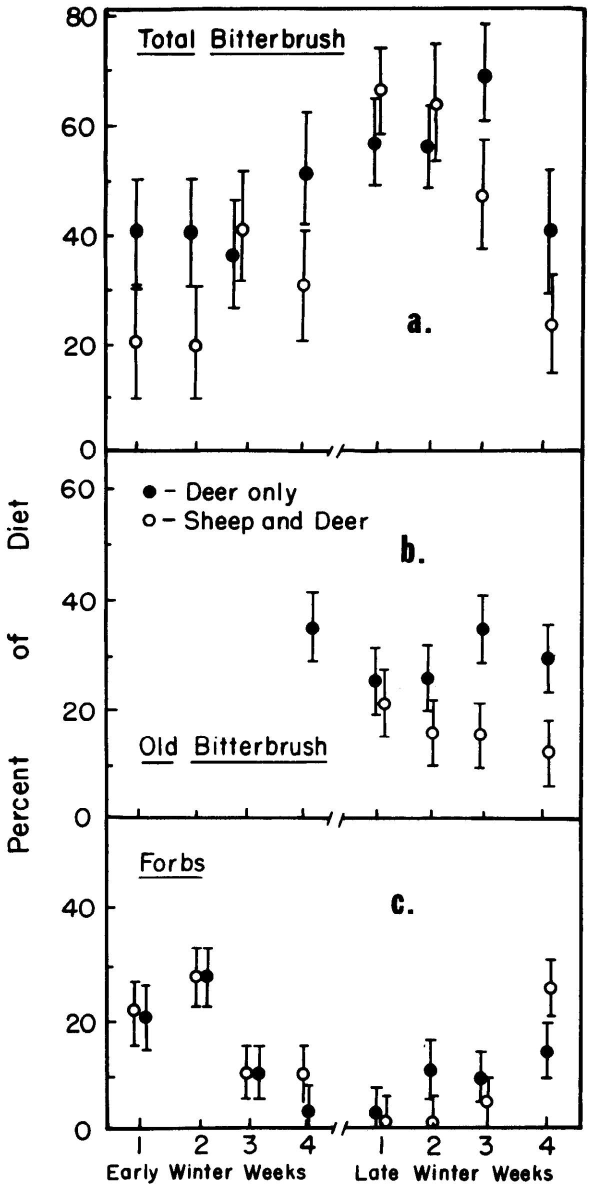


Fig. 1. *Trends of three forage components in diets selected by deer during early and late winter periods. Vertical bars represent 95% confidence intervals.*

the tall plants and they remained partially uncovered and available for consumption. However, by week 4 forb use in the sheep-deer pasture had greatly exceeded that in the deer-only pasture.

Summary and Conclusions

Mule deer grazing in the winter in a pasture grazed by sheep the previous spring selected a diet containing more herbaceous plant material and less shrub material than did deer in a similar pasture not grazed by sheep. Fulgham (1978) in a study concurrent with this found no large differences in overall nutritive quality of forage ingested by deer between the two treatments. These findings indicate that sheep grazing at the time and intensity used in this study will not detrimentally affect mule deer winter ranges in northern Utah. Moreover, the total stocking rate of the sheep-deer pasture (100 deer-da/ha + 150 sheep-da/ha) was more than 2× that of the deer-only pasture (100 deer-da/ha), indicating the potential for increased animal production per unit of land under dual-use grazing. We can offer no firm evidence on the length of time such relationships might persist without marked changes in the plant community structure necessitating changes in the grazing program. This facet is presently being pursued in a related longer-term study (Jensen et al. 1976). However, preliminary information based on 4 years of spring sheep grazing does not suggest major successional changes that would have a direct bearing on food species important to wintering mule deer (Jensen, upubl. data).

Seasonal dietary changes indicated that wintering mule deer will select green grass and some cured forbs as long as they are available in preference to shrubs, although shrubs (primarily bitterbrush) were always the largest single component of diets.

Major dietary components in order of importance by weight were bitterbrush 42%, green grasses 30%, Oregon grape 8%, miscellaneous forbs, 6%, mulesear wyethia 4%, low sagebrush 3%, Pacific aster 3%, and miscellaneous shrubs 2%. Big sagebrush, the co-dominant shrub on the site was totally rejected by deer as a food item probably because of the abundance of other more palatable forages.

Literature Cited

Aldous, C.M. 1945. A winter study of mule deer in Nevada. J. Wildl. Manage. 9:145-151.

Arnold, G.W. 1964. Factors within plant associations affecting the behavior and performance of grazing animals. p. 133-154. *In:* D.J. Crisp, ed. Grazing in Terrestrial and Marine Environments. Blackwell Sci. Publ., London.

Arnold, G.W., and R.A. Maller. 1977. Effects of nutritional experience in early and adult life on the performance and dietary habits of sheep. App. Anim. Ethol. 3:5-26.

Cook, C.W., and L.E. Harris. 1968. Nutritive value of seasonal ranges. Utah Agr. Exp. Sta. Bull. 472. 55 p.

Doman, E.R., and D.I. Rasmussen. 1944. Supplemental feeding of mule deer in northern Utah. J. Wildl. Manage. 8:317-338.

Draper, N.R., and H. Smith. 1966. Applied Regression Analysis. John Wiley and Sons, Inc., New York. 407 p.

Free, J.C., P.L. Sims, and R.M. Hansen. 1971. Methods of estimating dry-weight composition in diets of steers. J. Anim. Sci. 32:1003-1007.

Fulgham, K.O. 1978. Influence of spring sheep grazing on the forage intake and quality of diets consumed by pen-reared mule deer under winter range conditions. PhD Diss., Utah State Univ. Logan. 138 p.

Fulgham, K.O., J.C. Malechek, and M.A. Smith 1977. Forage quality of a deer winter range grazed by sheep in spring. Proc. 30th Annual Meeting, Soc. Range Manage., Portland, Ore. p. 56 (abstract).

Galef, B.G., Jr., and M.M. Clark. 1971. Social factors in poison avoidance and feeding behavior of wild and domesticated rat pups. J. Comp. Physiol. Psychol. 75:341-343.

Geiger, R. 1965. The Climate near the Ground. Harvard Univ. Press, Cambridge, Mass. 611 p.

Iskander, F.D. 1973. Factors affecting feeding habits of sheep grazing foothill ranges of northern Utah. PhD. Diss., Utah State University, Logan. 72 p.

Jensen, C.H., A.D. Smith, and G.W. Scotter. 1972. Guidelines for grazing sheep on rangelands used by big game in winter. J. Range Manage. 25:346-352.

Jensen, C.H., P.J. Urness, and A.D. Smith. 1976. Productivity of big game winter forage can be enhanced by grazing with domestic sheep. Proc. 29th Annual Meeting, Soc. Range Manage., Omaha, Nebraska. p. 17 (abstract).

McLean, A., and W. Willms. 1977. Cattle and deer feeding habits on winter range in southern British Columbia. Proc. 30th Annual Meeting, Soc. Range Manage., Portland Ore. p. 56 (abstract).

Neff, D.J. 1974. Forage preference of trained mule deer on the Beaver Creek watersheds. Arizona Game Fish Dep. Spec. Rep. No. 4. 61 p.

Reichert, D.W. 1972. Rearing and training deer for food habits studies. U.S. Dep. Agr. Forest Serv., Rocky Mountain Forest and Range Exp. Sta. Res. Note RM 208. 7 p.

Reppert, J.N. 1960. Forage preference and grazing habits of cattle at the eastern Colorado range station. J. Range Manage. 13:48-65.

Robinette, W.L., O. Julander, J.S. Gaswiler, and J.G. Smith. 1952. Winter mortality of mule deer in Utah in relation to range condition. J. Wildl. Manage. 16:289-299.

Short, H.L., R.M. Blair, and L. Burkart. 1972. Factors affecting nutritive values. p. 311-318. *In:* C.M. McKell, J.P. Blaisdell, and J.R. Goodin, eds. Wildland Shrubs-Their Biology and Utilization. U.S. Dep. Agr. Forest Serv. Intermountain Forest and Range Exp. Sta. General Tech. Rep. INT-1, 1972.

Smith, A.D. 1950. Sagebrush as winter feed for deer. J. Wildl. Manage. 14:285-289.

Smith, A.D., and D. Doell. 1968. Guides to allocating forage between cattle and big game on big game winter range. Utah State Div. Fish and Game Pub. No. 68-11. 32 p.

Smith, A.D., and R.L. Hubbard. 1954. Preference ratings for winter deer forages from nothern Utah ranges based on browsing time and forage consumed. J. Range Manage. 7:262-265.

Warren-Wilson, J. 1963. Estimation of foliage denseness and foliage angle by inclined point quadrats. Aust. J. Bot. 11:95-105.

The Western Harvester Ants: Their Density and Hill Size in Relation to Herbaceous Productivity and Big Sagebrush Cover

FORREST A. SNEVA

Abstract

Ant colony density decreased but the denuded disc area increased as big sagebrush crown cover increased and as herbaceous productivity decreased.

The western harvester ants (*Pogonomyrmex occidentalis* Cresson and *P. owyheei* Cole) have been of interest since the colonization of the Western range. McCook (1879, 1882 a&b, and 1883) made intensive and extensive studies of the harvester ant as far west as Reno, Nevada. Biological and ecological studies were sporadic through the close of that century and the beginning of this century. Agricultural interest relating to their impact on crop production resulted in studies by Johnson et al. (1938), Costello (1944), Hull and Killough (1951), Gilbert (1960), Sharp and Barr (1960), and Wight and Nichols (1966). Control of these ants was first reported in 1942 by Fritz and Vickers, but widespread control studies were not conducted until the 1950's and those are documented by the works of Knowlton (1966) in Utah, Lavigne and Fisser (1966) in Wyoming, Race (1966) in New Mexico, and Crowell (1963) in Oregon. The association of ants with, and their impact on, grazed ranges has not been totally resolved by the studies reported. Rogers (1972) associated an increase in hill density with pastures heavily grazed but Kirkham and Fisser (1972) were unable to produce this result after 10 years of grazing with various levels of grazing intensity. They did show, however, that soil texture was the most important factor influencing ant distribution. Similarly, while some workers have estimated productive losses due to the denuded disc, Rogers (1972) and Wight and Nichols (1966) reported increased growth on the disc perimeter which partially or wholly compensate for production loss on the disc area.

This note presents information of effects of harvester ant activity that spans a 40-year period. It relates changes in ant hill density and disc area with other measured attributes of their environment.

Study Site

The Squaw Butte Experiment Station lies within the cold, high desert province of eastern Oregon. It is typical of an extensive region that also includes parts of Idaho, Nevada, and California. The study area lies at approximately 1,370 m elevation and receives an average of 30.5 cm of precipitation, annually.

The vegetation-soil complex of some of these sites has been described by Eckert (1957). These data are derived from sites classified by him as the *Stipa thurberiana* phase of *Artemisia tridentata*/*Agropyron spicatum* habitat. Other important grass species are *Sitanion hystrix* (Nutt.) J.G. Smith, *Poa secunda* Presl., and *Koeleria cristata* (L.) Pers. In years of high precipitation and on disturbed areas *Bromus tectorum* L. is abundant. The dominant perennial forb is *Phlox diffusa* Benth.; *Collinsia parviflora* Dougl. ex Lindl. is the most abundant annual species.

Soils of this vegetative type are sandy loams overlying sandy-clay-loams in the B horizon and are part of a gently sloping fan derived from alluvial materials of basaltic and rhyolitic origin. A cemented pan, found at depths of 50.8 to 140 cm, restricts the growth of grass roots but is penetrated by shrubs.

Procedure

In 1962 and 1974, ant colony surveys took place within a fence-enclosed 16.2-ha range pasture that in 1952 had been treated with 2,4-D to control big sagebrush. Data in 1938 were obtained from surveys by Johnson et al. (1938) within a 64.8-ha pasture within 0.8 km of the previously mentioned pasture.

Surveys in 1962 and 1974 consisted of 400 sample points on a 6.1-m grid pattern. At each point the number of ant hills within a circular 37.2m² plot were tallied. Additionally, the longest diameter of the disc (denuded area) and the cross diameter at right angles to that axis at its midpoint for each hill were recorded. The mean of the two diameters was used to compute total disc area per hill and per sample ($A.=0.7854d^2$).

In 1938, all hills within the 64.8-ha pasture were located and tallied. Disc areas of 100 hills were estimated from several measurements per disc (Johnson et al. 1938).

Total herbaceous production by species on the 16.2-ha pasture was taken annually, after grass maturity, in the years 1950 through 1974. Yield was estimated from 60 random plots (4.5m²) harvested at ground level. Sagebrush cover estimates on control plots of an associated study within the 16.2-ha pasture were taken in 1950, 1951, and 1952 (Hyder and Sneva 1956). In 1970, 1972, and 1974 brush cover intercept was read from randomly located 30.5-m lines.

Herbage production and brush cover estimates were not measured by Johnson et al. in 1938. An estimate of herbage production was derived for the 64.8-ha pasture from the 1938 range inventory records on file at this station. An estimate of big sagebrush was developed from 1938 records of three, 6.1-m² permanent charted plots. Ten randomly placed lines per chart were read from which brush cover intercept was estimated.

Results and Discussion

Johnson et al. (1938) classified the ants in his study as *P occidentalis*, but it is now recognized that *P occidentalis* normally does not inhabit eastern Oregon. The species in their study was probably *P. owyheei*, (Cole 1968).

Brush cover data (Table 1) estimated from 1938 permanent-chart records were derived from a rather small sample, but nevertheless were believed to be reliable. Tueller (1962) reinventoried all such permanent plots on the Squaw Butte Station in 1960 and found only a small change in brush cover since 1938. Brush cover in the 16.2-ha pasture in the early 1950's before brush control also averaged 20%, (Hyder and Sneva 1956).

The research is a cooperative investigation of the U.S. Dep. Agr., SEA, Agricultural Research, and the Oregon State Agr. Exp. Sta., Squaw Butte Experiment Station, Burns. Technical Paper 4659 of the Oregon State Agr. Exp. Sta.

The author is range scientist, U.S. Department of Agriculture, Science and Education Administration, Agricultural Research, Burns, Oregon 97720.

Manuscript received January 16, 1978.

Table 1. Summary for ant, herbage, brush, and precipitation statistics.

Parameter	Measure	years 1938	1962	1974
Big sagebrush cover	(%)	20	5	14
Herbaceous yield	(kg/ha)	262	520	346
Sept. – June precipitation	(cm)	29.7	19.1	23.2
Crop-year yield index[1]	(%)	107	65	82
No. Ant hill/ha		32.4	80.1	56.5
Disc area	(m^2/hill)	9.3	0.9	1.5
Disc area	(m^2/ha)	301.3	72.1	84.8
Disc area	(%)	3.0	0.7	0.8
Yield loss (disc area)	(kg/ha)	7.9	3.6	2.7
Herbage available	(kg/hill)	8.1	6.5	6.1
Herbage available[2]	(kg/hill)	7.6	10.0	7.5

[1] Estimated from $y = 1.11 \times - 10.6$ where x is Sept. – June precipitation/long term crop-year median amount (27.9 cm) × 100. Sneva and Hyder (1962)
[2] Adjusted by the crop-year yield index

Brush Control in 1952 effectively killed most all sagebrush present. Plant mortality in 1953 was estimated to be in excess of 95%.

The 1938 herbaceous yield estimate of 262 kg/ha was derived from the 1938 range survey of four, 810-ha pastures on the Squaw Butte Station. The estimate is believed to be a fair approximation of the yield in this smaller but similarly vegetated pasture.

Herbage yield was mainly that of perennial grasses, with bluebunch wheatgrass (*Agropyron spicatum*) the primary contributor to yield. In the years 1962 and 1974 following brush control in 1952, downy bromegrass (*Bromus tectorum*) contributed 28 and 9% of the total yield, respectively. Annual and perennial broad leaf plants seldom exceeded 10% of the total yield weight.

Ant hill density ranged from 32.4 to 80.1 hills per hectare, the greater number per hectare being associated with the least amount of brush cover and the highest herbaceous productivity (Table 1). The amount of disc area around each hill was smallest in 1962 (averaging 0.9 m^2 per hill); and, despite the greater number of colonies per hectare, the total amount of disc area per hectare was the least (72.1 m^2)

The fewer number of hills per hectare but much greater area of the disc denuded in 1938 as compared with that in 1962 and 1974 may be due to location. The 64.8-ha pasture, although less than 0.8 kilometer from the later study area, was further out into the valley area. Situated thusly, the soils may be slightly shallower due to less deposition over the years. A shallower soil depth may cause the colony to expand itself greater in the horizontal plane. Also, in 1938, the area was in the process of recovering from the drought years and the measurements in 1938 may have been a reflection of conditions favorable or unfavorable to the ant in the preceeding years.

Ant hill density declined from 1962 to 1974 and this was associated with about 9% increase in brush cover. As the sagebrush returned, herbaceous production decreased from 755 kg/ha in years 1958-1963 to 346 kg/ha in the years 1971 to 1973. Grazing occurred in this pasture in all years following grass maturity, but the stocking rate was low with utilization guidelines allowing 336 kg/ha of herbage remaining or 50% utilization of the perennial grasses, whichever was the least in all years. It is unlikely that grazing contributed greatly to the increase of brush under those conditions.

Loss of herbaceous production based on the denuded disc area ranged from 1 to 3%. These are similar to percentage losses reported by other investigators. The quantitative yield loss in each of those years was 7.9, 3.6, and 2.7 kg/ha for 1938, 1962, and 1974, respectively. Willard and Crowell (1965) reported the foraging activity of *P. owhyeei* to be greatest within 15.2 m of the mound and that the harvesting activity was directed primarily toward seeds of annual species. Thus, at the densities measured in this study, the associated small loss of production and the assumption that the seeds of annual species are being harvested, the total return from ant control does not, in the author's opinion, justify the expense.

Ants are primarily seed gatherers; thus, an estimate of available herbaceous productivity per mound may not be realistic. Willard and Crowell (1965) concluded that where mound density ranged from 49 to 74 per hectare, the entire area was being foraged by the ant. Densities in the latter study were in this range. It is interesting to note that despite wide fluctuations in mound density and disc area, the quantity of herbaceous material available per hill remained fairly constant. The amounts varied from 6.1 to 8.1 kg/hill; and when herbage production was adjusted for year influence, it averaged 8.4 kg/hill.

Literature Cited

Cole, Arthur C. 1968. Pogonomyrmex Harvester Ants: A Study of the Genus in North America. Univ. of Tennessee Press. Knoxville.

Costello, David F. 1944. Natural revegetation of abandoned plowed land in the Mixed Prairie association of northeastern Colorado. Ecology 25:312-26.

Crowell, H.H. 1963. Control of the Western harvester ants, *Pogonomyrmex occidentalis* with poisoned baits. J. Econ. Entomol. 56:295-98.

Fritz, R.F., and W.A. Vickers. 1942. Damage to highways by the mound-building prairie ant. J. Econ. Entomol. 35: 725-727.

Gilbert, Harold. 1960. Sheridan man conducts survey of ant hills on Wyoming ranges. Wyoming Stockman-Farmer 66:29-63.

Hull, A.C. Jr., and J.R. Killough. 1951. Ants are consuming Big Horn Basin ranges. Western Farm Life, Annu. Livestock Rev. 53:70.

Hyder, D.N., and F.A. Sneva. 1956. Herbage response to sagebrush spraying. J. Range Manage. 9:34-38.

Johnson, et al. 1938. The influence of the harvester ant (*Pogomyrmex occidentalis* Cress), upon range vegetation. Unpubl. Rep. Squaw Butte Oregon Agr. Exp. Sta. 12 p.

Kirkham, D.R., and H.G. Fisser. 1972. Rangeland relations and harvester ants in north-central Wyoming. J. Range Manage. 25:55-60.

Knowlton, George F. 1966. Western harvester ants. A range and farm problem. Utah State Ext. Serv. Entomol. Mimeo Ser. 111, 1 p.

Lavigne, R.J. and H.G. Fisser. 1966. Controlling Western harvester ants. Mountain States Reg. Publ. 3, 4 p.

McCook, Henry C. 1879. Remarks on *Pogonomyrmex occidentalis* p. 22, *In:* Proceedings of Monthly Meetings of the Entomological Section on the Academy of Natural Sciences, Philadelphia. Trans. Amer. Entomol. Soc. 7, XLIV and 340 p.

McCook, H.C. 1882a. The Honey Ants of the Garden of the Gods, and the Occident Ants of the American Plains. Lippincott and Co., Philadelphia. 188 p.

McCook, H.C. 1882b. Ants as beneficial insecticides. Proc. Acad. Natural Sci., Philadelphia. 188:263-71.

McCook, H.C. 1883. The occident ant of dakota. Proc. Acad. Natural Sci., Philadelphia. 188:263-71.

Race, S.R. 1966. Control of Western harvester ants on rangeland. N. Mex. Agr. Exp. Sta. Bull. 502.

Rogers, Lee E. 1972. The ecological effects of the Western harvester ant (*Pogonomyrmex occidentalis*) in the shortgrass plains ecosystem. Unpubl. PhD. Thesis, University of Wyoming, Laramie. 114 p.

Sharp, L.A., and W.F. Barr. 1960. Preliminary investigations of harvester ants on southern Idaho rangelands. J. Range Manage. 13:131-34.

Sneva, Forrest A., and D.N. Hyder. 1962. Forecasting range herbage production in eastern Oregon. Oregon State Univ. Agr. Exp. Sta. Bull. 588. 11 p.

Tueller, Paul T. 1962. Plant succession on two *Artemisia* habitat types in southeastern Oregon. PhD. Thesis, Oregon State Univ., Corvallis.

Willard, J.R., and H.H. Crowell. 1965. Biological activities of the harvester ant. *P. owyheei*, in central Oregon. J. Ex. Entomol. 58:484-489.

Wight, J. Ross, and James T. Nichols. 1966. Effects of harvester ants on production of saltbush community. J. Range Manage. 19:68-71.

Survival of Alfalfa in Five Semiarid Range Seedings

M.D. RUMBAUGH AND M.W. PEDERSEN

Abstract

Selected cultivars and strains of alfalfa were seeded at five locations in Northern Utah during 1953 and 1954. Average annual precipitation ranged from 20 to 36 cm. Observations and detailed plant counts showed a decline in alfalfa stand densities at four of the five sites. The reduction in plant density at two sites was attributed primarily to livestock grazing and to severe damage by rabbits. Moisture stress was an additional factor at two other sites. Plant density has remained high at the fifth location for 23 years.

The value of alfalfa (*Medicago sativa* L. and *M. falcata* L.) as a legume component of tame pastures in humid and subhumid environments is commonly recognized. Attempts have been made to introduce these species into more arid situations to supplement range vegetation for some usages. The legumes have been seeded or interseeded after varying degrees of site preparation. The plantings have been based on the premises that (1) the alfalfa will itself be a major contributor to forage yield and quality, (2) the alfalfa will fix additional atmospheric nitrogen unavailable to the plant community, (3) the fixed nitrogen will result in increased productivity and protein content of the associated grasses, and (4) the increased quality and quantity of forage will increase livestock production per hectare.

The opportunity for increasing the productivity of many grazing areas by seeding is substantial. Thomas and Ronningen (1965) believed that on sites where seeding was feasible it might offer the greatest potential of all possible vectors for bringing about increased productivity. They also recognized that because of technological and economic limitations, only a small part of the range area can be improved by seeding. Interseeding of legumes into existing sods has been a widespread practice in the Aldelaide Hills region of South Australia since about 1930 (Grimmett 1967). Rumbaugh and Thorn (1965) were successful in establishing alfalfa in 9 of 16 such seedings on dryland sites in South Dakota.

Increased short-term forage yields following the introduction of alfalfa on range sites in the subhumid Northern Great Plains have been reported by Lorenz and Rogler (1962), Gomm (1964), and Miles (1969). Hervey (1960) cited lamb gains that were 65% higher during the third year of grazing when alfalfa and crested wheatgrass (*Agropyron desertorum* [Fisch. ex. Link] Schult.) had been seeded into native sod in Wyoming.

Alfalfa is long-lived in some semiarid environments when lightly utilized. Kilcher and Heinrichs (1965) found that the creeping-rooted cultivar, 'Rambler,' survived better than three other strains for 5 years on sites that received 32 and 38 cm precipitation per year during the experiment. These plantings were not subjected to grazing, but were cut twice each year. Pearse (1965) showed a picture of a 2,430-hectare field of alfalfa in a 20-cm rainfall zone of the USSR that had remained productive after 6 years. The method of utilization of the alfalfa was not indicated.

During the early 1950's, the junior author initiated a number of experiements with alfalfa on rangeland sites in northern and central Utah. Five of these have been permitted to progress through successional events for more than 20 years. This paper reports the present condition of the alfalfas included in these five seedings.

Materials and Methods

Site Descriptions and Stand Establishment

Rosebud

A shadscale saltbush (*Atriplex confertifolia* [Torr. & Frem.] S. Wats.-big sagebrush (*Artemisia tridentata* Nutt.) range site located approximately 24 km southwest of Rosebud, Utah, was selected. Elevation is about 1,654 m and soils are of the Xerollic Haplargids–Xerollic Calciorthids Association. Precipitation averages approximately 20 cm per year and is uniformly distributed.

The test area was plowed in August and again in September, 1952, to destroy the existing vegetation and to prepare the seedbed. Crested wheatgrass (*Agropyron cristatum* [L.] Gaertn., *A. desertorum* [Fisch. ex. Link] Schult.) was seeded in October at a rate of 6.7 kg/ha. Alfalfa (*Medicago sativa* L. and *M. falcata* L.) was planted March 23, 1953, with a grass drill equipped with large single discs and drag chains. The legume seeding rate was 2.8 kg/ha in rows spaced 81 cm apart. Each plot was 14.6 m wide and 69.2 m long.

The experimental design was a randomized complete block with four replications and eight legume treatments. The alfalfa cultivars and strains were the following: (1) *M. falcata* L. from Coal Springs, South Dakota, (2) 'Grimm', (3) 'Ladak', (4) 'Nomad', (5) 'Ranger', (6) 'Rhizoma', and (7) 'Sevelra'. The eighth treatment was non-scarified seed of the *M. falcata* strain used as the first treatment.

Grouse Creek

The experimental site was located approximately 2.5 km southwest of the village of Grouse Creek, Utah, in a big sagebrush rangeland area. Average annual precipitation was estimated to be 25 cm. The test site was plowed in August and again in September, 1952, and 6.7 kg/ha crested wheatgrass seed was planted in October. Legume treatments identical to those described for the Rosebud site were planted March 24, 1953, in rows spaced 46 cm apart. Plot size was 14.6 m by 56.4 m. A randomized complete block design with four replications was used. The soils are Xerollic Haplargids and Xerollic Calciorthids. Elevation is 1,600 m.

Snowville

The third experiment was situated about 2 km southeast of Snow-

Authors are research geneticist and research agronomist, U.S. Department of Agriculture, Science and Education Administration/Agricultural Research, Crops Research Laboratory Utah State University, Logan 84322.

This study is a contribution from the U.S. Dep. Agr. SEA/AR, in cooperation with the Utah Agricultural Experiment Station, Logan, Utah. Journal Paper No. 2248.

Manuscript received January 16, 1978.

ville, Utah, on a site that previously had been used for dryland wheat (*Triticum aestivum* L.) production. Alfalfa was seeded at a rate of 2.8 kg/ha on May 20, 1954, in a one replicate planting with plots 12.2 m wide and 76.2 m long on the contour of a slightly sloping field. The legume strains and cultivars seeded were those previously described plus 'Utah Common' alfalfa. Precipitation in the vicinity of the test is 28 cm annually and the elevation is 1,420 m. The soils are similar to those at Rosebud.

Cottonwood Spring

A juniper (*Juniperus osteosperma* [Torr.] Little)-big sagebrush site located approximately 74 km south of Ouray, Utah, on the Hill Creek Extension of the Uintah and Ouray Indian Reservation was cleared, tilled, and seeded with crested wheatgrass in the fall of 1953. Alfalfa was planted April 22 of the following year. The experimental design was a split-plot with alfalfa strains as the whole plot treatments in two replications. A fenced exclosure bisecting the replications in the center of the test area provided the split-plot treatment contrast of grazing versus no grazing.

The whole-plots were 36.6 m by 112.7 m for the last six cultivars listed in the Rosebud site description. The seventh entry at Cottonwood Springs, *M. falcata* from Coal Spring, South Dakota, was seeded in whole plots 6.1 m wide and the same length as plots of the other cultivars. Precipitation was estimated to be about 33 cm and the elevation is 2,285 m. Soils in this area belong to the Typic Argiboralls-Lithic Argiboralls-Typic Haploboralls Association.

Mud Spring

This test was situated in a valley dominated by big sagebrush located approximately 8 km north of Altonah, Utah, at 2,240 m elevation. Precipitation was estimated to average 36 cm per year. Plantings were established in the same way as at Cottonwood Spring with alfalfa seeded on April 16, 1954. Whole-plot size was changed to 32.6 m by 124.9 m for the six cultivars of alfalfa and to 8.2 m by 124.9 m for the *M. falcata* plots. The exclosure constructed in the center of the test area bisected the whole-plots of the two replications.

Grazing Management

Detailed information on management of the test sites is not available. The Rosebud and Grouse Creek locations were used for wintering sheep, but stocking rates are not known. Both locations had high populations of rabbits (*Sylvilagus auduboni* and *Lepus* sp.) during the first 2 or 3 years of the experimental period.

The Snowville test site was used as early spring pasture for cattle. The animals were removed before June each year. The Cottonwood Spring and Mud Spring tests were grazed by sheep, cattle, and horses with some utilization by elk, deer, and rabbits. The exclosure fencing in both experiments has been down at intervals of varying durations since 1954. On May 17, 1956, the junior author noted that the exclosure fence at Cottonwood Springs was in disrepair and that the entire test had been closely grazed. On May 24, 1960, it was observed that herdsmen had been using the exclosure for horse pasture. Rabbits were more of a problem at Mud Spring than at Cottonwood Spring when the plantings were observed in 1956 and 1960.

Data Acquisition

Different procedures were followed to estimate alfalfa stand density and productivity. During the first part of the test period, numbers of alfalfa plants per hectare were estimated by counting all plants in each plot whenever stands were sufficiently thin for this to be accomplished easily. In other cases, plants were counted in 0.914-m square quadrats. The estimates in 1977 were made by counting all plants in each plot and marking them with paint as they were tallied. Productivity was measured by using 0.914-m square quadrats or by using a circular sampling frame with a 1.066-m diameter and an area of 0.892 m^2.

Results and Discussion

The initial stands of crested wheatgrass were excellent in all tests where seeded. Population densities of the alfalfas varied among sites but in each case the numbers were considered adequate for maximum utilization of the available moisture. However, at four of the five locations, alfalfa populations, and consequently alfalfa forage production, declined rapidly.

The Rosebud experiment was in the lowest precipitation zone of the five tests. Despite this, seed germination was sufficient to provide the equivalent of 39,506 alfalfa plants per hectare in the growing season of 1953. Seedling mortality was high and by the end of the 1954 season, there were fewer than 7,000 plants per hectare. The planting continued to deteriorate; and during the spring of 1956, the alfalfa stand density was estimated to be 25 plants per hectare. Differences among the treatments were inconsequential. All alfalfa plants observed were small and were believed to have resulted from hard seeds which had germinated after the year of sowing. At no time did the legumes materially contribute to forage yield as the plants were killed by rabbits and moisture stress before they developed much beyond the seedling stage.

On May 6, 1960, only one alfalfa plant could be found and the vegetation had apparently stabilized with crested wheatgrass, shadscale saltbush, and halogeton (*Halogeton glomeratus* [M. Bieb.] C.A. Mey.) as dominant species. When searched in 1965 and again in 1977, no alfalfa plants were found at this location.

The experiment at Grouse Creek was observed on June 29, 1953, 3 months after tha alfalfa had been seeded. A fair stand was noted to be confined to the tractor tracks. It was possible that much of the seed was improperly covered at this site. The seedlings which were present were equivalent to 33,281 plants per hectare (Table 1). The plots of Ladak contained appreciably more seedlings than those of the other cultivars. Scarification of the *M. falcata* L. seeds almost doubled the stand of that strain. Rabbit damage was severe throughout the test.

Table 1. Numbers of alfalfa plants per hectare for several cultivars seeded at Grouse Creek, Utah, in 1953.

Cultivar or strain	Date				
	7-9-53	5-20-54	6-21-57	5-6-60	8-26-65 and 5-18-77
M. falcata (seed scarified)	33,580	9,111	1,494	12	0
M. falcata (seed not scarified)	19,185	8,395	2,580	37	0
Grimm	36,049	6,494	1,543	0	0
Ladak	60,000	10,074	2,731	12	0
Nomad	19,185	7,432	2,543	62	0
Ranger	12,000	8,395	1,877	0	0
Rhizoma	38,346	6,494	1,370	25	0
Sevelra	47,901	9,111	2,259	0	0
Mean	33,281	8,188	2,049	19	0

When examined on May 6, 1960, only 12 alfalfa plants could be found in the entire experiment. These were small, but were not seedlings. Sagebrush and crested wheatgrass provided most of the forage on the site with some halogeton present. When next viewed in August, 1965, and again in May, 1977, no alfalfa plants were seen.

Annual precipitation and available moisture at the Grouse Creek experimental site may approach the minimum level at which alfalfa can survive as a component of range vegetation. The decline in stand was quite rapid but mature plants did exist in appreciable numbers for 3 to 4 years (Table 1). The initial stand could probably have been improved by increasing the compaction of the soil above the seeds after sowing. Rabbit damage was severe throughout the early years of the test and undoubtedly contributed greatly to the stand loss observed in the

1953 to 1954 interval. Seeding of legumes on larger areas would reduce rodent damage and subsequent stand decline.

The experiment at Snowville was the most successful of the five described when judged by maintenance of the legume populations. Exact numbers of plants in the plots were not determined until 1977, but on May 12, 1959, the descriptions recorded varied from "poorest stand" and "stand thin but O.K." for the *M. falcata* entry to "good" for five of the eight alfalfas. Similar comments were noted in 1960, 1961, and 1966. Exact numbers of plants were obtained in July, 1977, and the equivalent density per hectare is shown in Table 2 for each treatment. These ranged from a low of 16,187 for Utah Common to 38,096 for Nomad. Phenotypically, the plants of Utah Common could not be distinguished from those of Ranger and the two populations had similar stands. The *M. falcata* entry which originally had the poorest stand rating contained more plants than any other entry except Nomad in 1977.

Alfalfa forage yields were estimated in 3 years (Table 2). Yields were high for this environment in 1956, averaging 3.90 metric tons of oven-dry forage per hectare. Precipitation at the nearest recording station 1.6 km from the plot area for the 12 months immediately prior to harvest totaled 32 cm and provided sufficient moisture to sustain an exceptional level of productivity. However, on June 3, 1960, there was insufficient growth to permit harvesting hay samples. Average yield was 0.74 and 0.46 metric tons/ha in 1961 and 1977, respectively. The most recent yield estimate was compared to that of an adjacent down-slope planting of crested wheatgrass seeded at the same time as the alfalfa. The grass produced 0.38 tons of forage per hectare or only 83% as much as the alfalfa.

Table 2. Oven-dry forage yields and numbers of alfalfa plants per hectare in a test seeded at Snowville, Utah, in 1954.

Treatment	Plants[1] per hectare (7-6-77)	Forage yield (ton/ha) 6-7-56	7-26-61	7-6-77
M. falcata	32,579	–	0.76	0.47
Grimm	17,155	3.90	0.49	0.45
Ladak	26,717	3.83	0.76	0.48
Nomad	38,096	3.41	0.78	0.40
Ranger	20,306	4.01	0.83	0.56
Rhizoma	30,019	3.59	0.56	0.34
Sevelra	26,254	4.06	0.92	0.53
Utah Common	16,187	3.99	–	0.43
Crested wheatgrass	–	–	–	0.38
Mean	25,914	3.90	0.74	0.46[2]
L.S.D. (0.05)	–	–	–	N.S.

[1] Plants one year old or older
[2] Alfalfa alone

The differences in productivity among the legume strains listed in Table 2 were not statistically significant ($P>.05$). Sevelra and Ranger were slightly superior to the other five entries. Nomad, the cultivar with the most plants per hectare, yielded next to least of the eight legumes. Three scientists who examined the plots 1 week before harvest had also visually ranked Nomad as the poorest of the eight. Plants of Nomad were markedly smaller and shorter than those of Sevelra in the adjoining up-slope plot and of Ranger on the adjoining down-slope plot.

The Snowville site was infested with Russian Thistle (*Salsola kali* L. var. *tenuifolia* Tausch). Forage yield of this species was determined from two samples per plot obtained the same day the alfalfa was cut in 1977. Average dry weight per hectare was computed to be 422 kg with no significant differences among the alfalfa populations.

The Cottonwood Spring and Mud Spring sites and plantings in eastern Utah were quite similar. The earliest notes now available were recorded on May 17, 1956, 2 years after planting. At that time, both sites had been closely grazed both inside and outside the exclosures by livestock and rabbits. Stands of alfalfa and crested wheatgrass at Cottonwood Spring were described as "satisfactory." Exact stand evaluations were not attempted at that time, but Grimm and Ranger were judged to be slightly inferior to the other cultivars. At Mud Spring, there was a "fairly good stand of all varieties" and Nomad and Rhizoma were showing a tendency to spread vegetatively. The ground cover was estimated to be 85% grass and 15% alfalfa.

In the spring of 1960, stands of Grimm and Ranger were still rated as inferior at Cottonwood Spring and stand density as well as forage composition at Mud Spring was about the same as in 1956. At the latter site, Grimm and Ranger plants were also throught to be less plentiful than those of the other entries.

All alfalfa plants surviving in the Cottonwood Spring and Mud Spring experiments were counted in mid-July, 1977. Averages of 176 plants per hectare within and 31 plants per hectare outside the exclosure were found at Cottonwood Spring. Numbers ranged from 230 plants per hectare for Nomad and Sevelra within the exclosure to 16 for Sevelra outside the exclosure. Although some of the experimental contrasts were statistically significant, the low population densities of the legumes indicate that they contributed very little to forage production on this range site in 1977. Those plants that were observed were small and only 10 were found to be sufficiently developed to permit flowering. Many of the alfalfa plants were intimately associated with sagebrush plants which provided protection from grazing. Only 30 alfalfa plants survived to 1977 in the Mud Spring experiment. Eighteen were within and twelve outside the exclosure. Several cottontail and jack rabbits were started from the test area both within and outside the exclosure. The comparative quantities of grass indicated that the exclosure had effectively excluded livestock during the 1977 growing season.

The only successful experiment, when evaluated in terms of alfalfa population density, was the one at Snowville. Although the Grouse Creek and Rosebud locations did not receive sufficient precipitation to sustain high forage yield levels, some alfalfa plants should have survived. We believe that the elimination of plants was due to close grazing by rabbits. Certainly the Cottonwood Spring and Mud Spring sites receive sufficient moisture to support more plants than were counted in 1977. The higher elevations of these two tests should have caused more efficient utilization of the precipitation than in other experiments. When compared to the Snowville planting, the major factors noted throughout the years which could have caused the differences in population density were livestock grazing and intensity of rabbit damage. A slight amount of foraging which appeared to have been done by rabbits was observed at Snowville during the summer of 1977, although no animals were seen. Several rabbits and some damage by them were noted the same year at Cottonwood Spring and Mud Spring. These latter two experiments were surrounded by thousands of hectares of brush rangeland which provided habitat for rodent populations. The Snowville test, however, had wheat and tame hay and pasture lands around it. The neartest native rangeland was approximately 1.6 km distant. This minimized the impact of rabbits on that planting.

Conclusions

The plant counts and forage yields in the Snowville experiment demonstrated that alfalfa can survive and remain productive when grazed for 23 years in a semiarid environment. At the end of that time period, the alfalfa yielded 121% as much oven-dry forage as crested wheatgrass in a adjacent planting.

Rabbits can cause rapid reductions in alfalfa stands even when the plantings receive 30 cm precipitation per year. This may not be as much of a problem in larger scale seedings as it was in the small tests considered in this report. Moisture stress may prohibit utilization of either *Medicago falcata* L. or *M. sativa* L. as range or permanent pasture species in localities with less than 28 cm annual precipitation.

Literature Cited

Gomm, F.B. 1964. A comparison of two sweetclover strains and Ladak alfalfa alone and in mixture with crested wheatgrass for range and dryland seeding. J. Range Manage. 17:19-22.

Grimmett, S.G. 1967. Rules for successful sod-seeding. Agr. Gaz. 78:7-13.

Hervey, D.F. 1960. Improving Great Plains rangelands by interseeding. Proc. 8th Int. Grassl. Congr. p. 216-220.

Kilcher, M.R., and D.H. Heinrichs. 1965. Persistence of alfalfas in mixture with grasses in a semiarid region. Can. J. Plant Sci. 46:163-167.

Lorenz, Russell J., and George A. Rogler. 1962. A comparison of methods of renovating old stands of crested wheatgrass. J. Range Manage. 15:215-219.

Miles, Arthur D. 1969. Alfalfa as a range legume. J. Range Manage. 22:205-207.

Pearse, C. Kenneth. 1965. Range study tour in the Soviet Union. J. Range Manage. 18:305-310.

Rumbaugh, M.D., and T. Thorn. 1965. Initial stands of interseeded alfalfa. J. Range Manage. 18:258-261.

Thomas, Gerald W., and Thomas S. Ronningen. 1965. Rangelands-our billion acre resource. Agr. Sci. Rev. 3:10-17.

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 18, 1978.
3. *Frequency of Issue:* Bimonthly
4. *Location of Office of Publication:* 2760 West Fifth Ave., Denver, Colo. 80204
5. *Location of General Business Office:* Same
6. *Names and Address of:*
   Publisher: Society for Range Management, 2760 West Fifth Ave., Denver, Colo. 80204
   Editor: Rex D. Pieper, Dept. of Animal and Range Sciences, New Mexico State Univ., Las Cruces, N. Mex. 88001
   Managing Editor: David A. Smith, 2760 West Fifth Ave., Denver, Colo. 80204
7. *Owner:* Society for Range Management, 2760 West Fifth Ave., Denver, Colo. 80204
8. *Known Bondholders, Mortgagees, etc.;* None
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*	6,907	6,665
B. *Paid Circulation*		
1. Dealers, counter sales	0	0
2. Mail subscriptions	6,374	6,321
C. *Total paid circulation*	6,374	6,321
D. *Free distribution*	35	35
E. *Total distribution*	6,409	6,356
F. *Copies not distributed*	498	309
G. *Total*	6,907	6,665

I certify that the statements made by me above are correct and complete.
—*David A. Smith,* Managing Editor.

Dry Matter Accumulation of Four Warm Season Grasses in the Nebraska Sandhills

WILLIAM L. GILBERT, L.J. PERRY, JR., AND J. STUBBENDIECK

Abstract

Grass development and seasonal growth patterns are used in making range management decisions. Plant development and dry matter accumulation of four warm-season grasses were studied in the Nebraska Sandhills. Development of the grasses were slowed during 1974 due to low precipitation. Plant, leaf blade, and stem dry matter accumulation per shoot increased with successive harvests and were considerably greater both years for the tall grasses, sand bluestem [*Andropogon hallii* Hack.] and switchgrass [*Panicum virgatum* L.], than for the mid-grasses, little bluestem [*Schizachyrium scoparium* (Michx.) Nash.] and sand lovegrass [*Eragrostis trichodes* (Nutt.) Wood]. Leaf blade to stem ratios decreased with successive harvests for all grasses. Dry matter accumulation of the tall grasses was affected more by the low rainfall in 1974 than that of the mid-grasses. At the last harvest, decrease in stem dry matter accumulation was considerably greater than the decrease in leaf blade dry matter accumulation in 1974 as compared to 1973.

Knowledge of development and seasonal growth patterns of grasses is used in making management decisions for proper range use. Development of plants can be altered by many climatic and management factors.

Time and height of growing point elevation of grasses is important in determining the reaction of shoots to herbage removal. The growing point remains below the soil surface during early vegetative growth and is elevated later in the growing season with internode elongation. If the growing point is removed after elevation, normal shoot development is arrested, and any further growth can only come from axillary buds at the shoot base (Cook and Stoddart 1953; Rechenthin 1956; Booysen et al. 1963; Hyder 1972).

Dry matter accumulation in grasses results from the interaction of the genetic constitution of the plant and environmental factors. Available soil moisture is probably the most important environmental factor influencing growth and development of grasses. High correlations have been found between available soil moisture and forage production (Cable 1971; Shiflet and Dietz 1974). Temperature affects precipitation effectiveness, as higher temperatures are associated with greater evapotranspiration losses.

Dry matter accumulation of a plant, when plotted, is generally represented by a sigmoid curve. The sigmoid curve can be separated into three growth periods: (1) early period of slow growth, (2) middle period of rapid growth, and (3) final period of slow growth (Stubbendieck and Burzlaff 1971). Early above-ground growth is primarily leaf material. Stem material is added later as the shoot and inflorescence develop during the middle period of rapid growth. In the last phase, dry matter accumulation continues, but at a slower rate (Sims et al. 1971; Sims et al. 1973; Pieper et al. 1974).

Four abundant grasses found in the Nebraska Sandhills are little bluestem [*Schizachyrium scoparium* (Michx.) Nash.], sand bluestem [*Andropogon hallii* Hack.], and sand lovegrass [*Eragrostis trichodes* (Nutt.) Wood], and switchgrass [*Panicum virgatum L.*]. They are important for soil stability and forage production. All four grasses are native, warm season, perennials. Sand bluestem and switchgrass are rhizomatous tall grasses, while little bluestem and sand lovegrass are mid-grasses and grow in bunches.

Objectives of this study were to examine stages of development and time of growing point elevation and to measure plant, leaf blade, and stem dry matter accumulation during two consecutive growing seasons.

Materials and Methods

The study was located in the Nebraska Sandhills near Halsey. The study area had a gently rolling topography and was classified as a sands range site. Range condition was excellent. Soil was a Valentine fine sand. Native tall and mid-grasses and forbs composed the dominant vegetation. No domestic livestock grazing had occurred since about 1935. About 70% of the annual precipitation falls within the April through September growing season.

In March, 1973 and 1974, 110 plants each of little bluestem, sand bluestem, sand lovegrass, and switchgrass were selected randomly throughout a 5-ha area. Dry matter accumulation was determined by harvesting the plants at weekly intervals beginning June 4, 1973, and May 27, 1974, and continued for 11 consecutive weeks. Stage of development was recorded at each harvest. Growing point height was measured in cm from the soil surface to the top of the shoot apex. Different plants were harvested each week with a minimum of 10 shoots per plant randomly clipped to a 2.5 cm height. Harvested shoots were separated into leaf blades and remaining topgrowth, hereafter referred to as stems. Forage was oven-dried at 70° C until a constant weight was obtained.

The study was conducted in a completely randomized design with ten replications. A factorial arrangement was used. Factors were years, grasses, and harvests with 2, 4, and 11 levels, respectively. An analysis of variance was computed for each variable. The treatment sum of squares was partitioned into years, grasses, and harvests, and their interactions. Years were considered a random effect and grasses and harvests fixed effects. Duncan's multiple range test was used to compare treatment means.

Results and Discussion

Annual and growing season precipitation were considerably lower in 1974 than in 1973. Between April 1 and July 31,

W. L. Gilbert, former graduate research assistant, is currently with Bureau of Land Management, Price, Utah 84501; L.J. Perry, Jr. (deceased) and J. Stubbendieck, were associate professors of Agronomy, University of Nebraska, Lincoln, at the time of the research.

This report is a contribution of the Nebraska Agricultural Experiment Station as Technical Paper Number 5328.

Manuscript received May 15, 1977.

precipitation was 28.6 cm in 1973 and 22.6 cm in 1974. Average air temperatures were higher in 1974 than in 1973. Average air temperatures during July were 3° C higher in 1974 than in 1973.

The grasses were at the 3- and 4-leaf stage of development at first harvest both years. At last harvest in early to mid August, little bluestem and sand bluestem inflorescences were beginning to emerge, sand lovegrass inflorescences were partially emerged, and switchgrass inflorescences were fully emerged. Sand lovegrass developed slowly by early harvests and more rapidly by later harvests. Rate of development of the grasses was slower during 1974 due to less precipitation. Little bluestem development was least affected by the climatic conditions of 1974 compared to 1973, and sand lovegrass was affected most.

Growing point elevation occurred in mid June for switchgrass, followed by little bluestem and sand bluestem in late June to early July. Sand lovegrass had the latest growing point elevation in mid to late July, but the rate of elevation was rapid

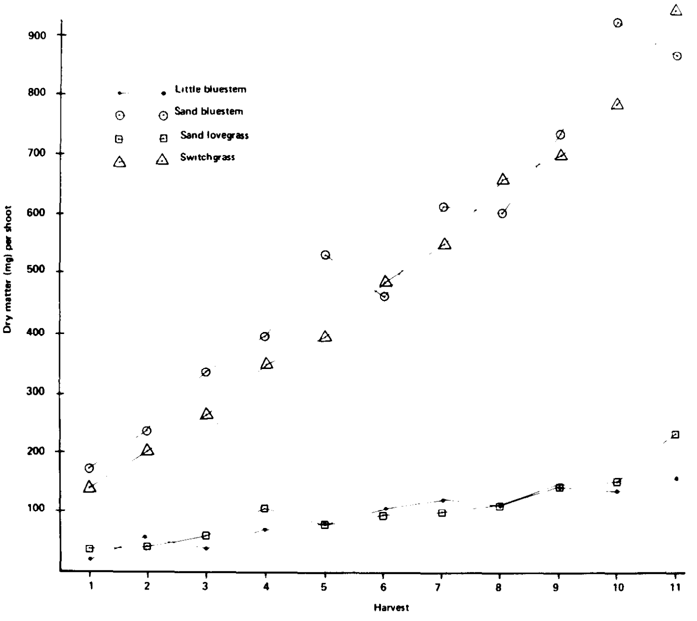


Fig. 1. *Plant dry matter accumulation of four warm-season grasses harvested at weekly intervals beginning June 4, 1973, near Halsey, Nebr.*

after that time. Growing points had elevated above the 2.5 cm height by late June for switchgrass, mid July for little bluestem and sand bluestem, and late July to early August for sand lovegrass. Branson (1953) suggested that the early vulnerability of the growing points of switchgrass could contribute to its rather rapid decrease in density under heavy grazing.

Plant dry matter accumulation per shoot generally increased with successive harvests for all four grasses in 1973 and 1974 as plant development advanced (Fig. 1 and 2). An increase in dry matter as the growing season progressed allowed for a greater forage supply, which was associated with potentially greater stocking rates. Dry matter accumulation occurred up to and including the last harvests; thus additional accumulation likely occurred after harvesting ceased.

Plant dry matter accumulation for each grass was nearly equal at the early harvests both years. At subsequent harvests, dry matter accumultion became progressively less in 1974 than in 1973, which was associated with the lower precipitation in 1974. Dry matter accumulation of the tall grasses was affected more by the reduced rainfall in 1974 than that of the mid-grasses. At the last harvest, dry matter production of the tall grasses was less in 1974 than in 1973, while the mid-grasses remained the same. Although the tall grasses still had greater dry matter production during the dry 1974 growing season, the mid-grasses can be important forage plants by maintaining a more stable forage production from year to year in spite of fluctuating climatic conditions.

Similar to plant dry matter accumulation, both leaf blade and stem dry matter accumulation generally increased with successive harvests for all grasses in 1973 and 1974 (Fig. 3, 4, 5, and 6.) Forage at the early harvests consisted of leaf material with little or no stem material. As the rate of stem dry matter accumulation increased, rate of leaf blade dry matter accumulation slowed. Therefore, leaf blade to stem ratios decreased with successive harvests.

Leaf blade and stem dry matter accumulation per shoot were significantly greater for the tall grasses than for the mid-grasses at the last harvests. Sand bluestem had the greatest leaf blade dry matter accumulation. Stem dry matter accumulation was significantly higher for switchgrass than for the other three grasses. This was associated with its advanced development. Leaf blade to stem ratio appeared to be greatest for sand bluestem and

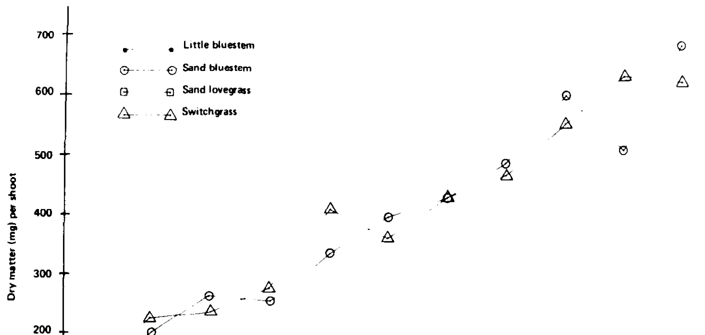


Fig. 2. *Plant dry matter accumulation of four warm-season grasses harvested at weekly intervals beginning May 27, 1974, near Halsey, Nebr.*

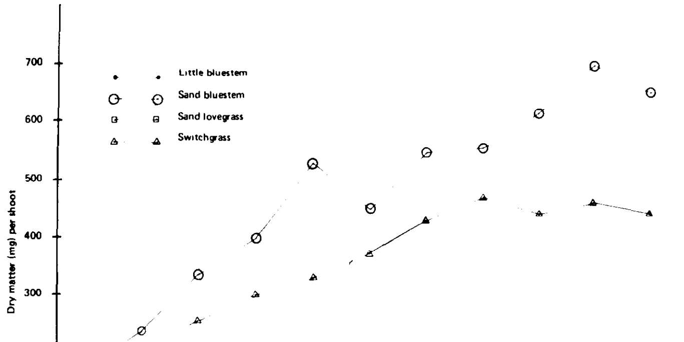


Fig. 3. *Leaf blade dry matter accumulation of four warm-season grasses harvested at weekly intervals beginning June 4, 1973, near Halsey, Nebr.*

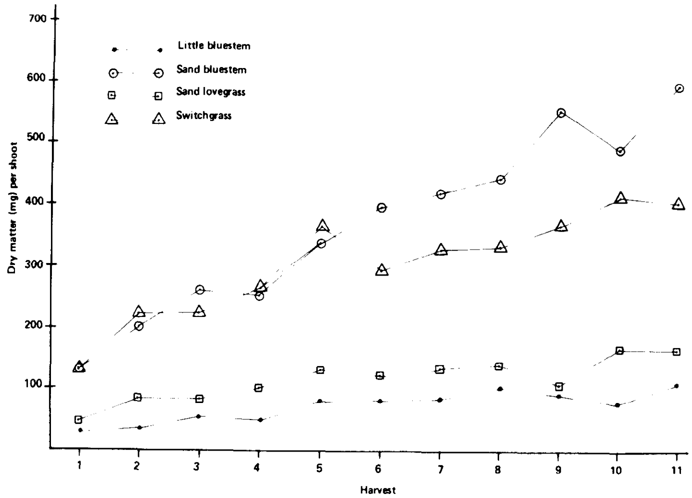


Fig. 4. *Leaf blade dry matter accumulation of four warm-season grasses harvested at weekly intervals beginning May 27,1974, near Halsey, Nebr.*

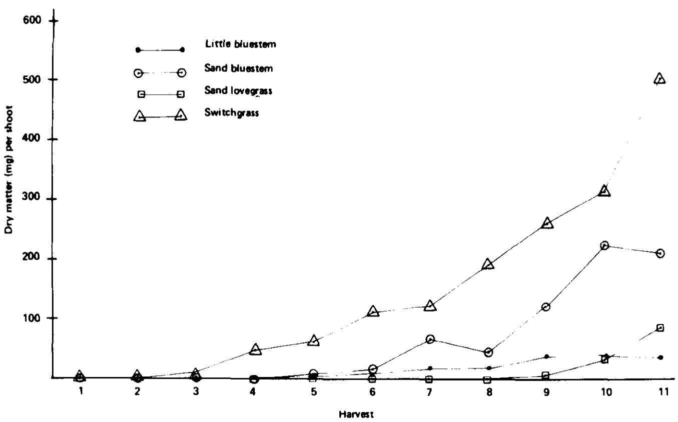


Fig. 5. *Stem dry matter accumulation of four warm-season grasses harvested at weekly intervals beginning June 4, 1973, near Halsey, Nebr.*

lowest for switchgrass, although few differences among the grasses were significant.

Both leaf blade and stem dry matter accumulation were significantly less at most harvests in 1974 than in 1973 for the tall grasses. At the last harvest, the decrease in stem dry matter accumulation, in 1974 as compared to 1973, was considerably greater than the decrease in leaf blade dry matter accumulation.

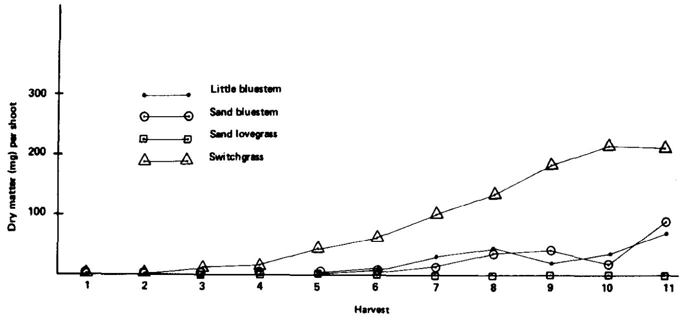


Fig. 6. *Stem dry matter accumulation of four warm-season grasses harvested at weekly intervals beginning May 27, 1974, near Halsey, Nebr.*

Thus the decrease in plant dry matter accumulation at the last harvest in 1974 can be attributed mostly to the decrease in stem dry matter accumulation. The lower dry matter accumulation was associated with the low precipitation in July of 1974, which occurred at a time when considerable leaf growth had occurred and stem growth was just beginning.

Literature Cited

Booysen, P. de V., N.M. Tainton, and J.D. Scott. 1963. Shoot-apex development in grasses and its importance in grassland management. Herbage Abstr. 33:209-213.

Branson, F.A. 1953. Two new factors affecting resistance of grasses to grazing. J. Range Manage. 6:165-171.

Cable, D.R. 1971. Growth and development of Arizona cottontop [*Trichachne californica* (Benth.) Chase]. Bot. Gaz. 132:119-145.

Cook, C.W., and L.A. Stoddart. 1953. Some growth responses of crested wheatgrass following herbage removal. J. Range Manage. 6:267-270.

Hyder, D.N. 1972. Defoliation in relation to vegetative growth. p. 304-317. *In:* V.B. Youngner and C.M. McKell (eds.), The Biology and Utilization of Grasses. Academic Press, New York. 426 p.

Pieper, R.D., C.H. Herbel, D.D. Dwyer, and R.E. Banner. 1974. Management implications of herbage weight changes on native rangeland. J. Soil and Water Cons. 29:227-229.

Rechenthin, C.A. 1956. Elementary morphology of grass growth and how it affects utilization. J. Range Manage. 9:167-170.

Shiflet, T.N., and H.E. Dietz. 1974. Relationship between precipitation and annual rangeland herbage production in southeastern Kansas. J. Range Manage. 27:272-276.

Sims, P.L., L.J. Auyko, and D.N. Hyder. 1972. Developmental morphology of switchgrass and sideoats grama. J. Range Manage. 24:357-360.

Sims, P.L., R.K. Lang'at, and D.N. Hyder. 1973. Developmental morphology of blue grama and sand bluestem. J. Range Manage. 26:340-344.

Stubbendieck, J., and D.F. Burzlaff. 1971. Nature of phytomer growth in blue grama. J. Range Manage. 24:154-156.

Evaluation of Fertilizer on Pronghorn Winter Range in Alberta

MORLEY W. BARRETT

Abstract

Nitrogen (N) alone, and in combination with phosphorus (P), was applied to sagebrush (*Artemisia cana*)-grassland vegetation which formed part of a traditional winter range for pronghorns (*Antilocapra americana*) in southeastern Alberta. Fertilizer was applied once, in April of 1975, and forage quality, forage production, and pronghorn response were monitored for the next three growing seasons. Forage quality on fertilized plots increased initially, but by late summer of each year, nutritional content was essentially similar in fertilized and control areas. Forage production increased markedly in each of the 3 years. The application of P in addition to N had little impact on forage quality and production. In year two and three following fertilizer treatment, N levels of 84, 168, and 252 kg/ha resulted in progressively more forage produced with each increase in N. Pronghorns selectively utilized the fertilized plots more heavily than adjacent control areas. The inability to increase protein content in cured samples of sagebrush and pasture sage through fertilizer treatment detracts from the value of this procedure for improving pronghorn winter ranges. The general increases in total forage production and hence total protein production and the preference of pronghorns for treated areas, however, suggest that the procedure should be evaluated further.

For many years wildlife managers have been investigating the nutritional requirements of most species of indigenous ungulates (Bandy et al. 1956; French et al. 1956: Dietz 1965; Murphy and Coates 1966; Ullrey et al. 1967; Nagy et al. 1969). More recently, greater emphasis has been placed on the interactions of range quality, environmental factors, and bioenergetics in determining the welfare of wildlife (Silver et al. 1969, 1971; Ullrey et al. 1970; Nordan et al. 1970; Wesley et al. 1973). There has also been a proliferation of literature concerning the nutrient content of a wide variety of plant species consumed by wildlife. Some authors have outlined nutritional limitations in forage available to ungulates (Nagy et al. 1969; Ullrey et al. 1971). Wallmo et al. (1977) have modelled the protein and energy requirements of mule deer (*Odocoileus hemionus hemionus*) and suggest that estimates of carrying capacity of ranges for wildlife should reflect the nutrient supplies available.

Range managers have conducted extensive research into the value of fertilizer as a tool for increasing the quality and quantity of forage produced for domestic livestock. Wight (1976) reviewed the effect of fertilizer in the Northern Great Plains region and concluded that nitrogen (N) in particular, greatly increased forage production, water-use efficiency, forage quality, and palatability. Fertilizer application on traditional big game ranges has been explored on a limited basis for years (Gibbens and Pieper 1962; Wood and Lindzey 1967; Bailey 1968; Abell and Gilbert 1974; Anderson et al. 1974; Bayoumi and Smith 1966; George and Powell 1977) but despite obvious potential, the practice has never become a widely used tool of wildlife management.

In Alberta, winter range is critical for the survival of pronghorns (*Antilocapra americana*), as the quality of forage and the distribution of suitable vegetation types within the pronghorn winter range are limited (Barrett 1974). Numerous fertilizer trials have been conducted on the semiarid grasslands of the northern Great Plains (Kilcher et al. 1965; Johnston et al. 1967; Lorenz and Rogler 1973) but no study has focussed on the sagebrush (*Artemisia cana*)-grassland vegetation type that constitutes the critical element of pronghorn winter ranges in Canada. Furthermore, no information appears available on the results of fertilizer on any pronghorn winter range.

The general objectives of this study were to evaluate the effects of nitrogen and phosphorus (P) fertilizer on a traditional pronghorn winter range in Alberta. Specifically, efforts were made to document changes in (1) nutrient content of forage, (2) forage production, and (3) pronghorn response to forage as a result of fertilizer application.

Study Area and Methods

The study area was a fenced 256-ha pronghorn enclosure located in the extreme southeastern corner of Alberta. The enclosure was established in 1973 and is situated on a portion of a traditional pronghorn winter range. As part of a long-term study on the carrying capacity of winter range, about 22 pronghorns were contained continuously in the enclosure at the time the fertilizer trials were conducted from April 1975 to November 1977. All fertilized plots were located within the enclosure but the total plot area represented less than 0.1% of the enclosure.

The study area is located in the Brown soil zone; the climate is semiarid. Mean annual precipitation (1941-1970) in the area as measured at the Agriculture Canada Research Sub-Station, Manyberries, 22 km southwest from the enclosure, is only 327 mm. Precipitation from April to July, inclusive, for the 3 years of the fertilizer trial was 295, 175, and 14 mm for 1975, 1976, and 1977, respectively (S. Smoliak, pers. comm.). General descriptions of the area have been presented by Coupland (1950; 1961) and by Mitchell and Smoliak (1971). Specifically, the fertilized sites reflected a sagebrush-grassland vegetation type (Fig. 1). The most prevalent browse, forb, and grass species, as determined by point quadrat analysis, were sagebrush, pasture sage (*A. frigida*), and western wheatgrass (*Agropyron smithii*). The sagebrush-grassland vegetation type was selected because of its importance in providing winter range for pronghorns in Alberta (Mitchell and Smoliak 1971; Barrett 1974).

The author is regional wildlife biologist, Department of Recreation Parks and Wildlife, Fish and Wildlife Division, Lethbridge, Alberta, Canada T1J 4C7.

Soil and forage analyses were conducted by the Soil and Feed testing Laboratory, Alberta Department of Agriculture, Edmonton. I thank L. Gudmundson, E. Hofman, H. Vriend, L. Windberg, and other members of the Albert Fish and Wildlife Division for assisting with field procedures, and R. Leech and S. Smoliak for reviewing the manuscript. This study was funded, in part, by the Alberta Buck for Wildlife program.

Manuscript received February 8, 1978.

Fig. 1. *Sagebrush-grassland range on which fertilized plots were located. This vegetation type is heavily used as winter range by pronghorns in Alberta.*

Three rates of N and three rates of N plus P were applied on test plots. Firstly, ammonium nitrate was applied in combination at the rates of 84N-39P, 168N-78P, and 252N-118P kg/ha. P was applied in the form of triple superphosphate. Each of the six treatments was replicated twice, producing a total of 12 experimental plots. Two adjacent areas were used as control plots for each replicate. Plot size was 6 × 15 m. Treatment was assigned to each plot on a completely random basis. A hand-held cyclone seeder was used to apply the single application of fertilizer on April 29, 1975; at that time no visible sign of spring growth was evident.

Forage for chemical analyses was collected from each of the fertilized plots and control areas on five occasions, namely, June 1975, September 1975, October 1975, August 1976, and August 1977. Each collection consisted of a composite sample of sagebrush, pasture sage and western wheatgrass, representing the dominant species of browse, forb, and grass, respectively. Portions of current year's growth collected from 20 to 40 individual plants of each species were pooled to obtain the forage class sample from each plot for chemical analyses. Using standard analytical techniques of the AOAC (1960) determinations for moisture, protein, calcium, phosphorus, and fiber were conducted. Values for treatments were averaged for presentation and all results are expressed on a dry weight basis.

During late October 1975, soil samples from each control area were collected from depths of 0–10 cm, 10–30 cm, and 30–60 cm; the three collections were analyzed separately. Using standard techniques N, P, potassium (K), conductivity, and pH values were obtained.

In August, after the growing season, forage production was determined for three consecutive years following fertilizer application. Twenty ¼ m² areas were clipped in each of the fertilized plots and control areas. Total annual production of browse, forbs, and grasses was separated, oven-dried and weighed. Data from each replicate are combined for presentation.

Leader lengths of sagebrush in each plot were sampled. In October of 1975, 1976, and 1977, 100 leaders were measured in each plot. In 1976 and 1977, an additional 400 leaders were measured from adjacent protected areas which received no ungulate browsing. Leader lengths reflected the current year's growth only. Values obtained for each treatment replicate are combined for presentation.

The plots were inspected periodically for evidence of use by pronghorns. In November of 1977, fecal pellet counts were made in ten 1-m² plots in each of the fertilized plots and 50 1-m² plots in the adjacent control areas. At the same time, the proportion of leaders browsed on sagebrush inside each fertilized plot and in the adjacent control areas were determined using Cole's (1963) method for random transects.

Differences between sets of means were examined for statistical significance using the *t* test. Minimum level of probability for statistical significance was $P<0.05$.

Results

Protein content of sagebrush, pasture sage and western wheatgrass is summarized for the fertilizer treatments at each sampling period in Table 1. Sagebrush sampled from fertilized plots had a mean protein value significantly greater than the respective control value on June 1975 and August 1976; no significance existed between the different fertilizer rates. Protein values in samples of sagebrush collected in late summer, while generally higher than control values, were not enhanced significantly by fertilizer. Similarly, pasture sage from fertilized plots collected after the growing season did not have significantly increased protein values relative to controls (Table 1). Differences in fertilizer application rates did not produce significant differences in the protein content of pasture sage. Western wheatgrass had significantly greater protein values in samples from fertilized plots as compared to controls on each sampling occasion except August, 1977 (Table 1). The mean protein content of western wheatgrass increased progressively with each increase in N fertilizer; the mean protein value for 252 kg/ha N plots was significantly ($P<0.05$) greater than the mean protein content in western wheatgrass from the 84 kg/ha N plots. The relative increase in protein content following the application of N was more pronounced in western wheatgrass than in pasture sage or sagebrush.

Table 1. Summary of protein content (%) of sagebrush, pasture sage, and western wheatgrass following fertilizer treatment in April, 1975[1].

Forage sampled	Sampling date				
	June 1975	Sept. 1975	Oct. 1975	Aug. 1976	Aug. 1977
Sagebrush					
Treatment mean	20.9a[2]	12.4a	7.3a	10.9a	12.2a
Control	16.7b	11.4a	7.3a	9.5b	11.6a
Pasture sage					
Treatment mean	18.7a	11.8a	8.9a	10.6a	9.7a
Control	13.6b	10.5a	8.2a	9.4a	8.7a
Western wheatgrass					
Treatment mean	17.0a	8.2a	5.6a	8.1a	8.8a
Control	10.1b	5.5b	3.9b	5.9b	7.3a

[1] For each sampling date, the mean value for each species reflects the average of all six fertilizer treatments.
[2] Within any column, the mean and control for a given forage species are significantly different ($P<0.05$) if the values are followed by a different letter.

Protein content of control samples collected in September 1975 and August 1976 and 1977 were compared for the three forage classes. Over the 3 years, the mean late summer protein content of sagebrush, pasture sage, and western wheatgrass was 10.8, 9.5, and 6.2%, respectively. The species means were significantly different ($P<0.05$).

No consistent changes in calcium, phosphorus, calcium/-phosphorus ratio, or fiber content of sagebrush, pasture sage, and western wheatgrass were evident as a result of fertilizer application. Consequently, analytical values obtained for fertilized and control samples were pooled (Table 2). The August and September samples of sagebrush had significantly more calcium and phosphor content than did samples of pasture sage or western wheatgrass. Of all parameters examined sagebrush contained higher nutrient values than did pasture sage or western wheatgrass (Table 2).

Analytical data for soil collected from the control areas are presented in Table 3. In general, soil in the test areas was deficient in nitrogen and rich in phosphorus and potassium.

Table 2. Chemical analyses of forage collected on pronghorn winter range in Alberta in late summer of 1975 to 1977, inclusive.

	Forage sampled								
	Sagebrush			Pasture sage			Western wheatgrass		
Parameter	n	Mean*	*S.D.*	n	Mean	*S.D.*	n	Mean	*S.D.*
Calcium (%)	48	0.98a	0.24	43	0.76	0.16	48	0.55c	0.16
Phosphorous (%)	48	0.36a	0.08	41	0.22b	0.03	48	0.14c	0.03
Calcium/phos. ratio	48	2.72a	0.73	41	3.45b	1.06	48	3.93b	1.32
Fiber (%)	48	34.42a	3.36	41	40.26b	3.06	48	41.39b	2.36

* Each mean was derived by pooling data for all fertilizer levels and control areas, and represent August and September samples only.
[a] Within any row, means which are significantly different ($P<0.05$) are denoted by a different letter.

Forage Production

Increases in grass and total forage production were evident at each level of fertilizer application in the year of treatment (Table 4). The largest increases occurred for the grass component. Although the general conditions for plant growth deteriorated from 1975 through 1977, the increased yield of vegetation in response to fertilizer treatment was apparent in each year. The values in Table 4 do not include cactus (*Opuntia* sp.) growth because of the sporadic distribution of this species and the potential of distorting forb production for any treatment plot. Slight increases in grass and browse production, although not significant, were still evident on fertilized plots after three growing seasons (Table 4).

Increased forage production as a result of N+P application was not evident when compared to corresponding levels of N fertilizer alone (Table 4). Consequently, forage produced for each level of N, with and without P, was combined to further examine the differences between the three levels of N application (Fig. 2); these values reflect total forage produced, including cactus. In 1975, total forage production on the fertilized plots was significantly higher ($P<0.05$) for each level of N than on control plots but no significant difference existed between the fertilizer levels. In 1976 and 1977, forage production increased consistently with each corresponding increase in N application. The 1976 and 1977 forage increases, while biologically important, were not statistically different between fertilizer levels or between each fertilizer level and control.

Sagebrush Growth and Pronghorn Utilization

The mean leader lengths of sagebrush in response to different

Table 3. Analytical data for soil collected from control plots in October, 1975. Data from the four control plots were averaged to obtain values below.

	Soil elements (kg/ha)				
Depth of sample (cm)	N	P	K	Soil pH	Conductivity (mmhos.)
0–10	5.9	69.1	1003.7	7.3	0.2
10–30	2.8	36.2	1047.2	7.9	0.3
30–60	2.0	28.1	879.3	8.5	0.9

levels of N are summarized in Table 5. Consistently longer leaders were documented only in 1975, but presumably as a result of the great variability in individual leader lengths, the differences between the values for fertilized and control plots were not statistically significant. In each year, the growth of sagebrush in fertilized plots appeared more vigorous than in control areas, but the differences were not measurable by October of each year. By comparison, mean leader lengths of sagebrush in areas protected from browsing was 8.1 cm in 1976 and 10.5 cm in 1977.

On numerous inspections each summer, increased use of the fertilized plots by pronghorns was evident. All species of grass,

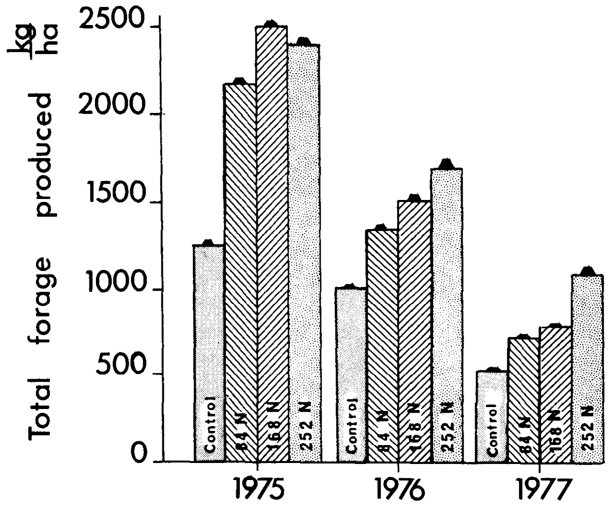


Fig. 2. *Annual forage production on pronghorn winter range following fertilizer application in April, 1975. Projection at apex of each histogram represents one standard deviation.*

Table 4. Annual forage production (kg/ha) on sagebrush-grassland vegetation type in Alberta as determined one, two, and three growing seasons after fertilizer treatment.

Fertilizer rate (kg/ha)		Forage production (kg/ha)											
		First growing season, 1975				Second growing season, 1976				Third growing season, 1977			
N	P	Grasses	Forbs*	Browse	Total*	Grasses	Forbs*	Browse	Total*	Grasses	Forbs*	Browse	Total*
84	0	1403.9[a]	35.2	141.6	1580.7[a]	964.6	6.0	111.5	1082.1	134.2	24.4	240.2	398.8
84	39	1701.3[a]	29.6	806.1[a]	2537.0[a]	1063.7[a]	12.4	96.7	1172.8[a]	308.7	13.4	230.3	552.4
168	0	1883.9[a]	45.8	615.2	2544.9[a]	839.2	7.7	199.5	1046.4	337.2	4.2	378.7	720.1
168	78	1788.7[a]	42.8	483.8	2315.3[a]	1002.4[a]	6.8	55.3	1064.5	297.5	2.6	206.5	506.6
252	0	1717.7[a]	37.0	657.6	2412.3[a]	964.7	3.9	405.9	1374.5[a]	284.9	4.0	441.3	730.2
252	118	1640.2[a]	39.0	354.5	2033.7[a]	919.2	26.3	202.3	1147.8	298.5	20.0	304.5	623.0
Control		928.2	30.8	264.9	1223.9	747.7	21.4	190.1	959.2	275.1	17.9	177.5	470.5

* These forage production values do not include data for *Opuntia* sp. which was encountered sporadically.
[a] Within any column, values which are significantly different ($P<0.05$) than control values, are denoted by a letter.

Table 5. Mean leader lengths (cm) of sagebrush associated with different levels of nitrogen fertilizer on pronghorn winter range.

Nitrogen rate[a] (kg/ha)	n	Mean leader length[b] (cm) 1975 Mean	1975 S.E.	1976 Mean	1976 S.E.	1977 Mean	1977 S.E.
84	400	9.28	0.28	6.23	0.20	5.28	0.18
168	400	9.90	0.33	7.08	0.20	5.78	0.20
252	400	9.80	0.33	6.70	0.23	6.30	0.20
Control	400	7.63	0.25	6.65	0.15	5.75	0.23

[a] Fertilizer applied on April 29, 1975.
[b] Based on current year's growth as measured in October of each year.

forbs, and browse appeared to be more heavily utilized inside each fertilized plot than in adjacent areas. A count of pronghorn fecal pellets in November 1977 indicated that 20.8% more pellets were located in fertilized plots than in adjacent control areas. Similarly, a browse use study conducted in November 1977, showed that 34.4% of the 420 sagebrush leaders examined inside fertilized plots were browsed while only 17.5% of 350 leaders examined in adjacent control areas were browsed; these differences were high significant ($P<0.01$). Although supporting quantitative data are unavailable, signs indicated that pronghorns consumed significantly more grasses and forbs from within fertilized plots than from control areas.

Discussion

Forage Quality

The lack of persistent increases in protein content of forbs and browse sampled from fertilized plots represents a limitation in the value of the technique for improving pronghorn winter range in Alberta. Although forage quality of cured plants was not enhanced greatly by fertilization, increased dry matter production, and hence increased total protein yield, resulted. Protein content in winter samples of sagebrush collected from Alberta winter ranges was only 7.6 (Barrett 1974) and appears to be less than optimal for overwintering pronghorns. Murphy and Coates (1966) reported that deer restricted to dietary protein rations of only 7% were less productive, had lower survival, and were in poorer condition than animals on a higher protein diet; pronghorn requirements may be similar to those of deer.

Pronghorns in Alberta do not appear restricted in terms of available summer nutrition and therefore little emphasis was placed on monitoring the forage quality during the growing season. Pronghorns would derive the most benefit by increasing protein values in sagebrush and pasture sage during the fall and winter. Our findings, however, were consistent with most studies conducted in the Great Plains which showed that fertilizer generally increases protein content of forage most significantly during the growing season (Goetz 1975a, 1975b; Hanson et al. 1976; Wight 1976). Goetz (1975b) reported a progressive decline in protein content of all grass species as they approached maturity, irrespective of fertilizer treatment. He also reported that fertilizer treatment accelerated the rate of protein loss in late summer. In my study, fall samples of western wheatgrass from fertilized plots (Table 1) reflected the effect of fertilizer application more than did corresponding samples of cured sagebrush or pasture sage. During fall and winter, however, pronghorns in Alberta consume practically no grass (Mitchell and Smoliak 1971; Barrett 1974).

The addition of P in combination with N, produced few consistent benefits in terms of increasing forage production or quality. A similar lack of significant response to P application was reported by Goetz (1975a), Bayoumi and Smith (1976), and Wight (1976). The phosphorus content in winter samples of sagebrush in Alberta was only 0.16% and probably reflected a near minimum concentration for overwintering pronghorns (Barrett 1974). Phosphorus content in cured forage did not appear to be augmented by the application of P fertilizer. By contrast, Johnston et al. (1968) observed an increase in P content of rough fescue (*Festuca scabrella*) on southern Alberta grasslands in the Black soil zone that received much higher rates of P fertilizer than used in my study.

Forage Production

Total forage production generally increased each year as a result of the single application of fertilizer (Table 4, Fig. 2). These findings are consistent with most reports on the effects of fertilizer on native range in the Northern Great Plains (Wight 1976). Treatment differences in total forage production as a result of differences in the rate of N application rates were not detected until the second and third growing seasons following fertilizer application (Fig. 2). Similarly, Wight (1976) stated that single applications of N at 56 kg/ha or less show limited carry-over effect, while applications of N over 112 kg/ha may have a residual effect for several years. Kilcher et al. (1965) reported that residual effects of 67 kg/ha N on grasslands in western Canada were evident for several years, probably as a consequence of low annual precipitation.

The production of forbs on fertilized plots was difficult to assess. Frequent visual inspections suggested that forb production on fertilized sites increased markedly each year but because pronghorns preferentially consumed them during the growing season, forb production was not accurately measured in August clippings. Also, growth of forbs in 1977 may have been restricted by the dry conditions during the growing season. An initial large increase in forb production following N fertilization, particularly at high application rates, has been reported by several authors (Kilcher et al. 1965; Johnston et al. 1967; Wight 1976). Wight (1976) indicated that pasture sage, in particular, responds readily to fertilizer but that the response decreases after the first year. Contrary to objectives for cattle grazing, increased forb production following fertilizer application would enhance the range for pronghorns but if the response of forbs is short-lived as Kilcher et al. (1965) suggested, then the technique is of less value.

Despite heavy utilization by pronghorns, increased browse production was a consistent measurable response to fertilizer treatment (Table 4). Increased leader length and a proliferation in growth of lateral twigs were most evident. The substantial increase in sagebrush production on fertilized plots, 3 years after treatment, was encouraging in view of the importance of sagebrush in the diet of pronghorns in Alberta (Mitchell and Smoliak 1971; Barrett 1974). The deep root system of sagebrush may account for the continuing response to fertilizer. Bayoumi and Smith (1976) reported an increase in production of big sagebrush (*A. tridentata*) in Utah following fertilizer application but they observed very little carry-over effect.

The great variation in total forage production between the 3 years of this study (Fig. 2) is a direct response to differences in precipitation. As the April to July precipitation declined from 295 mm in 1975 to only 175 mm and 114 mm in 1976 and 1977, respectively, forage production of grasses declined proportionately. The close relationship between spring precipitation and annual forage production in southeastern Alberta has been demonstrated by Smoliak (1956). Forage production may be particularly enhanced on dry years by fertilizer because of the better water use efficiency.

Palatability

Pellet group counts and forage utilization surveys indicated conclusively that pronghorns spent more time in fertilized plots and consumed significantly more of the available forage therein. Increased preference for fertilized range by domestic livestock has been a consistent finding. Similarly, fertilized range is usually preferentially utilized by wildlife (Gibbens and Pieper 1962; Anderson et al. 1974; Bayoumi and Smith 1976). Johnson et al. (1967) reported that hare (*Lepus townsendi*) pellets on native range increased proportionately with increased levels of N and N-P fertilizer. The ability of pronghorns to select higher quality forage in winter has been documented previously (Bruns 1969; Barrett 1974). The continuation of their selection for fertilized range during the growing season, when most plants are comparatively high in palatability, underscores the sensitivity of their ability to detect differences in forage quality.

This paper represents the first published information available on the influence of fertilizer application on pronghorn range and consequently, the results should be considered as preliminary. Some of the findings are encouraging and further studies are required to more fully evaluate the technique. Particular attention appears warranted on the long range effect of fertilizer on forb and browse production, species composition, and palatability of forage for pronghorns.

Literature Cited

Abell, D.H., and F.F. Gilbert. 1974. Nutrient content of fertilized deer browse in Maine. J. Wildl. Manage. 38:517-524.

Anderson, B.L., R.D. Pieper, and V.W. Howard, Jr. 1974. Growth response and deer utilization of fertilized browse. J. Wildl. Manage. 38:525-530.

A.O.A.C. 1960. Official methods of analysis (9th Ed.). Washington, D.C.

Bandy, P.J., I. McT. Cowan, W.D. Kitts, and A.J. Wood. 1956. A method for the assessment of the nutritional status of wild ungulates. Can. J. Zool. 34:48-52.

Bailey, J.A. 1968. Effects of soil fertilization on the concentration of crude protein in witchhobble browse. New York Fish and Game J. 15:155-164.

Barrett, M.W. 1974. Importance, utilization, and quality of *Artemisia cana* on pronghorn winter ranges in Alberta. Proc. Sixth Antelope States Workshop. 26-57.

Bayoumi, M.A., and A.D. Smith. 1976. Response of big game winter range vegetation to fertilization. J. Range Manage. 29:44-48.

Bruns, E.H. 1969. A preliminary study of behavioural adaptations of wintering pronghorn antelopes. M Sc Thesis, Univ. Calgary, Calgary, Alta. 60 p.

Cole, G.F. 1963. Range survey guide. U.S. Dep. Int., Nat. Park Service, Moose, Wyo.

Coupland, R.T. 1950. Ecology of mixed prairie in Canada. Ecol. Monogr. 20:272-315.

Coupland, R.T. 1961. A reconsideration of grassland classification in the Northern Great Plains of North America. J. Ecol. 49:135-167.

Dietz, D.R. 1965. Deer nutrition research in range management. Trans. North Amer. Wildl. Nat. Res. Conf. 30:275-285.

French, C.E., L.C. McEwen, N.D. Magruder, R.H. Ingram, and R.W. Swift. 1956. Nutrient requirements for growth and antler development in the white-tailed deer. J. Wildl. Manage. 20:221-232.

George, J.F., and J. Powell. 1977. Deer browsing and browse production of fertilized American elm sprouts. J. Range Manage. 30:357-360.

Gibbens, R.P., and R.D. Pieper. 1962. The response of browse plants to fertilization. California Fish and Game 48:268-281.

Goetz, H. 1975a. Availability of nitrogen and other nutrients on four fertilized range sites during the active growing season. J. Range Manage. 28:305-310.

Goetz, H. 1975b. Effect of site and fertilization on protein content of native grasses. J. Range Manage. 28:380-385.

Hanson, C.L., G.A. Schumaker, and C.J. Erickson. 1976. Influence of fertilization and supplemental runoff water on production and nitrogen content of western wheatgrass and smooth brome. J. Range Manage. 29:406-409.

Johnston, A., S. Smoliak, A.D. Smith, and L.E. Lutwick. 1967. Improvement of southeastern Alberta range with fertilizers. Can. J. Plant Sci. 47:671-678.

Johnston, A., L.M. Bezeau, A.D. Smith, and L.E. Lutwick. 1968. Nutritive value and digestibility of rough fescue. Can. J. Plant Sci. 48:351-355.

Kilcher, M.R., S. Smoliak, W.A. Hubbard, A. Johnston, A.T.H. Gross, and E.V. McCurdy. 1965. Effects of inorganic nitrogen and phosphorus fertilizers on selected sites of native grassland in western Canada. Can. J. Plant Sci. 45:225-237.

Lorenz, R.J., and G.A. Rogler. 1973. Growth rate of mixed prairie in response to nitrogen and phosphorus fertilizer. J. Range Manage. 26:365-368.

Mitchell, G.J., and S. Smoliak. 1971. Pronghorn antelope range characteristics and food habits in Alberta. J. Wildl. Manage. 35:238-250.

Murphy, D.A., and J.A. Coates. 1966. Effects of dietary protein on deer. Trans. North Amer. Wildl. Nat. Res. Conf. 31:129-139.

Nagy, J.G., T. Hakonson, and K.L. Knox. 1969. Effects of quality on food intake in deer. Trans. North Amer. Wildl. Nat. Res. Conf. 34-146-154.

Nordan, H.C., I. McT. Cowan, and A.J. Wood. 1970. The feed intake and heat production of the young black-tailed deer (*Odocoileus hemionus colubianus*). Can. J. Zool. 48:275-282.

Silver, H., N.F. Colovos, J.B. Holter, and H.H. Hayes. 1969. Fasting metabolism of white-tailed deer. J. Wildl. Manage. 33:490-498.

Silver, H., J.B. Holter, N.F. Colovos, and H.H. Hayes. 1971. Effect of falling temperature on heat production in fasting white-tailed deer. J. Wildl. Manage. 35:37-46.

Smoliak, S. 1956. Influence of climatic conditions on forage production of shortgrass rangeland. J. Range Manage. 9:89-91.

Ullrey, D.W., W.G. Youatt, H.E. Johnson, L.D. Fay, and B.L. Bradley. 1967. Protein requirements of white-tailed deer fawns. J. Wildl. Manage. 31:679-685.

Ullrey, D.E., W.G. Youatt, H.E. Johnson, L.D. Fay, B.L. Schoepke, and W.T. Magee. 1970. Digestible and metabolizable energy requirements for winter maintenance of Michigan white-tailed does. J. Wildl. Manage. 34:-863-869.

Ullrey, D.E., W.G. Youatt, H.E. Johnson, L.D. Fay, D.B. Purser, B.L. Schoepke, and W.T. Magee. 1971. Limitations of winter aspen browse for the white-tailed deer. J. Wildl. Manage. 35:732-743.

Wallmo, O.C., L.H. Carpenter, W.L. Regelin, R.B. Gill, and D.L. Baker. 1977. Evaluation of deer habitat on a nutritional basis. J. Range Mange. 30:-122-127.

Wesley, D.E., K.L. Knox, J.G. Nagy. 1973. Energy metabolism of pronghorn antelopes. J. Wildl. Mange. 37:563-573.

Wight, J.R. 1976. Range fertilization in the Northern Great Plains. J. Range Manage. 29:180-185.

Wood, G.W., and J.S. Lindzey. 1967. The effects of forest fertilization on the crude protein, calcium, and phosphorus content of deer browse in a mixed oak forest. Pennsylvania Coop. Wildl. Res. Unit Pap. 126.

Carbohydrate Levels and Control of Blackjack Oak and Winged Elm Treated with Tebuthiuron and 2,4,5-T

J.P. SHROYER, J.F. STRITZKE, AND L.I. CROY

Abstract

The effects of tebuthiuron N-[5(1,1-dimethylethyl)-1,3,4-triadiazol-2-yl]-*N,N'* dimethylurea) and 2,4,5-T[(2,4,5-trichlorophenoxy) acetic acid] on total nonstructural carbohydrates (TNC) in the roots of blackjack oak (*Quercus marilandica* Muench.) and winged elm (*Ulmus alata* Michx) were evaluated. Tebuthiuron was applied to the soil in February 1976 at 2.24 kg/ha and 2,4,5-T was foliar applied at 2.24 kg/ha in May 1976. Tree kill 1 year after treatment with tebuthiuron was 100% for both woody species. No tree kill resulted from treatment with 2,4,5-T, and canopy reduction after 1 year was 50 and 70% for winged elm and blackjack oak, respectively. The TNC content of both winged elm and blackjack oak roots was significantly reduced following application of 2,4,5-T and tebuthiuron. The TNC content of roots from trees growing in tebuthiuron-treated areas did not significantly increase after treatment (TNC contents of 6 and 7%, respectively for blackjack oak and winged elm on October 13). There was some increase in TNC content of roots from trees sprayed with 2,4,5-T, and by October the TNC content in blackjack oak and winged elm roots was 10 and 19%, respectively. This compared to TNC contents of 36 and 32%, respectively for untreated blackjack oak and winged elm.

Phenoxy herbicides, such as 2,4,5-T, have been the herbicides most commonly used for brush control. Elwell (1964) and Darrow and McCully (1955) indicated that two aerial applications of 2,4,5-T totaling 3.36 to 4.48 kg/ha, with not more than 2 years between treatments, were required to effectively control blackjack oak (*Quercus marilandica* Muench.) and post oak (*Quercus stellata* Wangenh.). Elwell (1968) concluded that foliar applications of 2,4,5-T did not effectively control winged elm (*Ulmus alata* Michx.). Stritzke (1975) found that the addition of ammonium thiocyanate to 2,4,5-T consistently increased control of winged elm compared to 2,4,5-T alone. Canopy reduction after treatments with 2,4,5-T was often short-lived since resprouting soon occurred. This resprouting has been attributed to carbohydrate reserves in the roots of the treated trees.

Tebuthiuron has shown promise for control of certain brush species. Soil treatments of 2.24 kg/ha on mixed brush have given excellent control of elms (*Ulmus spp.*) and oaks (*Quercus spp.*), (Stritzke 1976, Nickels and Stritzke 1977). Baur and Bovey (1975) observed good control of yaupon (*Ilex vomitoria* Ait.), post oak, and blackjack oak with soil applications of tebuthiuron using 2.24 to 4.48 kg/ha. There is usually only the initial defoliation of trees treated with 2,4,5-T; whereas, there are several repeated defoliations caused by tebuthiuron during the first season following application, and some additional defoliations have been noted into the second and third years after treatment.

The objectives of this study were to evaluate the control as well as defoliation and resprouting of blackjack oak and winged elm treated with 2,4,5-T and tebuthiuron, and to determine the total nonstructural carbohydrate (TNC) levels in roots of both species.

Materials and Methods

Individual winged elm and blackjack oak trees located near Stillwater, Oklahoma, were utilized in the study. Winged elm trees were planted on a 3-m^2 grid in 1971. The soil type was a Port silt loam (fine silty, mixed, Thermic Cumulic Haplustolls). The blackjack oak trees were resprouts growing on a Bates fine sandy loam site (fine loamy, siliceous, Thermic Typic Argiudolls) that had been bulldozed in 1964.

On February 12, 1976, 125 winged elm trees were each treated with 7.5 grams of tebuthiuron (10% pellets) applied on a 1.8m^2 area around each tree (equivalent to 2.24 kg/ha). In the blackjack oak area five plots (15.2m^2) were treated at the same rate with tebuthiuron. On May 28, 1976, three blackjack oak plots (15.2 m^2) and 60 winged elm trees were foliar treated with a solution of 2,4,5-T, butoxyethanol ester. The solutions were as follows: blackjack oak—95 ml of 2,4,5-T (480 g/l) plus 95 ml of diesel in 18.9 liters of water foliar applied with a hand sprayer until the solution dripped from the leaves; winged elm—a mixture of 63 ml of 2,4,5-T (480 g/l) in 3.8 liters of water sprayed for 9 seconds with a hand sprayer (both treatments equivalent to 2.24 kg/ha of 2,4,5-T).

Sampling of roots of both species for untreated trees began on February 12, 1976. Trees treated with tebuthiuron were first sampled April 26, 1976, and sampling for trees treated with 2,4,5-T began on June 8, 1976. Sampling was done twice monthly until September 15, 1976, once each in October (1976), April (1977), and June (1977). Root samples were collected from five trees within each treatment on each sampling date, except that on the September and October dates only two winged elm trees were sampled from the tebuthiuron areas since three of the trees were dead.

Roots that were sampled, ranging from 0.5 to 3.0 cm in diameter, were placed in an oven (65° C) and dried for 48 hours. After drying, the bark was removed by scraping with a pocket knife and the roots were ground in a Wiley mill to pass through a 2-mm screen. After the root samples were ground, 0.5 gm of the root sample was placed in a 250-ml beaker with 50 ml of 0.2 N HCl and allowed to boil slowly for 1 hour. The root solution was then filtered into a 100-ml volumetric flask. The beaker and filtrate were washed with 50 ml deionized water, and the solution was then brought to 100 ml volume. Then 0.1 ml of this sample was placed into a 20-ml test tube with 0.9 ml of deionized water. The Anthrone reagent, as described by Yemm and Willis (1954), was used to determine the TNC content. The Anthrone reagent (5.0 ml) was then added to the root extract and agitated. The samples

Authors are, graduate research assistant and associate professors, Department of Agronomy, Oklahoma State University, Stillwater, Oklahoma 74074. Mr. Shroyer is currently extension agronomist, Iowa State University.

Journal Article 3411 of the Agricultural Experiment Station, Stillwater, Oklahoma.
Manuscript received January 3, 1978.

were then placed in a hot water bath for 15 minutes, followed by 20 minutes in a cold water bath. Optical density of the samples was determined with a spectrophotometer (B and L Spectronic 20) at 620 nm. Standards containing 0, 40 80, 120, 200 μg glucose/ml water served for comparison with the unknown TNC content of the root samples.

The vegetative stage and percentage defoliation of each tree was visually estimated on each sampling date. Also, canopy and tree mortality was determined on May 25, 1977. Trees were considered dead if there were no resprouts and cambium at ground level was dead.

The design was a randomized complete block and difference were separated by Duncan multiple range test.

Results

Tebuthiruon injury to winged elm was detected earlier than injury to black jack oak, and by July 8 the winged elm trees were completely defoliated (Table 1). Defoliation of blackjack oak treated with tebuthiuron increased with time and by September 15 they were completely defoliated. Defoliation was less with 2,4,5-T, and by October 13 the average defoliation was 80% for both blackjack oak and winged elm. Leaves on untreated trees were still green at this time. At the May 25, 1977, evaluation, all winged elm and blackjack oak trees treated with tebuthiuron were dead (no leaves on the original stems, no sign of resprouts, and no green cambium at ground level). At the May 1977 evaluation, none of the trees sprayed with 2,4,5-T were dead, although canopy kill averaged 50 and 70%, respectively, for winged elm and blackjack oak with no basal sprouting.

Table 1. Defoliation (%) of blackjack oak and winged elm on various sampling dates after treatment with tebuthiuron and 2,4,5-T[1].

	Defoliation			
	Blackjack oak		Winged elm	
Sampling date	Tebuthiuron	2,4,5-T	Tebuthiuron	2,4,5-T
1976				
4/26	10	—[2]	30	—
5/13	25	—	45	—
5/25	30	—	90	—
6/8	50	20	90	25
6/23	45	70	90	60
7/8	90	50	100	60
7/21	90	70	100	50
8/4	90	65	100	50
8/18	90	70	100	65
9/1	90	70	90[3]	50
9/15	100	90	90[3]	70
10/13	100	80	90[3]	80
1977				
5/25	100	70	100	50

[1] Tebuthiuron applied February 12, 1976, and 2,4,5-T applied May, 28 1976.
[2] — = No data taken.
[3] Contains only two observations.
[4] Defoliation taken in May, 1977, is considered to be canopy kill since data was taken 1 year after treatment.

On the first sampling date (February 12, 1976) the roots of untreated winged elm contained 23% TNC (Fig. 1). There was a decline in TNC levels with leaf initiation in early spring and TNC was less than 14% by April. After the leaves were full size (4 to 6 cm long) TNC began to increase, and by the October sampling the roots contained 32% TNC. The TNC content in the roots of untreated blackjack oak in February was essentially the same as that for the untreated winged elm (Fig. 2). The major difference was that the rate of decline of TNC in the roots of blackjack oak was delayed, resulting in a greater TNC content in the blackjack oak roots in late March and early April. By May

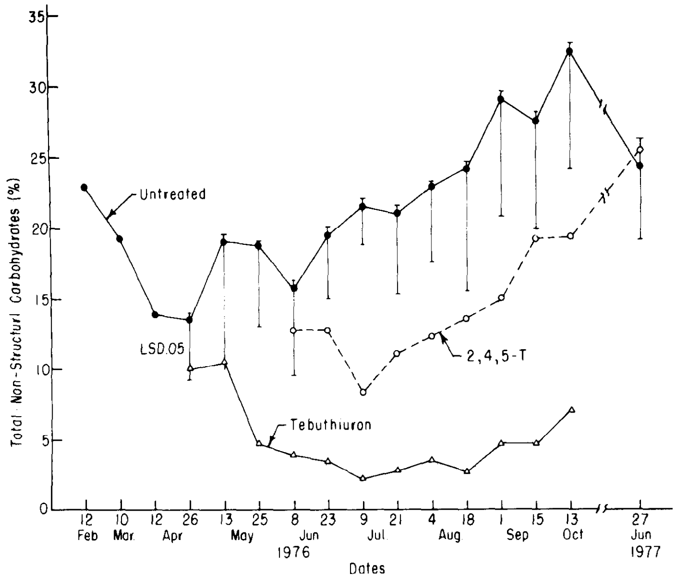


Fig. 1. *Nonstructural carbohydrate levels in roots of winged elm at various dates and influence of tebuthiuron and 2,4,5-T on these concentrations. Trees were dormant at the February sampling, budding at the March sampling, leaves expanding during April, and some leaves full size by May.*

13 the leaves were fully developed and the TNC began to accumulate. This type of TNC pattern exhibited by the untreated trees was in agreement with previous reports by Kramer and Kozlowski (1960).

On April 26 winged elm treated with tebuthiuron had a TNC content in the roots of 10% compared to 13% in the roots from untreated trees. The TNC content in roots of the treated trees continued to decline and by August 18 it was only 3%. The cambium at ground level of some of the trees was dead by the September sampling. TNC content in roots of live trees averaged 4% on September 1, 5% on September 15, and 7% on October 13. Defoliation of these trees averaged 90% on all three sampling dates. None of the winged elm trees were alive by the

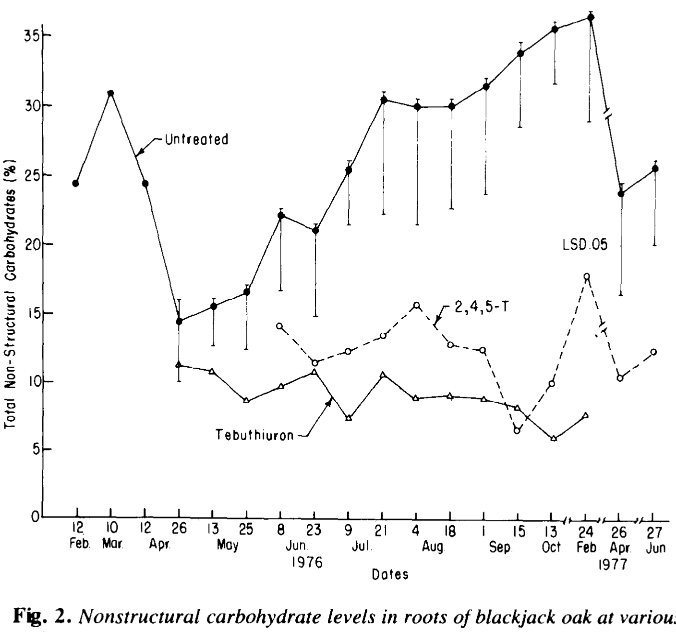


Fig. 2. *Nonstructural carbohydrate levels in roots of blackjack oak at various dates and influence of tebuthiuron and 2,4,5-T on these concentrations. Trees were dormant at the February samplings, budding at the March samplings, expanding during April and May, and full size by June samplings.*

following spring (May 1977); therefore sampling was discontinued.

The TNC content in roots of winged elm sprayed with 2,4,5-T was also influenced but the effect was not as dramatic and long lasting as with the tebuthiuron treatments (Fig. 1). The lowest TNC content (18%) occurred on July 8. After July 8, there was an increase in TNC in roots of winged elm treated with 2,5,5-T which essentially paralleled the increase in untreated trees. This increase in TNC evidently resulted from activity of leaves remaining on the trees, since 30% or more of the canopy remained alive through October. By the following year (June 27, 1977), there was no difference in the TNC content between untreated trees and those treated with 2,4,5-T. Boo and Pettit (1975) reported the same type of recovery of TNC in roots of sand shinnery oak (*Quercus harvardii* Rydb.) after mechanical shredding.

When blackjack oak trees treated with tebuthiuron were first sampled (April 26), the roots contained 11% TNC (Fig. 2). This was only 3% less than the untreated trees on the same date. However, treated trees had lower TNC than untreated trees on May 13. The percent TNC in roots of tebuthiuron-treated trees was between 7 and 11% for most of the summer, reaching a low of 6% by the October 13, 1976, sampling.

The TNC content of roots of blackjack oak was also significantly reduced by the 2,4,5-T treatment (Fig. 2). For most of the summer the reduction was similar to that of trees treated with tebuthiuron. The main difference was the increase of TNC content in roots of trees sprayed with 2,4,5-T. By February 1977, the TNC content was 18% compared to 8% in roots from tebuthiuron-treated trees. No comparison of TNC levels in roots 1 year after treatment was made between the two herbicides since all trees treated with tebuthiuron were dead.

Tebuthiuron was more effective than 2,4,5-T in reducing the TNC content in roots of both blackjack oak and winged elm in this study. There was also better defoliation of existing stems and tree kill with the tebuthiuron treatment. This was in agreement with results obtained by Scrifres and Mutz (1977) for white brush (*Aloysia lycioides* Cham.) and Berlandier wolfberry (*Lycium berlandieri* Dun.) where they observed no resprouting from trees 2 years after being treated with tebuthiuron. This more effective tree kill and lack of resprouting when using tebuthiuron should significantly increase the longevity of effective brush control.

Literature Cited

Baur, J.R., and R.W. Bovey. 1975. Herbicidal effects of tebuthiuron and glyphosate. Agron. J. 67:547-553.

Boo, Robert M., and R.D. Pettit. 1975. Carbohydrate reserves in roots of sand shin oak in west Texas. J. Range Manage. 28:469-472.

Darrow, R.A., and W.G. McCully. 1955. Aerial application of herbicides for control of post and blackjack oaks. Proc. So. Weed Conf. 8:265-268.

Elwell, Harry M. 1964. Oak brush control improves grazing land. Agron. J. 56:411-415.

Elwell, Harry M. 1968. Winged elm control with picloram and 2,4,5-T with and without additives. Weed Sci. 16:131-133.

Kramer, P.J., and T.T. Kozlowski. 1960. Physiology of Trees. McGraw-Hill, New York 642 p.

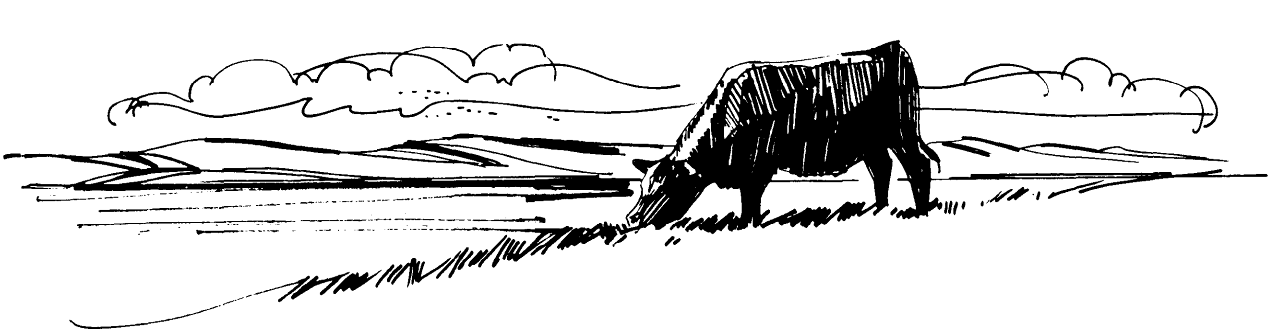
Nickels, J.K., and J.F. Stritzke. 1977. Some potential uses of tebuthiuron and 3-cyclohexyl-6-(dimethylamino)-1-methyl-1,3,5,-triazine-2,4(1H, 3H)-dione in pine management. Proc. So. Weed. Conf. 30:246.

Scifres, C.S., and J.L. Mutz. 1977. Brush control and range forage production following aerial application of tebuthiuron. Proc. So. Weed Conf. 23:131-136.

Stritzke, J.F. 1975. Chemical mixtures for control of winged elm. Weed Sci. 23:131-136.

Stritzke, J.F. 1976. Use of tebuthiuron for control of undesirable vegetation in pastures and range. Weed Sci Abstr. 38 p.

Yemm, E.W., and A.J. Willis. 1954. The estimation of carbohydrates in plant extracts by anthrone. Biochem. J. 57:508-514.



Response of *Bouteloua eriopoda* (Torr.) Torr. and *Sporobolus flexuosus* (Thurb.) Rybd. to Season of Defoliation

RICHARD F. MILLER AND GARY B. DONART

Abstract

Production, total nonstructural carbohydrates, and crown diameters were measured to evaluate the effects of season of clipping on black grama and mesa dropseed. Vegetative reproduction was also monitored for black grama. Early defoliation of both black grama and mesa dropseed had less impact on plant vigor than continuous defoliation or defoliation during the last half of the growing season. Black grama plants clipped during or after flowering, or continuously through the growing season, produced less herbage in the following year than those plants clipped during the vegetative stage. Removal of 65% of the current year's growth any time during the growing season significantly reduced stolon numbers on black grama. Mesa dropseed clipped during maturity, during flowering, or clipped continuously throughout the growing season was negatively affected on one or more of the plant parameters measured. Clipping during the vegetative state had little apparent effect on plant vigor.

Knowledge of plant responses to defoliation during various seasons, frequencies, and intensities is essential for proper management on rangelands. Limited data exist on season, frequency, and intensity of use on native plants occurring on Southwestern rangelands. Nelson (1934) and Canfield (1939) concluded that persistent heavy grazing significantly reduced the vigor of black grama (*Bouteloua eriopoda* (Torr.) Torr.), an ecological dominant of much of the Southwest. Valentine (1970) found the number and length of stolons per black grama plant were closely correlated with intensity of winter grazing. Paulsen and Ares (1962) reported cyclic changes in black grama basal area were closely correlated with precipitation during the growing season.

Paulsen and Ares (1962) reported that temperature requirements for mesa dropseed (*Sporobolus flexuosus* (Thurb.) Rybd.), another important Southwestern range plant, were less limiting than for black grama. Mesa dropseed seedlings establish well on open areas (Nelson 1934), especially during the first favorable growing season following drought (Dittberner 1971).

While ecological relationships and limited information on grazing tolerance are available, the impact of defoliation at different stages of phenological development on physiological and morphologcal characteristics have not been established for this area. Similarly, time necessary for recovery of vigor of important range plants in the Southwest has not been defined. The purpose of this study was to measure the effect of six defoliation patterns over a 3-year period on forage harvested, total nonstructural carbohydrates (TNC), and crown diameter for black grama and mesa dropseed and vegetative reproduction of black grama. Such information is an integral portion of grazing strategies.

The authors are assistant professor, Rangeland Resources Program, Oregon State University, Corvallis; and associate professor, Department of Animal and Range Sciences, New Mexico State University, Las Cruces, respectively. Miller was formerly graduate research assistant, Department of Animal and Range Sciences, New Mexico State University, Las Cruces.

This report was submitted as Journal Article 665, New Mexico Agricultural Experiment Station, Las Cruces. This paper reports on work supported in part by Bureau of Land Management Contract YA-512-CT6-205.

Manuscript received April 29, 1978.

Study Area

The study area was located on the New Mexico State University College Ranch, located 32 km north of Las Cruces in Dona Ana County. Average annual rainfall is 22 cm. Of this total, 55% occurs during the growing season of July, August, and September (Agr. Res. Serv. 1975). Precipitation during the growing season was 107% above the mean in 1974, 26% above the mean in 1975, and 28% below the mean in 1976. Most summer rainfall comes from high intensity convectional thunderstorms (Paulsen and Areas 1962). Annual rainfall is highly variable, and drought is common throughout these desert ranges. The frost-free period is approximately 200 days, with the growing season ranging between 90 to 100 days, depending on rainfall distribution.

Soils ranged from sandy loams to light loamy sands on the black grama and mesa dropseed study areas (Valentine 1970). Soil depth varied between 15 to 90 cm to a highly fractured calcium carbonate hardpan. Vegetation associated with these two sites consisted of fluffgrass (*Erioneuron puchellum* (H.B.K.) Takeoka), three awn (*Aristida* sp.), broom snakeweed (*Xanthocephalum sarothrae* (Pursh.) Shinners), soaptree yucca (*Yucca elata* Englm.) and honey mesquite (*Prosopis juliflora* (Sw.) D.C.). The two study areas have been protected from cattle grazing since 1965.

Methods

Criteria used in measuring plant response to defoliation were levels of TNC, forage harvested, and plant growth characteristics. The six clipping treatments were (1) *vegetative*, plants clipped only in the vegetative stage once each year during the 3-year period; (2) *VFS*, plants clipped once in the vegetative stage in 1974, once during flowering in 1975, and once during leaf senescence in 1976; (3) *VSV*, plants clipped once in the vegetative stage in 1974, once in leaf senescence in 1975, and once in the vegetative stage in 1976; (4) *maturity*, plants clipped once in leaf senescence and once during quiescence in 1974, 1975, and 1976; (5) *continuous*, plants clipped once in each the vegetative, flowering, leaf senescence, and quiescence stages during each of the 3 years; and (6) *control*, nondefoliated plants. The four phenological stages designating the period of defoliation were the third to fouth leaf stage for vegetative, dough stage for flowering, after seed ripening for leaf senescence, and chlorophyll absent from about 90% of the leaf tissue for quiescence. Defoliation for all treatments was accomplished by clipping 65% on a weight basis of the current annual growth.

Plants were excavated from each of the three replications 7 days after defoliation, placed on ice in the field, and brought into the

Table 1. Percent TNC between defoliation treatments for black grama roots and mesa dropseed roots collected during quiescence, 1976.

Species		Stage of defoliation					
	1974	Control	Vegetative	Vegetative	Vegetative	Maturity	Continuous
	1975	Control	Vegetative	Flowering	Senescence	Maturity	Continuous
	1976	Control	Vegetative	Senescence	Vegetative	Maturity	Continuous
Black grama							
Black grama		16.0[a1]	15.2[a]	15.3[a]	15.8[a]	15.2[a]	14.9[a]
Mesa dropseed		18.8[a]	16.6[ab]	17.3[ab]	18.4[a]	14.6[b]	14.8[b]

[1] Data in rows followed by a different letter are significantly different at the 95% level by Tukey's *w*-procedure.

laboratory, where they were dried at 68°C for 48 hours. Total available carbohydrates were extracted from a 0.5-g root sample in 0.8 N H_2SO_4 (Smith et al. 1964). All samples were refluxed on a crude fiber apparatus. An extension of Forsee's photocolorimetric ferricyanide method was used for determining TNC levels (Morrell 1941).

Clipped material was collected and bagged for each plant during defoliation for dry matter yield determinations. Crown diameters were measured at the end of each growing season for all six treatments on black grama and mesa dropseed. The number of stoloniferous culms on black grama were counted in 1976 prior to defoliation in the vegetative stage and at the end of the growing season. Precipitation data were recorded on each site from U.S. Weather Bureau standard rain gauges.

Analysis of variance, Turkey's *w*-procedure and the pooled-*t* test were used to analyze data at the 95% confidence level (Steel and Torrie 1960).

Results and Discussion

Black Grama

At completion of the 3-year study, no significant differences occurred in percent TNC for black grama among the six defoliation treatments (Table 1). This indicated that season of clipping had no effect on black grama food storage reserves. However, concentrations of TNC in black grama were highly variable between plants within the same treatment and phenological stage. If defoliation did affect TNC levels, this response was obscured by variation in food storage levels among plants. Variability in TNC levels among plants within the same treatment and the apparent lack of response in TNC levels to defoliation were similar to data on blue grama (*Bouteloua gracilis* (H.B.K. Lag.) in Colorado (Menke and Trlica 1972), *Dupontia fisheri* R. Br. in Alaska (Mattheis et al. 1972), and western wheatgrass (*Agropyron smithii* Rydb.) in a hydroponic solution (Bokari and Singh 1974).

Season of clipping black grama did not significantly affect the percent root TNC (Table 1) or crown diameter (Table 2). The smallest crown diameter increases were measured from plants clipped continuously through the growing season or in maturity. These trends were consistent with available forage trends. Season of clipping did significantly affect the amount of forage being harvested during the current growing season, the following year's forage production and the vegetative reproduction potential. When 65% of the current year's growth was clipped in the first year (1974), 50% less forage was harvested on plants defoliated during the vegetative stage (3.9 g/plant) as compared to either the continuous or mature treatments (7.2 and 7.9 g/plant, respectively). However, both continuous and late defoliation decreased forage harvested in the following growing season (Table 3). Plants clipped in the 1974 growing season during the vegetative stage produced significantly more forage during the vegetative, flowering, and leaf senescent stage in 1975 than either the continuous or defoliation at maturity treatments. Plants clipped only once during the vegetative stage in 1974 produced more forage during this same stage in 1975 than did plants that had been clipped in the continuous or mature treatments.

In 1976, plants defoliated only in the vegetative stage for two consecutive years had significantly more forage during the initial third and fourth leaf stage of growth than either the VSV or continuous treatments (Table 3). Little additional growth occurred in August and September, probably because of low rainfall. Forage harvested from the VFS, maturity and continuous defoliation treatments during senescence in 1976 were not significantly different. It appeared that clipping black grama during flowering in 1975 reduced forage production potential (1.1 g/plant) for the following year. Low rainfall on the black grama sites during the 1976 growing season (34% below average) may have obscured treatment effects on production between VFS, maturity, and continuous treatments.

One of the more detrimental effects of clipping black grama was the reduction of stolon numbers. Vegetative reproduction is very important for increasing black grama stands since this plant produces few viable seed (Valentine 1970). Black grama

Table 2. Mean change in crown diameter (cm) for black grama and mesa dropseed plants during the 1975 and 1976 growing seasons.

Species and date							
	1974	Control	Vegetative	Vegetative	Vegetative	Maturity	Continuous
	1975	Control	Vegetative	Flowering	Senescence	Maturity	Continuous
	1976	Control	Vegetative	Senescence	Vegetative	Maturity	Continuous
Black grama							
1975		1.4[a1]	2.1[a]	2.1[a]	2.0[a]	0.4[a]	1.3[a]
1976		−0.6[a]	0.0[a]	−1.0[a]	−1.2[a]	−1.3[a]	−2.8[a]
Mesa dropseed							
1975		1.4[a]	−1.1[ab]	0.2[ab]	0.7[ab]	−4.7[c]	−2.0[bc]
1976		0.7[ab]	1.4[a]	−1.1[ab]	0.1[ab]	−5.7[c]	−3.2[bc]

[1] Data in rows followed by a different letter are significantly different at the 95% level by Tukey's *w*-procedure.

Table 3. Mean dry weight (g) of forage harvested per plant of black grama and mesa dropseed from five defoliation treatments during 1974, 1975, and 1976. Data are accumulative within years across phenology stages.

Species and treatment	Phenology at time of harvest											
	1974				1975				1976			
	Veg[1]	Flow	Sen	Quies	Veg	Flow	Sen	Quies	Veg	Flow	Sen	Quies
Black grama												
Veg[1]	3.9^{a}[2]				4.3^{a}				3.6^{a}			
VFS	4.2^{a}					5.1^{a}					1.1^{a}	
VSV	3.6^{a}						7.2^{a}		1.2.^{b}			
Sen & Quies			5.3^{a}	7.9^{a}			3.2^{b}	3.2^{a}			1.0^{a}	1.0^{a}
Continuous	3.2^{a}	4.3	5.9^{a}	7.2^{a}	1.2^{a}	2.7^{b}	3.4^{b}	3.4^{a}	0.5^{b}	1.0	1.1^{a}	1.1^{a}
Mesa Dropseed												
Veg	4.1^{a}				4.3^{a}				2.7^{a}			
VFS	4.8^{a}					7.0^{a}					3.0^{a}	
VSV	4.9^{a}						10.1^{a}		2.0^{ab}			
Sen & Quies			7.7^{a}	16.5^{a}			10.4^{a}	13.4^{a}		5.3^{a}	5.3^{a}	5.3^{a}
Continuous	3.7^{a}	5.7	8.5^{a}	13.3^{a}	1.2^{b}	3.6^{b}	3.6^{b}	4.0^{b}	1.0^{b}	2.1	2.9^{b}	2.9^{b}

[1] The abbreviations are: Veg = Vegetative, Flow = Flowering, Sen = Senescence, Quies = Quiescence. These treatments reflect period of defoliation for 1974, 1975, and 1976, respectively.

[2] Data in columns followed by a different letter are significantly different at the 95% level by Tukey's *w*-procedure.

produces a true stolon, which is generally located toward the outer portion of the plant base. Occasionally, the true stolons may develop and form sets within the same year, when precipitation and length of growing season are adequate (Nelson 1934). The true stolon, usually prostrate, may be elevated a few centimeters from the soil surface. When the stolon set is formed and nodal roots develop, the set is generally in contact with, or in close proximity to, the soil surface.

A second type of stolon activity was observed from flowering culms and identified as a stoloniferous culm. This form of stolon generally develops from the interior portion of the plant over a 2-year period. Inflorescence-bearing reproductive culms developed during the first year. Simultaneously, culms began elongating with development, depending upon growing conditions during and after flowering. During the winter the meristematic tissue in the stolon culms persisted in a quiescent stage. It was observed that this material constituted a large percentage of the palatable stem bases that remained green throughout the winter. Under favorable conditions the following growing season, these stems all quickly elongated during the initial stages of growth and developed axillary vegetative branching and nodal roots, giving the same appearance of a stolon set. At this stage of development, inflorescences formed in the previous year could be found at the tip of the culm. These stoloniferous culms generally remained several centimeters above the ground and were thus readily exposed to defoliation. The nodal roots seldom appeared to make contact with the soil surface in the second year, thus limiting the capability of vegetative reproduction in the second year.

Defoliation during or after flowering significantly decreased the vegetative reproduction potential of these plants in the following growing season primarily through removal of stoloniferous culms (Table 4). Because of the vulnerability of these elevated stolons to defoliation, reduction of these vegetative reproductive parts was simply caused by physical removal. Plants defoliated in the vegetative stage in 1974 and 1975 had significantly more stolons in the initial stages of growth in 1976 than did plants in any other defoliation treatment (Table 4). Stolon potential on plants defoliated in the vegetative stage during the previous two growing seasons was similar to that of nondefoliated plants. However, the current year's potential for stolon development for those plants defoliated in the vegetative stage during the two previous growing seasons was removed when the plants were clipped in the vegetative state in 1976 (Table 4). The still-elevated stolons, developed during the previous growing season, were easily removed by clipping in the second year of formation during the vegetative stage, which significantly reduced the reproductive potential. Few stoloniferous culms were present at the end of the 1976 growing season for the five treatments in which clipping occurred. Low rainfall promoted little development of new stoloniferous culms. Although the nondefoliated plants had significantly more stolons than any of the defoliated plants, most of these had been produced during the 1975 growing season.

Mesa Dropseed

After 3 years of defoliation, season of forage removal had a significant affect on TNC, amount of forage being harvested

Table 4. Mean change in stolon numbers of black grama plants during the vegetative stage prior to clipping and during quiescence in 1976.

Treatment		Stage of defoliation					
	1974	Control	Vegetative	Vegetative	Vegetative	Maturity	Continuous
	1975	Control	Vegetative	Flowering	Senescence	Maturity	Continuous
	1976	Control	Vegetative	Senescence	Vegetative	Maturity	Continuous
Vegetative		8.3^{a}[1]	11.3^{a}	1.3^{b}	0.0^{b}	0.0^{b}	0.0^{b}
Quiescence		8.0^{a}	1.9^{a}	0.4^{b}	2.4^{b}	2.4^{b}	0.3^{b}

[1] Data in rows followed by a different letter are significantly different at the 95% level by Tuckey's *w*-procedure.

during the current growing season, the following year's forage production, and crown diameters of mesa dropseed.

Concentrations of TNC were not highly sensitive to defoliation. Variability of food reserves between plants was generally greater than that caused by herbage removal. However, after three consecutive years of clipping, TNC levels in plants defoliated continuously or during maturity were significantly less than levels present in nondefoliated plants (Table 1).

Defoliating plants before or after flowering did not affect production of forage harvested (Table 3). However, defoliating plants during flowering or continuously throughout the growing season significantly reduced production the following growing season. Removal of 65% of the current annual production present during the vegetative stage in 1974 resulted in about 70% less forage being harvested than if plants were clipped continuously or during maturity at the same intensity. Clipping 65% of the current annual growth on mesa dropseed during the 3 to 4 leaf stage harvested approximately 19 to 20% of the annual forage available.

During the 1975 growing season, plants that had been clipped in the vegetative stage in 1974 yielded significantly more forage in the vegetative stage, flowering stage, and senescence stage than plants that had been continuously defoliated (Table 3). Plants clipped at maturity during 1974 and 1975 also produced significantly more forage during the 1975 growing season than did continuously clipped plants.

In 1976 continuously defoliated plants produced significantly less during the vegetative stage than did plants defoliated at the vegetative stage (Table 3). During leaf senescence in 1976, plants that had been clipped continuously or during flowering in 1975 produced significantly less than plants clipped during maturity in 1976.

Low yields for plants from the VFS treatment indicated defoliation during flowering was detrimental to the following year's forage production. However, this was based on 1 year of data, in which growing season rainfall was 28% below average on the mesa dropseed study area. No measurable amount of forage was produced during the latter part of senescence, probably because of lack of precipitation and cool temperatures.

Crown diameters for control plants were significantly larger than diameters of plants clipped continuously or at maturity during the 1975 and 1976 growing seasons (Table 2). Although this was not totally consistent with production data, it did correlate with TNC data in the last year. As crown diameters decreased, TNC levels decreased during the quiescence stage in 1976.

Conclusions

Total available carbohydrates and crown diameters of black grama showed little response to season of clipping. However, the amount of forage harvested was sensitive to season of clipping. Black grama plants continuously defoliated throughout the growing season, or during senescence and quiescence, during flowering, or during senescence, produced less forage in the following year than did those plants clipped only during the vegetative stage. Early clipping allowed for substantial regrowth, probably enabling plants to adequately complete normal growth requirements. In 1974 less than half of the total forage yield was present during the three to four leaf stage. Defoliation at a level of 65% during this period removed only 30% of the plant total. This was consistent with levels of winter use required to maintain or improve stands of black grama reported by Campbell and Crafts (1939) and Valentine (1970). However, removing 65% of the current year's growth during the vegetative stage significantly reduced the number of stolons produced during the following growing season. Later use at this intensity removed the current year's production of stolons. Due to the vulnerability of stolons, 65% removal of the current year's production any time during the growing season will impair the ability of black grama to increase vegetatively, thus greatly decreasing its competitive ability. Probably a more effective scheme for managing black grama would be to harvest 30 to 35% of the total annual production throughout the growing season. This should decrease grazing pressure on stoloniferous culms.

The responses of TNC, production, and crown diameter in mesa dropseed to season of clipping were not consistent. Continuous defoliationg at 65% intensity significantly reduced TNC levels and crown diameter below that of the control plants, and significantly reduced production below the level of plants clipped in the vegetative stage. Crown diameters and TNC levels were also significantly reduced in plants clipped during senescence and quiescence although productivity was not affected. Clipping during flowering significantly reduced productivity in the following year but had no effect on crown diameters and TNC levels. Of the five clipping treatments, both the vegetative and VSV treatments had no apparent effect on plant vigor. As with black grama, less than half the total annual yield was present during the three to four leaf stage. Removing 65% of the vegetative growth during this period harvested 19% of the total.

Since mesa dropseed becomes unpalatable and low in nutrients when it matures (Paulsen and Ares 1962), it would benefit beef production to graze this plant during the growing season. If plants are to be continuously grazed during active growth or grazed during or after flowering, utilization should be less than 65%. In summary, these plants can withstand heavier use prior to flowering than during the remainder of the growing season.

Early use of both black grama and mesa dropseed had less impact on plant vigor than late season or continuous defoliation. Several factors are possibly involved. Early defoliation occurs during a time when environmental parameters (mainly soil moisture and air temperature) are adequate to allow for quick regrowth. As plants mature, these conditions become less optimal and plants have less time to complete important growth functions. Besides environmental factors affecting regrowth, the elapse of time for chemical processes to attain peak rates with defoliation increases with leaf age (Hodgkinson 1974).

Both species were unable to tolerate continuous clipping at 65% herbage removal. However, care must be taken in the interpretation of continuous clipping. Continuous clipping and continuous grazing may be two different things. Continuous grazing would decrease plant vigor under the assumption that herbivores will continually remove plant material from these plants during the growing season. However, cattle do not consistently graze one species or the same plant unit of a given species during the entire growing season under desert conditions. Also, lighter use would be made during the growing season under a continuous year-long grazing system.

Literature Cited

Agricultural Research Service. 1975. File data. U.S. Dep. Agr. Las Cruces, N.M.

Bokhari, V.G., and J.S. Singh. 1974. Effects of temperature and clipping on growth, carbohydrate reserves and root exudation on western wheatgrass in a hydroponic culture. Crop Sci. 14:790-794.

Buwai, M., and M.J. Trlica. 1977. Multiple defoliation effects on herbage yield, vigor and total nonstructural carbohydrates of five range species. J. Range Manage. 30:164-171.

Campbell, R.S., and E.C. Crafts. 1939. How to keep and increase black grama on southwestern ranges. U.S. Dep. Agr. Leaflet No. 180. 8p.

Canfield, R.H. 1939. The effect of intensity and frequency of clipping on density and yield of black grama and tobosa grass. U.S. Dep. Agr. Tech. Bull. 681. 39p.

Dittberner, P.L. 1971. A demographic study of some semidesert grassland plants. MS Thesis. New Mexico State Univ., Las Cruces. 81p.

Hodgkinson, E.C. 1974. Influence of partial defoliation on photosynthesis, photorespiration and transpiration by lucerne leaves at different ages. Aust. J. Plant Physiol. 1:561-578.

Mattheis, P.J., L.L. Teszen, and M.C. Lewis. 1976. Response of *Dupontia fischeri* to simulated grazing in an Alaskan arctic tundra. Ann. Bot. 40:179-197.

Morrell, S.A. 1941. Rapid determination of reducing sugars. Ind. Eng. Chem. (Anal. Ed.). 13:249-251.

Nelson, E.W. 1934. The influence of precipitation and grazing on black grama range. U.S. Dep. Agr. Tech. Bull. 409. 32p.

Paulsen, H.A., and F.N. Ares. 1962. Grazing values and management of black grama and tobosa grasslands and associated shrub ranges of the southwest. U.S. Dep. Agr. Tech. Bull. 1270. 56p.

Smith, D., G.M. Paulsen, and H.A. Raguse. 1964. Extraction of total available carbohydrates from grass and legume tissue. Plant Physiol. 39:960-962.

Steel, R.G.D., and J.H. Torrie. 1960. Principles and Procedures of Statistics. McGraw-Hill Book Co., Inc., New York. 481p.

Valentine, K.A., and J. Gerard. 1968. Life history characteristics of the creosotebush (*Larrea tridentata*). New Mexico State Univ. Agr. Exp. Sta. Bull. No. 526. 32p.

Valentine, K.A. 1970. Influence of grazing intensity on improvement of deteriorated black grama range. New Mexico State Univ. Agr. Exp. Sta. Bull. No. 533. 21p.

Soil Ingestion by Mule Deer in Northcentral Colorado

W.J. ARTHUR, III AND A.W. ALLDREDGE

Abstract

Soil ingestion rates calculated from titanium concentrations in feces from mule deer (*Odocoileus hemionus*) feeding in a grassland-shrub community in northcentral Colorado in g/day ($\bar{x}\pm$ *SD*) were: spring, 29.6±20.1; summer, 7.7±10.2; fall, 8.8±6.5; and winter 18.3±10.8. Based on observations of feeding tame deer, intake in winter appeared to be primarily due to direct soil ingestion from pocket gopher (*Thomomys talpoides*) mounds, roads, and other areas of exposed soil. The greatest intake during spring was likely due to indirect consumption of soil adhering to ingested vegetation. Soils from locations where tame deer had consumed soil were analyzed for trace elements (Ca, Cu, Fe, Mg, Mn, P, K, Na, and Zn) and compared to areas where no soil intake was observed. No significant differences (α=0.05) in mean levels of these elements was detected between areas. Most likely, deer at Rocky Flats were not selecting soils based strictly on mineral content, but instead were consuming soil indiscriminately. Ingested soil may provide a source of trace elements as well as a mode of entry for environmental pollutants.

Ingestion of soil and grit by both domestic and wild ruminants has been indicated as a possible source of trace elements (Healy 1968, Healy et al. 1970, Mayland et al. 1975, and Skipworth 1974) as well as a potential intake pathway for environmental pollutants (Mayland et al. 1977). In our study, which was designed to measure plutonium intake by mule deer (*Odocoileus hemionus*) feeding in a radioactively contaminated area at Rocky Flats Nuclear Weapons Plant, Colorado, it became necessary to quantify soil ingestion rates. Little (1976) reported that the majority of the plutonium contamination at Rocky Flats was associated with soil, and our observations of wild and tame deer during their foraging indicated that these animals consumed soil either directly (Fig. 1) or with ingested vegetation.

Healy (1968) and Mayland et al. (1975, 1977) quantified soil ingestion in cattle by measuring concentrations of a trace element, titanium, in feces, but we know of no reports quantifying soil intake in wild ruminants. We employed the titanium tracer technique, and it is the purpose of this report to describe

Fig. 1. *Field observations of tame deer indicated that these animals consumed soil while feeding at Rocky Flats Nuclear Weapons Plant.*

Arthur's present address is U.S. Department of Energy, Environmental Sciences Branch, Idaho National Engineering Laboratory, Idaho Falls, ID 83401.

Authors express appreciation to the following: W.B. Healy of the Soil Bureau, New Zealand, and H.F. Mayland of the Snake River Conservation Research Center, Idaho, for helpful suggestions; R. Keiss of the Colorado Division of Wildlife for trace element analysis on soil samples; W. Ferguson and D. Bigelow of the Colorado State University Analytical Chemistry Facility for conducting titanium analysis; G.S. Hiatt for aid in sample collection; D. Hein, for critical review of this manuscript. This research was funded through Energy Research and Development Administration Contract No. E(11-1)-1156 with Colorado State University.
Manuscript received February 27, 1978

our methods and to present daily soil intake rates for mule deer feeding in a grassland-shrub community during each season from December 1975 to December 1976.

Study Area

Research was conducted on property owned by the U.S. Department of Energy (DOE) surrounding the Rocky Flats Nuclear Weapons Plant 12 km northwest of Denver, Colorado. Portions of this property have been accidentally contaminated with plutonium (Krey and Hardy 1970; Krey and Krajewski 1972), which has led to numerous studies including our own.

Primarily a grassland, the area has a mean elevation of 1,800 m and is characterized by flat, wind-scoured plateaus interspersed with ravines. Vegetation communities described by Clark and Webber (1975) were dominated by moist meadows; principal species were slender wheatgrass (*Agropyron trachycaulum*), cheatgrass (*Bromus tectorum*), bluegrass (*Poa* spp.), and salsify (*Tragopogon dubius*). Upland sites were occupied by dry prairie consisting of junegrass (*Koeleria gracilis*), slender wheatgrass, mountain muhly (*Muhlenbergia montana*), needlegrass (*Stipa comata*), little bluestem (*Schizachyrium scoparium*), sage (*Artemesia ludoviciana*), golden aster (*Heterotheca villosa*), and pussytoes (*Antennaria parvifolia*). Streamside vegetation occurred on approximately 5% of the study area and was dominated by shrub species: snowberry (*Symphoricarpos occidentalis*), plains cottonwood (*Populus sargentii*), willow (*Salix* spp.), and lead plant (*Amorpha fruticosa*).

Mule deer were the most conspicuous wild mammal utilizing the study area, with 90 to 100 of these animals frequently being observed on approximately 25 km^2 of DOE-owned property (Hiatt 1977).

Methods

Measurement of soil ingestion using titanium as a tracer has been discussed by Healy (1968) and Mayland et al. (1975), who reported that titanium, relatively abundant in soil (1,000 to 3,000 ppm), is contained in amounts less than 1 ppm in plants and is not taken up by the ruminant body (Miller et al. 1975). If these assumptions are correct, then by knowing the daily mass of fecal excretion and titanium concentrations in soil and feces, one could calculate the daily soil intake.

To measure titanium concentration in soil at Rocky Flats, five representative soil samples were collected from the upper 3 cm of the soil profile. Samples were oven-dried for 48 hours at 80°C, sieved through a 2-mm mesh screen, and analyzed for titanium using a Gilford spectrophotometer at the Colorado State University Analytical Chemistry Facility. All titanium analysis conducted on soil, vegetation, feces, and tissue samples was done according to a procedure described by Bigelow (unpublished manuscript, Colorado State University Analytical Chemistry Facility 1976) and Yoe and Armstrong (1947).

Four vegetation samples were collected each season for titanium analysis and were selected as being representative of Rocky Flats vegetation consumed by deer. Vegetation composites were clipped, placed in an ultrasound bath, and washed with water. Duration of washes varied, depending upon the amount of soil associated with the plants, but in all cases washing was continued for 0.5 hour after no soil was visible in the wash pan. Samples were then oven-dried at 80°C for 72 hours, milled through a 2-mm mesh screen, and analyzed. The mill was cleaned after each sample to assure that no cross-contamination of samples occurred. A two-way analysis of variance was used to test for differences in titanium concentrations among samples and seasons.

In addition to vegetation, we also conducted titanium analysis on liver, kidney, and metacarpal bone samples from two deer that were killed by automobiles in our study area. Liver and kidney samples were oven-dried for 72 hours at 105°C and bone samples were ashed at 600°C for 48 hours. Samples were ground until powdered and then analyzed.

Each season, 20, fresh, non-soil-contaminated, fecal groups were collected from the Rocky Flats property. Because we had observed fecal groups which contained pellets that appeared to be almost entirely soil, and doubted that ingested soil was uniformly distributed throughout the fecal group, we carefully collected all pellets belonging to a group. Feces were processed in the same manner as vegetation samples. Duplicate cross samples were prepared and analyzed each season to ascertain analytical error. Titanium concentrations in sample preparation solutions ranged from 0 to 4 ppm ($\bar{x}$ = 2.5 ppm); therefore all fecal, vegetaion, soil and tissue samples were corrected for this potential error source.

Titanium concentrations measured in Rocky Flats vegetation were much higher than values previously reported (Healy 1968) and because of this, we corrected all titanium concentrations measured in feces for the contribution that could have come from vegetation. The following calculations made for daily soil ingestion during spring are provided to illustrate our approach:

$$\text{I.}\quad \frac{242.8\ \text{ppm titanium}}{\text{g-feces}} \times \frac{401.3\ \text{g-feces}}{\text{deer-day}} = \frac{97435.6\ \text{ppm titanium}}{\text{deer-day}}$$

$$\text{II.}\quad \frac{8.8\ \text{ppm titanium}}{\text{g-plant}} \times \frac{1390.2\ \text{g-plant}}{\text{deer-day}} = \frac{12233.8\ \text{ppm titanium}}{\text{deer-day}}$$

$$\text{III.}\quad 97435.6 - 12233.8 = \frac{85201.8\ \text{ppm titanium}}{\text{deer-day}}$$

$$\text{IV.}\quad \frac{85201.8\text{ppm titanium}}{\text{deer-day}} \times \frac{\text{g-soil}}{2880\ \text{ppm titanium}} = \frac{29.6\ \text{g-soil}}{\text{deer-day}}$$

Part I calculates the total amount of titanium from all sources that is excreted in one day. The amount of feces defecated each day was estimated by collecting complete pellet groups from the Rocky Flats area. Individual pellet group mass was multiplied by 13.2 (Smith 1964) to obtain daily fecal mass excreted. Results for spring, summer, fall, and winter were 401, 527, 351, and 396 g/day, respectively (Arthur 1977). Analysis of variance for differences in mean weight per pellet group over seasons was not significant at the α=0.05 level ($F_{3,115}$=1.99).

Part II calculates titanium intake from vegetation, based on measured concentrations in vegetation that had been ultrasound washed. Forage intake rates of deer of 1,390 g/day for spring, summer and fall seasons, and 1,145 g/day for winter were obtained from Alldredge et al. (1974). Part III, above, calculates the amount of titanium in feces that came from ingestion of soil. In part IV titanium concentrations in daily fecal excretion are related to soil excretion by using measured titanium concentrations in Rocky Flats soils. If we assume that a steady state condition exists and that no titanium is being absorbed from the gut, then the amount of soil excreted each day should equal the amount of soil ingested each day.

A portion of our study involved the "bite count" technique (Wallmo and Neff 1968) for determination of food habits, and in the process of observing tame deer feeding at Rocky Flats, we noticed them consuming soil. Soil ingestion by tame deer was categorized as either attachment to plant roots, attachment to above ground plant parts, or direct intake. When ingested soil was associated with plant material, the species of plants was recorded. Specific areas where direct intake was observed were noted, and soil from these areas was collected.

In order to determine whether or not deer were selecting soil on the basis of trace element content, samples were collected from the upper 3 cm of soil from under vegetation litter, along roads and from pocket gopher mounds. Roads and pocket gopher mounds were areas where deer often consumed soil. Soil samples were screened through a 24-mesh screen, extracted in a 0.1N HCl solution for 24 hours on a shaker, and analyzed on a flame photometer for calcium, copper, iron, magnesium, manganese, phosphorus, potassium, sodium, and zinc. Mean concentrations of these elements were log normalized, plotted against collection areas and analyzed for consistency among peaks at specific areas.

Results

Titanium concentrations in soil ranged from 2,600 to 3,100 ppm ($\bar{x}$ = 2,880, *SD* = 192 ppm), with the highest value coming from a sample collected from a pocket gopher mound. The mean titanium concentration in vegetation was 17.3 ppm (*SD* = 8.1 ppm) with a range of values of 8.8 ppm in spring to 21.8 ppm during the fall season. Analysis of variance revealed no significant differences (α = 0.05) between concentrations in vegetation among seasons or areas. Titanium concentrations in mule deer bone samples were less that 1 ppm, while kidney samples had a mean concentration of 20.5 ppm (*SD* = 6.5 ppm), and liver samples had a mean of 22.0 ppm (*SD* = 2.0 ppm). Table 1 lists mean titanium concentrations in mule deer feces for each season. The highest concentration occurred in spring (x = 242.8 ppm) and the lowest in summer (x = 87.2 ppm). Analysis of variance was significant ($F_{3,74}$=9.69) for differences in seasonal mean concentrations of titanium. Duncan's test (Duncan 1965) showed that the spring mean was significantly greater than the summer and fall means, but not the winter mean. *T*-tests conducted on titanium concentrations in fecal samples from sampling areas at Rocky Flats were not significant (α = 0.05) indicating no area differnces. Blind duplicate error for 20 fecal samples averaged 19.7% (*SD* = 20.9%) and was believed to be associated with our method of dividing samples.

Table 1. Seasonal titanium concentrations in mule deer feces at Rocky Flats Nuclear Weapons Plant, Colorado, 1976.

	Winter (75-76)	Spring (76)	Summer (76)	Fall (76)
$\bar{x}$ (ppm titanium)	195.7	242.8	87.2	155.1
SD (ppm titanium)	78.5	144.3	55.7	59.4
Coefficient of variation (%)	40.1	59.4	63.9	38.3
Range (ppm titanium)	89-375	57-530	45-250	24-250
Sample size	18	20	20	20

Mean daily rates of soil intake were calculated for each season by correcting for titanium concentrations in vegetation (Table 2). Soil ingestion was highest during winter and spring with a daily intake of 18.3 and 29.6 g of soil, respectively. Analysis of variance showed significant difference (α = 0.05) in mean daily soil intake between seasons. Duncan's test indicated that spring mean was significantly greater than those for fall and summer, but not for winter.

Results of trace element analysis from Rocky Flats soils are presented in Table 3. A log-transformation of mean element concentrations and a *t*-test conducted on means between areas where soil was seen ingested versus areas where none was observed ingested indicated that there were no significant differences (α = 0.05) in trace element concentrations among any samples.

Table 2. Seasonal soil ingestion rates for mule deer at Rocky Flats Nuclear Weapons Plant, Colorado, 1976.

	Winter (75-76)	Spring (76)	Summer (76)	Fall (76)
$\bar{x}$ (grams soil per deer per day)	18.3	29.6	7.7	8.8
SD (grams soil per deer per day)	10.8	20.1	10.2	6.5
Coefficient of variation (%)	59.0	67.9	132.5	73.9
Range	3.7-43.0	3.7-69.6	0.0-37.6	0.0-20.0
Sample size	18	20	20	20

Discussion

Our measured titanium concentrations in soil fell within the ranges reported by Healy (1968). Small variations of titanium concentrations in soils were found to exist locally in our study area, but a greater variability might be expected over wider geographical areas because of varying geologic conditions.

Titanium concentrations in vegetation collected in our study were higher than those cited in the literature (Healy 1968: 1 ppm). Either Rocky Flats' vegetation contained more titanium than was reported in other studies (Healy 1968; Mayland et al. 1975, 1977) or there were differences in analytical capabilities. Our wet chemistry method had a lower detection limit of approximately 10 ppm as compared to a lower limit of 50 ppm for the X-ray fluorescence techniques used in other work (H.F. Mayland, personal communication 1977). Another possibility is that vegetation samples had soil particles adhered to their surfaces. Using our measured titanium concentrations in soil, approximately 120 mg of soil would need to be associated with a 20-g vegetation sample to result in a concentration of 17 ppm titanium. A quantity this large should have been seen, and it is doubtful that ultrasound washing would have failed to remove that much soil from plant samples. Therefore, we believe that titanium concentrations we measured were the result of titanium in vegetation, and improved analytical sensitivity may best explain our higher values.

We also measured higher titanium concentrations in mule deer liver and kidney than had been previously reported for terrestrial mammals (Bowen 1966). Because our samples came from deer that had been killed by automobiles, these samples could have been contaminated with soil, resulting in the higher

Table 3. Trace element concentrations (ppm) in upper 3 cm of soils collected under vegetation, from roads, streambanks, and gopher mounds at Rocky Flats Nuclear Weapons Plant, Colorado.

Source		K	Cu	Fe	Zn	Mg	Na	Ca	P	Mn
Under vegetation	$\bar{x}$	537.5	11.3	575	17.5	487.5	42.5	3350	1500	287.5
(n = 2)	*SD*	62.5	1.9	75	0.0	37.5	5.0	250	250	12.5
Road	$\bar{x}$	433.3	14.8	633	10.0	916.7	68.3	6100	833	233.7
(n = 3)	*SD*	77.3	9.4	103	2.0	117.9	30.6	2844	312	35.6
Streambank	$\bar{x}$	312.5	8.5	950	10.0	700	70.0	8200	1000	156.5
(n = 2)	*SD*	12.5	1.6	200	2.5	500	37.5	4100	250	18.5
Gopher mound	$\bar{x}$	496.4	7.0	561	11.4	582	47.9	3257	1071	264.4
(n = 7)	*SD*	49.0	1.1	122	4.6	96	14.8	420	319	40.5
Total	$\bar{x}$	462.5	9.5	634	11.8	657	54.6	4586	1071	245.7
(n = 14)	*SD*	88.5	5.5	184	4.3	255	25.1	2773	359	52.5

titanium values. Greater analytical sensitivity could also explain our higher values. Miller et al. (1975) reported that titanium absorption in domestic sheep did not exceed 0.5% and concluded that titanium could be used as a satisfactory index for soil ingestion by ruminants. We assumed titanium absorption by mule deer was negligible.

The largest daily intake of soil for mule deer feeding at Rocky Flats occurred during the winter and spring seasons, with spring being significantly greater than the other seasons. Observations made on tame deer feeding at Rocky Flats during the winter season (Table 4) indicated that the main portion of their soil intake was taken directly from pocket gopher mounds, roads and other areas where soil was exposed. In spring the high soil consumption of 29.6 g/day may have been primarily due to soil attached to roots of low growing grasses and forbs (cheatgrass, bluegrass, pasture sage, filaree (*Erodium cicutarium*), and musineon (*Musineon divarcatum*), that made up a large portion of deer diets at this time (Arthur 1977). Observations made on tame deer (Table 4) indicated that the majority of their soil intake came about in this manner, which is in agreement with the findings of Mayland et al. (1975) for cattle on a grassland range in southern Idaho. Skipworth (1974) found the largest grit intake by bighorn sheep (*Ovis canadensis*) occurred in spring, but he did not indicate how this intake came about.

Table 4. Frequency of soil ingestion for tame mule deer observed during food habits trails [1] at Rocky Flats Nuclear Weapons Plant, Colorado.

Source	Number of soil ingestion observations			
	Spring	Summer	Fall	Winter
Root of grass, forb	27	27	34	59
Above-ground plant portion	1	2	0	10
Direct soil	11	19	15	27
Gopher mound	5	0	8	7
Road	1	2	2	5
Total number of times soil ingested	45	50	59	108
Percent of food trials where soil ingested	50.0	58.1	61.2	54.2
Mean number of soil ingestions per food trial	0.98	1.16	1.20	1.30

[1] A food haibts trial consisted of a period of time, usually 1 to 3 hours when deer were allowed to forage freely over the study area.

During summer and fall months, soil consumption declined sharply to 7.7 and 8.8 g per day, respectively. Plants in the growing state are higher in trace elements (Cu, Fe, K, Mg, P, Se, and Zn; Keiss 1977) and animals may receive adequate trace elements from forage during these periods. For our tame deer it appeared that soil consumption during these seasons was due to material adhering to above-ground plant parts, and other incidental intake while foraging (Table 4).

While data in Table 2 came from analysis of fecal material from resident wild deer at Rocky Flats and should be representative of their soil intake, data presented in Table 4 were obtained from observations on our tame deer during food habits trials at Rocky Flats. We present these data as an indication of sources of soil ingestion by deer. In addition, the frequency of soil ingestion events observed in tame animals correlates with seasonal fluctuations in calculated soil intake rates for resident wild deer. The manner in which wild and tame deer ingest soil may be similar, but we would not actually expect that the frequency of direct soil ingestion would be similar in these animals. When tame deer were not being used at Rocky Flats, they were maintained in a facility at Fort Collins, Colorado, where they were provided with a commercial ration that was believed to contain adequate amounts of trace elements. Therefore, during the brief periods (5 to 8 days) when these animals were feeding at Rocky Flats they likely would not be stimulated to seek additional trace elements that may have been lacking in vegetation. Regretfully, we have no data on trace elements in vegetation at Rocky Flats.

Comparison of trace element content in soils collected from areas where tame deer ingested soil to areas where no soil intake was observed indicated no significant differences in elemental concentrations. If deer were selectively ingesting soil, trace element content does not appear to be the criteria of selection. However, we suspected that these animals were probably eating soil as a source of trace elements, and thus concluded that mule deer at Rocky Flats probably did not select soil, but consumed it indiscriminately from areas where it was exposed. To our knowledge, there are no natural mineral licks in the area.

Soil intake rates measured for mule deer in this study ranged from 0.6 to 2.1 percent of the weight of their total daily dry matter intake. Healy et al. (1970) reported that dairy cattle in New Zealand consumed as much as 450 kg per year, which was approximately 2% of their dry matter intake over the year; and Mayland et al. (1977) estimated that cattle feeding on an Idaho range in June consumed 0.73 kg of soil per day, which was approximately 7% of their daily dry matter intake. These and other investigators (Skipworth 1974) have suggested that foraging ruminants may consume soils as a source of trace elements lacking in vegetation.

Conclusions

Soil intake rates in grams per day for free-ranging, mule deer feeding at Rocky Flats, Colorado were ($x \pm SD$): spring, 29.6± 20.1; summer, 7.7±10.2; fall, 8.8±6.5; and winter, 18.3± 10.8. While we did not have data to indicate reasons for soil consumption, intake patterns measured in wild deer and observed in tame deer were inversely correlated with reported trace element concentrations in vegetation. Trace element analysis conducted on soil samples from out study area indicated that deer were probably not selecting specific soil for any trace elements in our analysis.

Observations on tame deer feeding at Rocky Flats indicated that deer may consume soil directly, consume it in association with plant roots, or take it in indirectly with above-ground portions of plants. The manner in which soil is ingested appears to be related to season of the year and species of plants in the deer diet. The greatest soil ingestion rate in spring was 29.6 g/day, and based on observations of tame deer the principal mode of entry was soil associated with plant roots. The second largest intake rate, 18.3 g/day in winter, may have come primarily from direct ingestion of soil. Low intake rates of 8.8 g/day and 7.7 g/day in fall and summer likely arose from ingestion of soil attached to above-ground plant parts.

While ingestion of soil may be an important source of trace elements for mule deer, at Rocky Flats Nuclear Weapons Plant, where soils contain measurable amounts of plutonium, the intake of even small quantities of soil can result in the animal's consuming measurable amounts of this radioactive contaminant. The intake and subsequent fate of ingested plutonium by mule deer at Rocky Flats will be the subject of future reports. We recommend that future studies attempting to quantify soil ingestion using the titanium tracer technique should examine titanium in vegetation and correct for these concentrations.

Literature Cited

Alldredge, A.W., J.F. Lipscomb, and F.W. Whicker. 1974. Forage intake rates of mule deer estimated with fallout Cesium-137. J. Wildl. Manage. 38:508-516.

Arthur, W.J. III. 1977. Plutonium intake by mule deer at Rocky Flats, Colorado. MS Thesis, Colorado State Univ., Fort Collins. 123 p.

Bowen, H.J.M. 1966. Trace Elements in Biochemistry. Academic Press. New York. 241 p.

Clark, S., and P.J. Webber. 1975. Brief descriptions of the vegetation units recognized on the Rocky Flats map. Inst. of Arct. and Alpine Res., and Dep. of Environ., Pop., and Organ. Biol., Univ. of Colorado, Boulder. 18 p.

Duncan, D.B. 1955. Multiple range and multiple f tests. Biometrics 11:1-42.

Healy, W.B. 1968. Ingestion of soil by dairy cows. New Zealand J. Agr. Res. 11:487-499.

Healy, W.B., W.J. McCabe, and G.F. Wilson. 1970. Ingested soil as a source of microelements for grazing animals. New Zealand J. Agr. Res. 13:503-521.

Hiatt, G.S. 1977. Plutonium dispersal by mule deer at Rocky Flats, Colorado. MS Thesis. Colorado State, Fort Collins. 143 p.

Keiss, R.E. 1977. Evaluation of the nutritonal requirements of bighorn sheep. Colorado Div. Wildl. P-R Proj. Rep. W-41-R-26. pp: 1-56.

Krey, P.W., and E.P. Hardy. 1970. Plutonium in soil around the Rocky Flats Plant. USAEC Rep. HASL-235. 44 p.

Krey, P.W., and B.T. Krajewski. 1972. Plutonium isotopic ratios at Rocky Flats. USAEC Rep. HASL-249. p: 67-94.

Little, C.A. 1976. Plutonium in a grassland ecosystem. PhD Thesis, Colorado State Univ., Fort Collins. 170 p.

Mayland, H.F., A.R. Florence, R.C. Rosenau, V.A. Lazar, and H.A. Turner. 1975. Soil ingestion by cattle on semiarid range as reflected by titanium analysis of feces. J. Range Manage. 28:448-452.

Mayland, H.F., G.E. Shewmaker, and R.C. Bull. 1977. Soil ingestion by cattle grazing crested wheatgrass. J. Range Manage. 30:264-265.

Miller, J.K., F.C. Maasen, and S.L. Hansard. 1975. Titanium-44 metabolism in ruminants. J. Anim. Sci. 42:279. (Abstr.)

Smith, A.D. 1964. Defecation rates of mule deer. J. Wildl. Manage. 28:435-444.

Skipworth, J.P. 1974. Ingestion of grit by bighorn sheep. J. Wildl. Manage. 38:880-883.

Wallmo, O.C., and D.J. Neff, 1968. Direct observation of tame deer to measure their consumption of natural forage. P. 105-110. *In:* Range Wildlife Habitat Evaluation U.S. Dep. Agric. Misc. Publ. 1147, 220 p.

Yoe, J.H., and A.R. Armstrong. 1947. Colormetric determination of titanium with disodium-1, 2-dihydroxybenzene-3, 5-disulfonate. Anal. Chem. 19:100-102.

Arrowleaf Balsamroot and Mules Ear Seed Germination

JAMES A. YOUNG AND RAYMOND A. EVANS

Abstract

The germination of arrowleaf balsamroot (*Balsamorhiza sagittata*) and mules ear (*Wyethia amplexicaulis*) was studied. Both species are important coarse forbs on sagebrush (*Artemisia*) rangelands in western North America. Germination of the seeds (achenes) of both species was enhanced by cool-moist stratification, 4 weeks at 2 or 5° C for mules ear and 12 weeks for arrowleaf balsamroot. After stratification, mules ear seeds germinated at a wide range of constant and alternating temperatures. Germination of arrowleaf balsamroot seeds was greatly enhanced by stratification, but even after stratification, germination was restricted to comparatively low temperatures.

Arrowleaf balsamroot (*Balsamorhiza sigittata*) and mules ear (*Wyethia amplexicaulis*) are both robust, tap-rooted perennial forbs with large, usually solitary, flower heads. The ray flowers are showy, and usually yellow. Other than historical practice, there probably is no reason to treat *Wyethia* and *Balsamorhiza* as separate genera (Cronquist 1955). Both genera are widely distributed from the Pacific Northwest to Nevada and east to Colorado. There are apparently few barriers to hybridization among species of either genus (Cronquist 1955). Numerous hybrids have been identified in local areas.

Both arrowleaf balsamroot and mules ear have wide ecologic distribution in numerous plant communities (Anonymous 1937). However, both species are most abundant in the more mesic sagebrush (*Artemisia*) grasslands. These are the sites at higher elevations and north-facing slopes where more moisture is available for plant growth. Both species are also common in woodland or seral timber communities at elevations above the sagebrush zone. Densities of arrowleaf balsamroot and mules ear generally increase after range communities are burned (Young and Evans 1977). This increase is especially evident if degraded plant communities are burned. In some areas where these coarse forbs have greatly increased, they represent serious competition for forage grasses and other forbs (Young and Evans 1978).

Young basal leaves of these species are springly grazed by livestock. Arrowleaf balsamroot generally grows in mixed stands with grasses, other forbs, and shrubs. Mules ear is generally less preferred as forage and it grows to the exclusion of other, more desirable forage species. Mature herbage is generally too coarse for use by livestock. Cattle, sheep, and horses will graze on the flower heads and, in years with good seed production, livestock will eat the seeds.

Reproduction of these two species is entirely by seeds and species increase at the expense of forage grasses. With their attractive and showy flowers, both arrowleaf balsamroot and mules ear may be desirable revegetation species for mining spoils and other disturbed areas where they are adapted. A knowledge of seed germination and seedbed ecology is necessary for successful revegetation with these species.

The authors are range scientists, U.S. Department of Agriculture, SEA Agricultural Research, Renewable Resource Center, University of Nevada, Reno 89512.

This study is a contribution from U.S. Dep. Agr. SEA, Agricultural Res., and the Agr. Exp. Sta., Univ. of Nevada, Reno. Journal Series No. 391.

Manuscript received February 7, 1978.

Our purpose in this investigation was to investigate the germination of these two species.

Methods

Seeds of mules ear and arrowleaf balsamroot were collected from numerous stands in northern Nevada and northeastern California from 1970 through 1976. Seeds from numerous plants at each location were composited in a single collection for each species. Preliminary trials showed that most seeds of both species were dormant and that this dormancy was not broken with dry storage. These trials also showed that dormancy could be broken with cool-moist stratification.

Using results of the preliminary trials, a comprehensive stratification experiment was designed. Seeds for each species from two different sources were used, and the results were averaged for presentation. Four replications of 100 seeds were used in each experiment. Cellulose was used instead of sand or vermiculite as the stratification medium so that the seeds could be easily observed during the stratification period. Seeds were placed on a single thickness of expanded cellulose in petri dishes, and the dishes were covered with a single thickness of germination paper for stratification. The paper and cellulose were kept moist during the entire stratification period. Stratification treatments were at 0, 2, 5, and 10°C in dark germinators for 2, 4, 6, 8, 10, and 12 weeks. At the end of each stratification period seeds were removed and incubated for 4 weeks at 10/25°C (10°C for 16 hr and 25°C for 8 hr daily) for mules ear and at 10°C for arrowleaf balsamroot. Results of preliminary trials indicated that these temperatures were optimaly effective, with optimum effectiveness defined as not being significantly (P=0.05) different from maximum germination. Germination counts were made after 1, 2, and 4 weeks of incubation. Seeds were considered to have germinated when the radicle had emerged 1 cm.

Temperature profiles were developed for pretreated (stratified) and unstratified seeds of each species. To develop germination profiles as affected by temperature, we incubated seeds of both species for 4 weeks at constant temperatures of 0, 2, 5, 10, 15, 20, 25, 30, 35, and 40°C. In addition, seeds were incubated at each of these constant temperatures for 16 hr in alternation with each possible higher temperature for 8 hr in each 24 hr period. For example, 0°C was alternated with 2, 5, 10, 15, 20, 25, 30, 35, and 40°C wheras 35°C was alternated with 40°C only.

Results and Discussion

The germination of seeds of both mules ear and arrowleaf balsamroot was enhanced by cool-moist stratification to break dormancy. Other than this generalization, there was little resemblance in the germination characteristics of the two species.

Mules Ear

Some seeds of mules ear germinated without stratification (Table 1). However, cool-moist stratification greatly enhanced their germination. Stratification of mules ear seeds for 4 weeks was required for near maximum germination (Fig. 1). Temperatures of 2 to 5°C were required. Microbial decomposition prevented germination of mules ear seeds after 8 weeks of stratification at 10°C. This temperature never resulted in enhancement of germination. At the other extreme, stratification at 0°C never enhanced germination and resulted in a slow decline in germinability.

Nonstratified seeds of mules ear germinated in about one-half of the 55 constant-and alternating temperature regimes tested (Table 1). When seeds were stratified at 2°C for 4 weeks and then exposed to the same temperature regimes, some germination occurred at all temperatures but a constant 0°C.

There were three optimum alternating temperature regimes for nonstratified and five optima for stratified mules ear seeds (Table 1). Three of the optima, 5/20, 5/25, and 5/30°C, were the same for each treatment. The additional optima for stratified seeds, were 10/25 and 10/30°C. Although the optima occurred in the same general range of alternating temperatures, the magnitude of germination at the optima differed greatly between nonstratified and stratified seeds. The mean germination at the optimum temperatures was 45% for nonstratified

Table 1. Germination (%) of mules ear seeds at constant and alternating temperatures with and without previous moist stratification. Incubation for 4 weeks.[1]

	Cool period °C – 16 hr	Warm period °C – 8 hr. 0	2	5	10	15	20	25	30	35	40
Germination after 4 weeks stratification at 2°C	0	0	4q-s	9p-s	7q-s	18l-s	20j-s	24j-r	20k-s	15m-s	6q-s
	2		7q-s	10o-s	26j-r	41f-j	23j-s	65c-e	68b-e	36h-n	15m-s
	5			16m-s	32i-n	61c-f	76a-d	81a-c	92a	30j-o	16m-s
	10				31j-n	54e-h	66c-e	94a	88ab	24j-r	28j-p
	15					24j-r	30k-n	68b-e	58d-g	40f-k	11n-s
	20						16m-s	53e-i	42f-j	20k-s	8p-s
	25							38g-l	22j-s	14n-s	2s
	30								5q-s	9p-s	4q-s
	35									4q-s	2s
	40										3r-s
Germination with unstratified seed	0	0	0	0	0	2g	26b-f	9e-g	4g	0	0
	2		0	0	2g	13d-s	29b-e	31b-d	24c-g	0	0
	5			1g	5g	15d-g	45ab	52ab	39a-c	0	0
	10				5g	11e-g	16d-g	27b-f	19d-g	0	0
	15					13d-g	13d-g	16d-g	15d-g	0	0
	20						3g	8f-g	3g	0	0
	25							0	0	0	
	30								0	0	0
	35									0	0
	40										0

[1] All means followed by the same letters are not significantly different at the 0.01 level of probability as determined by Duncan's multiple range test stratification and control compared separately. For readers' convenience, means not significantly different from maximum are underlined.

Table 2. Germination (%) of arrowleaf balsamroot seed at constant and alternating temperatures with and without previous moist stratifications incubation for 4 weeks.[1]

	Cool period °C – 16 hr	Warm period °C – 8 hr 0	2	5	10	15	20	25	30	35	40
Germination after 4 weeks stratification at 2° C	0	6m-o	2 0j-o	69a-e	68a-e	76a-c	72a-d	47e-i	28i-m	0	0
	2		36g-k	80ab	67a-e	69a-e	43f-j	27i-n	30i-l	15k-o	0
	5			87a	86ab	65a-f	57b-h	43f-j	50d-i	3 0	0
	10				69a-e	34i-k	43f-j	35h-k	21j-o	3 0	0
	15					36g-k	20j-o	8L-O	19k-o	0	0
	20						27i-n	9L-O	6m-o	0	0
	25							4no	3o	1o	0
	30								6m-o	0	0
	35									0	0
	40										0
Germination with unstratified seed	0	0	0	0	0	2	0	0	0	0	0
	2		0	0	0	0	0	2	0	0	0
	5			4	0	2	8	0	0	0	
	10				18	2	0	4	0	0	0
	15					0	0	0	0	0	0
	20						0	0	0	0	0
	25							0	0	0	0
	30								0	0	0
	35									0	0
	40										0

[1] All means of stratified seed followed by the same letters are not significantly different at the 0.01 level of probability as determined by Duncan's multiple range test. For reader's convenience, means not significantly different from maximum are underlined.

seeds and 86% for stratified seeds.

Without stratification, mules ear seeds did not germinate with cool-period temperatures higher than 20°C or warm-period temperatures higher than 30°C. Alternation with extremes of low temperatures also inhibited germination.

With stratification, none of the temperature regimes tested prevented germination of mules ear seeds except a constant 0°C, but germination tended to be quite low at extremes of high and low temperatures.

Arrowleaf Balsamroot

For seeds of arrowleaf balsamroot, in contrast to the seeds of mules ear, germination without stratification was very low and erratic (Table 2). A 12 week period of stratification was required for enhancement of germination and for maximum germination (Fig. 2).

As with mules ear seeds, the highest stratification temperature tested (10°C) was not effective, and the most effective temperatures were 2 and 5°C. At the lowest temperature (0°), stratification for 12 weeks was required for enhancement of germination (Fig. 2).

Stratification for 8 weeks at 5°C was the pretreatment used for development of the temperatures for arrowleaf balsamroot profile. We chose 8 weeks, even though germination after this stratification period was only 50% of that obtained after 12

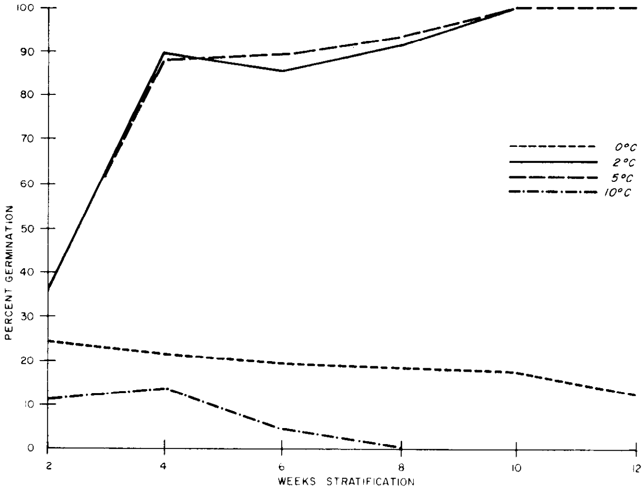


Fig. 1. *Germination (%) of mules ear seeds after moist stratification at 0, 2, 5, or 10°C from 2 through 12 weeks. Seeds were then incubated at 10/25°C (10°C for 16 hr/25°C for 18 hr daily) for weeks before germination percentages were determined.*

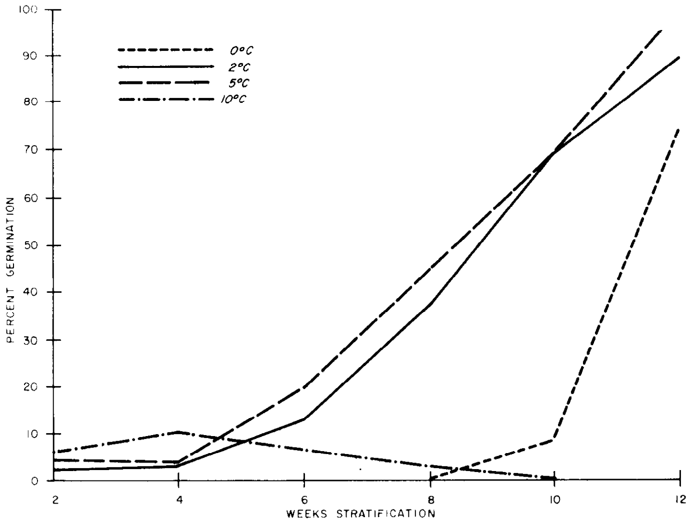


Fig. 2. *Germination (%) of arrowleaf balsamroot seeds after moist stratification at 0, 2, 5, or 10°C from 2 through 12 weeks. Seeds were then incubated at 10°C for 4 weeks before germination percentages were determined.*

weeks of stratification, because some seeds germinated during stratification. The problem is that optimum temperatures for germination were essentially temperatures for the optimum stratification. This complicates stratification of arrowleaf balsamroot seeds before sowing in the field or nursery, because of the danger that emerging radicles will be damaged.

Nonstratified arrowleaf balsamroot seeds germinated at only 15% of the temperature regimes tested (Table 2). Stratified seeds germinated at 55% of the temperature regimes.

There were no significant differences among germination percentages for nonstratified seeds. In contrast, 11 temperature regimes were optima for germination of stratified seeds (Table 2). The warmest of these regimes was a constant 10°C and the coldest was 0/5°C. All of the optima temperatures were very low for germination in comparison with optima for other species. A temperature of 35°C reduced germination and a warm-period temperature of 40°C prevented germination.

Significance of Stratification Requirements

Although stratification is essential for the germination of many seeds of species in such economically important families a Rosaceae, Juglandaceae, and Pinaceae, we do not know by what processes stratification affects germination. Come and Tissaoui (1972) provided an enlightening discussion on the probable mode of action of cool-moist stratification in transferring oxygen to dormant embryos through restrictive seedcoats.

In a previous study (Young and Evans 1977) we found that for seed of bitterbrush (*Purshia tridentata*) cool-moist stratification requirements may be extended if stratification is interrupted by varying temperatures or moisture stress. Seeds of mules ear require only 4 weeks of stratification, so a cool-moist period in the fall could satisfy the stratification requirement. However, we must remember that stratification temperature must remain above 0°C and below 10°C for best germination of mules ear seeds.

The 3-month stratification requirement of arrowleaf balsamroot seeds is long for many rangeland seedbed, even through 0°C appears to be an acceptable stratification temperature for this species. The 0°C environment we used for stratification did not crystalize the water. In other studies (Young and Evans 1977), we have shown that in species in which germination is enhanced by stratification at 0°C, exposure to −2°C reduces or prevents the enhancement; i.e., the range of acceptable temperatures is very restricted. The only environment on sagebrush rangelands that might have a satisfactory stratification of arrowleaf balsamroot seeds is at the snow-litter-soil interface in sites with continuous snow cover for at least 3 months. This may explain the occurrence of dense communities of arrowleaf balsamroot on north-facing slopes where snow drifts accumulate. The snow-soil interface as a germination environment has been studied by Bleak (1959) and Hull (1960).

Literature Cited

Anonymous. 1937. Range plant handbook. Forest Serv., U.S. Dep. Agr., Government Printing Office, Washington, D.C.

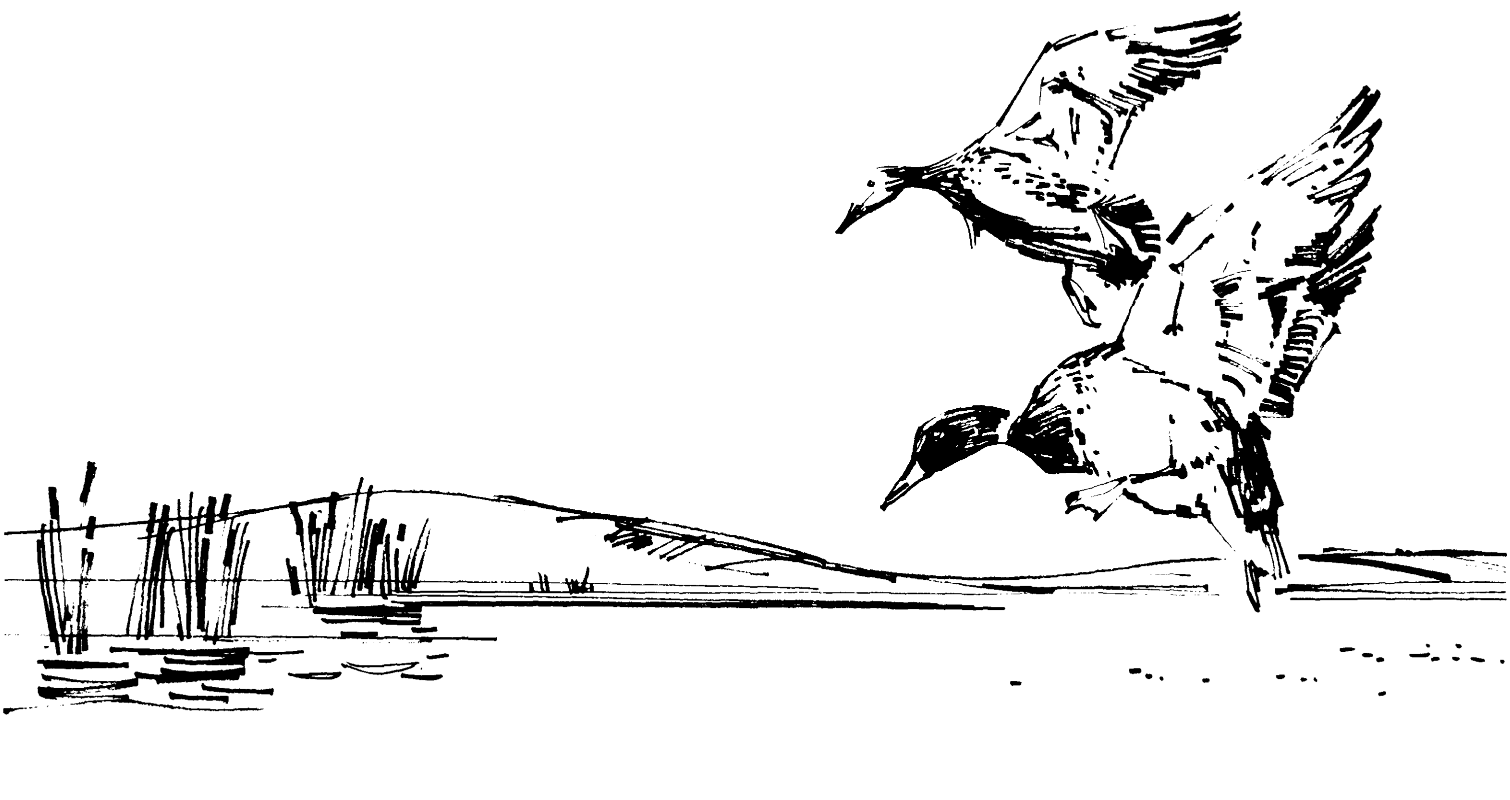
Bleak, A.T. 1959. Germination characteristics of seeds under snow. J. Range Manage. 12:298-302.

Come, D., and T. Tissaoui. 1972. Interrelated effects of inhibition, temperature and oxygen on seed germination. p. 157-168. *In:* W. Heydecker (Ed.). Seed Ecology. Penn. State Univ. Press, Univ. Park, Pa.

Cronquist, A. 1955. Part 5. Compositae. p. 99. *In:* C.L. Hitchock, A. Cronquist, M. Ownbey, and J.W. Thompson (Eds.). Vascular plants of the Pacific Northwest. Univ. of Washington Press, Seattle, Wash.

Hull, A.C., Jr. 1960. Winter germination of intermediate wheatgrass on mountain lands. J. Range Manage. 13:257-260.

Young, J.A., and R.A. Evans. 1978. Population dynamics after wildfires in sagebrush grasslands. J. Range Manage 31:283-290.



TECHNICAL NOTES

A Simple, Lightweight Point Frame

STEVEN H. SHARROW AND DWIGHT A. TOBER

Abstract

A simple, lightweight, yet rugged point frame is described. This frame can be easily constructed at a relatively low cost (1975 cost of materials=$6.00 per frame).

Heady and Rader (1958) described a four-legged steel point frame which they found well suited to sampling California annual rangelands. Since then, several modifications of this basic frame have been proposed. Smith (1959) described a three-legged frame constructed from angle aluminum. The modified design, using aluminum, was 8.5 kg lighter than the 19-kg steel frame and was equally sturdy. In addition, the hinged third leg allowed easy positioning of the frame at any desired pin angle regardless of slope. Rader and Ratliff (1962) replaced the holes previously used to guide sampling pins in the cross arms with notches. This eliminated much of the drudgery of repeatedly raising pins. It also reduced sampling time by allowing repeated use of a single pin rather than the ten pins previously required. An added advantage was that the pin could be easily removed for transit, thus reducing the chance of bending pins while moving from one sampling area to another. The purpose of this paper is to describe a further modification of the point frame which incorporates many of the best features of the above designs.

This frame (Fig. 1) is somewhat similar in appearance to one previously described by Neal et al. (1969) but differs significantly in materials and construction. It can be constructed with ordinary shop tools in about one man day. Material costs are realatively low. Cost per frame in 1975 was only $6.00.

Three legs, each 57 cm long, and two cross arms, each 30 cm long, are cut from 20 × 20 × 3 mm-angle aluminum. They are fastened in place with two small bolts per joint. The back leg is attached to the frame using a 5-cm piece of angle aluminum and a 2.5 × 2.5-cm hinge (Fig. 2). The hinged third leg gives the frame stability while allowing the operator to select a wide range of pin angles or to compensate for steep topography by simply positioning the leg closer to or farther from the main body of the frame. A small chain attaches between the leg and the main body of the frame to facilitate positioning of the pins at a preselected angle. A wide range of angles can be easily obtained by adjusting the length of the chain.

Ten 6 mm deep V-shaped notches are cut at 2.5-cm intervals into the cross arms with a triangular file. A longer distance between adjacent notches may be required where vegetation is very sparse or tends to be contagiously distributed (Crocker and Tiver 1948). However, the authors found the 2.5 cm spacing worked well for sampling blue grama (*Boutelous gracilis*) rangelands in New Mexico.

Fig. 1. *Point frame and piano wire pin used to sample New Mexico rangelands.*

During sampling, the single pin is held in position by ceramic magnets positioned directly behind each notch. In order for the magnets to hold the pins firmly, they must be placed as close as possible to the pins. This is accomplished by using a 2.8 × 28 × .3 cm thick wooden spacer strip to which the magnets are held flush with the vertexes of the notches by a small screw. The spacer strip is held in place by two bolts.

Ten points per frame are obtained by moving a single pin from notch to notch. This proves to be a very rapid procedure. When the tenth point has been recorded, the point is removed and the frame folds easily for transit to the next location.

The notches of the frame will accept a wide range of different types and sizes of pins. In contrast to previously used pins (Heady and Rader

The report is submitted as Technical Paper No. 4748. Oregon Agricultural Experiment Station, Corvallis.

Authors are, respectively, assistant professor, Rangeland Resources Program, Oregon State University, Corvallis, 97331; and range research technician, Department of Animal and Range Science, New Mexico State University Las Cruces 88003.

Manuscript received January 23, 1978.

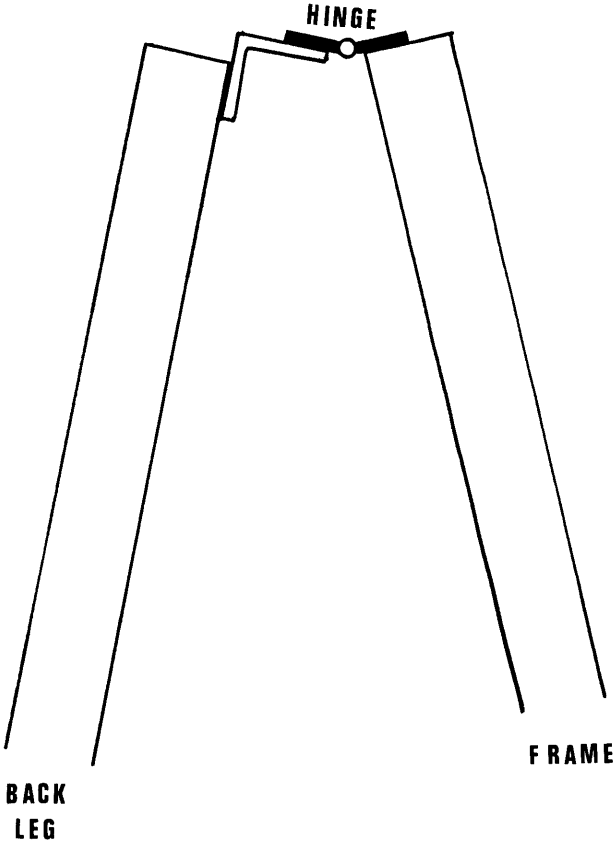


Fig. 2. *Diagram showing attachment of hinged third leg to the body of the point frame.*

1958; Smith 1959) made from welding rod, which tended to bend, the pins employed here are piano wire. Piano wire is quite resilient and not only resists warping but also tends to stay in the notches well by absorbing some of the torque exerted on the pins during sampling. Small diameter piano wires (<2 mm), however, tend to be too limber, while large wires (>6 mm) are too massive to be firmly held by the magnetic brakes. A 3-mm diameter pin works well.

In summary, the authors have found the frame described here to be well suited to sampling blue grama rangeland in New Mexico. It proved to be sturdy, lightweight (approximately 1.1 kg), and easy to use.

Literature Cited

Crocker, R.L., and N.S. Tiver. 1948. Survey methods in grassland ecology. J. Brit. Grassland Soc. 3:1-26.

Heady, H.F., and L.R. Rader. 1958. Modifications of the point frame. J. Range Manage. 11:95-96.

Neal, D.L., R.L. Hubbard, and C.E. Conrad. 1969. A magnetic point frame. J. Range Manage. 22:202-203.

Rader, L.R., and R.D. Ratliff. 1962. A new idea in point frames. J. Range Manage. 15:182-183.

Smith, J.G. 1959. Additional modifications of the point frame. J. Range Manage. 12:204-205.

The Value of Fresh-stripped Topsoil as a Source of Useful Plants for Surface Mine Revegetation

GENE S. HOWARD AND MARILYN J. SAMUEL

Abstract

Topsoil from nearby undisturbed areas was stripped and directly laid over regraded overburden to a depth of about 20 cm at Kemmerer, Wyo., and Oak Creek, Colo. Native plant response was determined after two growing seasons with only natural precipitation. Rhizomatous species were the most valuable for establishing the perennial plants. Plant density averaged 4.16 and 1.77 plants/m^2 at Kemmerer and Oak Creek sites, respectively, but the density was too low to meet State and Federal revegetation standards without additional seeding. Plants established from fresh-stripped topsoil are a plus in revegetation as opposed to stockpiled topsoil where these plants are lost.

Rangeland topsoil contains seed, rhizomes, and other vegetative plant parts of many native species. Beauchamp et al. (1975), who studied Wyoming topsoil as a seed source for reseeding stripmine spoils, concluded that viable seed of desirable species was plentiful in the top 2 inches of soil. However, they indicated that seeding or transplanting of desired species would also be required to meet State reclamation standards. Knipe and Springfield (1972), working in New Mexico, found that natural reproduction from seed of desirable range plants was subject to high loss by wind, water, animals, or insects, and unfavorable conditions for seedling establishment, thus limiting natural reseeding of disturbed lands.

A survey was conducted in fall 1977 at two locations to determine species establishment and plant density on spoils that were topsoiled in 1976 with fresh-stripped topsoil.

Authors are horticulturist and botanist, respectively, Department of Agriculture-Science and Education Administration, High Plains Grassland Research Station, Cheyenne, Wyoming 82001.

This study is a contribution from SEA-AR, U.S. Dep. Agr. in cooperation with the Wyoming Agricultural Experiment Station, University of Wyoming, Laramie. It was supported in part by the Environmental Protection Agency Interagency Agreement Funds: EPA-IAG-D5-E763.

Manuscript received February 8, 1978.

Study Area

Study areas were located at the Kemmerer Coal Co. near Kemmerer, Wyo., and the Pittsburg and Midway Coal Co. near Oak Creek, Colo.

Elevation at the Kemmerer site is about 2,317 m. The experimental topsoil came from a big sagebrush (*Artemisia tridentata*) plant community. Major plant species included western wheatgrass (*Agropyron smithii*), slender wheatgrass (*A. trachycaulum*), big sagebrush, fourwing saltbush (*Atriplex canescens*), and Indian ricegrass (*Oryzopsis hymenoides*). The average annual precipitation at Kemmerer is 23.52 cm. Topsoil at Kemmerer is a Ustic torriorthent with a clayey, montmorillinitic calcareous, frigid, shallow family and loamy, skeletal mixed calcareous family. The slope is about 15%.

At Oak Creek the elevation is about 2,286 m. The topsoil came from a mix-shrub plant community. Major plant species were saskatoon serviceberry (*Amelanchier alnifolia*), gambels oak (*Quercus gambeli*), quaking aspen (*Populus tremuloides*), big sagebrush, snowberry (*Symphoricarpos albus*), chokecherry (*Prunus virginiana*), and mountain brome (*Bromus marginatus*). The average annual precipitation at Yampa, Colo. which is 13 km south of the Oak Creek site, is about 39.37 cm. The topsoil at Oak Creek is an unnamed complex having a slope of about 25%.

Materials and Methods

In spring 1976, topsoil from nearby undisturbed areas was stripped with earthmovers and immediately spread as uniformly as possible over reclaimed overburden to a depth of about 20 cm at each site. Topsoil was stripped at Kemmerer to depths of 10 to 60 cm and at Oak Creek to depths of 45 to 60 cm.

On June 16, 1977, at Kemmerer and on June 29, 1977, at Oak Creek, all plant species within the topsoiled plots were listed to determine plant establishment after spring seed germination. On September 26 at Oak Creek and on September 27 at Kemmerer, quadrats along transects were laid out within the topsoiled plots. At Kemmerer, six transects were randomly located in each of six plots (6 m wide by 69 m long for a total of 414 m). At Oak Creek, six transects were randomly located in each of 6 plots (7 m wide by 46 m long for a total of 276 m). Populations of species were counted along the transects at .9-m intervals. We counted 450 quadrats at Kemmerer and 300 quadrats at Oak Creek. Tillers were counted for rhizomatous species, and plants were counted for the other species.

Results and Discussion

Precipitation for the 16 months preceding the plant density survey was about 12.62 and 27.94 cm for Kemmerer and Oak Creek, respectively.

Despite drouth conditions, we found 39 species growing in the new topsoil at Kemmerer, about 14 months after treatment. At Oak Creek, we found 41 species. Most of these species did not survive over summer and were not counted in September. Hence they only have been transitory or too few to be significant in disturbed-land reclamation.

The topsoiled plot and an adjacent overburden experimental plot at Oak Creek were densely covered with Russian thistle (*Salsola kali*). Seed was probably transported by wind from nearby areas.

Table 1 gives the density, as determined by the quadrat survey, from the Kemmerer and Oak Creek areas. The density of grasses was greater at Kemmerer than at Oak Creek, probably because of the rhizomatous habit of western wheatgrass. The density of perennial forbs was also greater at Kemmerer than at Oak Creek, whereas the density of woody shrubs was the same at both sites.

Table 1. Species density (no./m²) at the test sites, after two growing seasons, in September, 1977.

Species	Common name	Kemmerer	Oak Creek
Perennial Grasses			
Agropyron smithii var. *molle**	Western wheatgrass	2.19	–
Agrostis scabra	Rough bent	.15	–
Bromus marginatus	Mountain brome	–	.66
Elymus cinereus	Basin wildrye	.18	–
*Poa arida**	Plains bluegrass	.52	.70
Total		3.04	1.36
Perennial Forbs			
*Achillea millefolium lanulosa**	Common yarrow	.19	.03
*Aster engelmanni**	Engelmann aster	.75	–
Cirsium drummondi	Drummond thistle	–	.04
Meliolotus officinalis	Sweet clover	–	.04
*Vicia americana**	American vetch	–	.04
Viguiera multiflora	Showy goldeneye	–	.08
Total		.94	.23
Woody Shrubs			
Artemisia tridentata	Big sagebrush	.08	.08
Chrysothamnus viscidiflorus	Douglas rabbitbrush	.05	–
Rosa woodsii	Woods rose	.02	–
Symphoricarpos albus	Common snowberry	.03	.10
Total		.18	.18
Total of the 3 above groups:		4.16	1.77
Annuals			
Capsella bursa-pastoris	Shepherdspurse	.15	–
Chenopodium album	Lambsquarter goosefoot	–	.02
C. strictum	– – – –goosefoot	.27	–
Hordeum jubatum	Foxtail barley	–	.03
Kochia scoparia	Belvedere summer-cypress	72.68	–
Lactuca scariola	Wild lettuce	–	.07
Lappula redowski	Common stickseed	–	.28
Moldavica parviflora	Dragonhead	–	.13
Polygonum aviculare	Prostrate knotweed	.03	.04
Salsola kali	Russian thistle	88.0	952.0

**rhizomatous*

Conclusions

Topsoil that is stripped in early spring and immediately spread is a good source for some useful reclamation plants. In arid regions, this source is important, not so much as a seed source as for the transfer of rhizomes and other vegetative plant parts that will grow after they are moved. The value of certain rhizomatous species is shown by their survival at Kemmerer, despite the low precipitation, as compared with the lower survival of all plant types at Oak Creek, which had about twice the precipitation. The lower survival at Oak Creek may be attributed to a different plant community as well as to drouth conditions during the test period.

The average plant density, for all perennial species, was 4.16 plants/m² at Kemmerer and 1.77 plants/m² at Oak Creek. This is not an adequate plant population to meet State and Federal revegetation standards. However, these native plants may serve as seed and rhizome sources for increased plant density in later favorable years. Seeding of range species or irrigating sites during the establishment period should enhance adequate revegetation at the Kemmerer site. Seeding selected species would probably suffice at Oak Creek, where precipitation is not so limited.

Literature Cited

Beauchamp, H., R. Lang, and M. May. 1975. Topsoil as seed source for reseeding strip mine spoils. Univ. of Wyoming, Agr. Exp. Sta., Res. J. 90. 8 p.

Knipe, O.D., and H.W. Springfield. 1972. Germinable alkali sacaton seed content of soils of the Rio Puerco Basin, West Central New Mexico. Ecology 53 (5): 965-968.

Cattle Grazing Impacts on Small Cleared Areas in Dense American Elm Woodlands

JAMES F. GEORGE AND JEFF POWELL

Abstract

Removal of overstory canopy of American elm (*Ulmus americana*) greatly increased the utilization of understory herbaceous vegetation by cattle. Cattle browsing killed all the elm sprouts.

American elm (*Ulmus americana*) is an important component of stream-course and flood plain woodlands of central Oklahoma and is invading contiguous uplands (Rice and Penfound 1959). This increase in overstory cover not only decreases production of forage species, but also decreases palatability of those plants present (Welton and Morris 1928; Halls and Epps 1969).

In a study in northern Oklahoma, Dwyer (1961) found that cattle browsed American elm, often maintaining individual trees in a shrub-like state. Dalrymple et al. (1965) reported that Winged elm (*U. alata*), a similar species, was heavily browsed by cattle in Oklahoma.

The objectives of this study were to determine the effects of top removal and fertilization of an American elm woodland on utilization of understory herbaceous vegetation and woody sprouts by cattle.

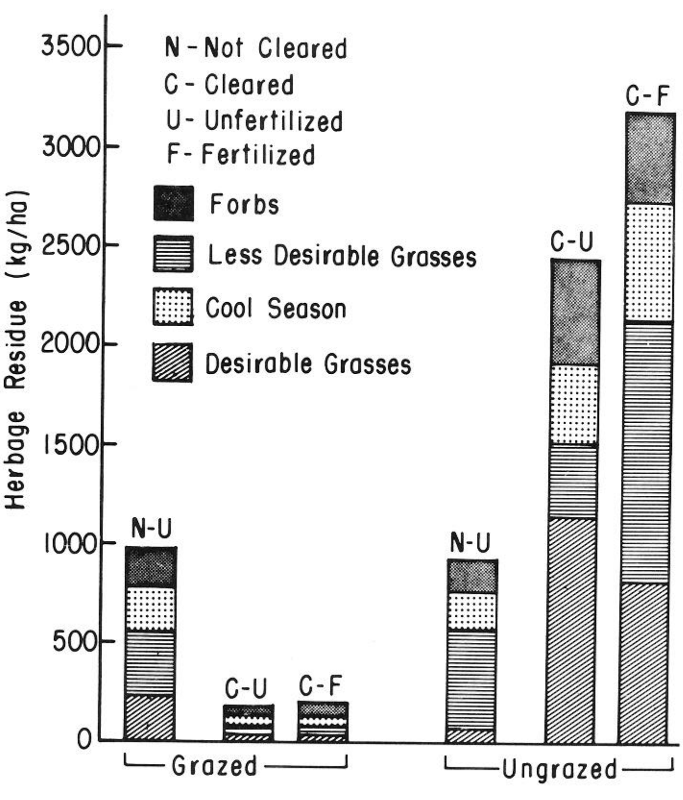


Fig. 1. *Herbage residue (kg/ha oven-dry) remaining at end of 1973 growing season.*

Authors are research assistant and associate professor, Department of Agronomy, Oklahoma State University, Stillwater. James George is, at present, range scientist, El Paso Natural Gas Company, El Paso, Texas.

The research is a contribution of the Oklahoma Agricultural Experiment Station as Journal Article Number 3424.

Manuscript received February 21, 1978.

Study Area

The study area is located in Payne County, Oklahoma, about 18 km west of Stillwater. The study site is a transition zone between an upland tallgrass prairie and a flood plain woodland. The site was cultivated prior to the mid-1930's and has since been invaded by American elm.

The annual precipitation averages 820±250 mm. The average precipitation distribution during the 210-day growing season is 21% during April and May, 28% during the June-August period, and 17% during September and October.

The overstory vegetation consisted of a dense stand of uniform-sized trees, 97% of which were American elm. The stand contained about 2,500 trees per hectare, with an average basal diameter of 10.0±2.2 cm. The herbaceous species were grouped into four species classes. Dominant desirable grasses (preferred by cattle) included *Schizachyrium scoparium*, *Tridens flavus*, and *Panicum scribnerianum*. Less desirable grasses were predominately *Andropogon virginicus*, *Bothriochloa saccharoides*, *Leptoloma cognatum*, *Setaria* spp. and *Sporobolus asper*. Cool-season grasses and grass-like plants included *Bromus japonicus*, *Carex* spp., and *Elymus virginicus*. Dominant forbs were *Ambrosia psilostachya*, *Veronia baldwinii*, and *Desmodium sessilifolium*.

Methods

The study was conducted in a grazed paddock of 9.7 ha and an adjacent, ungrazed area. The grazed area was moderately stocked with

Fig. 2. *View of (A) ungrazed and (B) grazed plots.*

Fig. 3. *American elm sprouts in (A) ungrazed and (B) grazed areas.*

6 steers, averaging 250 kg initially, from May to October. About 20% of the grazed area was wooded, whereas most of the ungrazed area was wooded and maintained as a wildlife area.

The randomized block experimental design in the grazed area consisted of four replications of two fertilizer treatments (0 and 74 kg/ha each of nitrogen and phosphorus) on 5 × 7 m plots cleared of trees in May 1973. Trees were cut at a height of 5 to 10 cm with chain saws. The adjacent ungrazed area consisted of three replications of the same treatments on plots of 15 × 30 m. Smaller plots were used in the grazed area to provide an adequate number of plots similar in elm density and herbaceous species composition to those in the ungrazed area.

One plot per replication was randomly selected to be left uncleared and unfertilized as a control in both the grazed and ungrazed areas. There were no uncleared, fertilized plots. Herbage production, grazing residue and sprout length data were collected at the end of the 1973 growing season. The height of the tallest sprout per stump was determined at the end of the growing season in 1974 and 1975.

Statistical analyses of differences in herbage production within the ungrazed areas, grazing residue within the grazed area and sprout length averages within each area were by analyses of variance. Statistical analyses of differences in herbage standing biomass, whether grazed or ungrazed, and sprout length averages between the grazed and ungrazed areas were by the unpaired t−test method (Steele and Torrie 1960). The level of significance of differences discussed was 5% or greater.

Results and Discussion

Total herbage production on the uncleared and unfertilized, grazed area (1,000 kg/hectare) was no less than that on the uncleared and unfertilized ungrazed area (Fig. 1). However, the amount of grazing residue on grazed cleared areas at the end of the 1973 growing season was less than 20% of that on grazed uncleared areas. There was no difference in grazing residue due to fertilizer treatments although fertilization increased herbage production on cleared ungrazed areas.

Herbage data from the ungrazed area show that overstorage removal greatly increased herbage production (Fig. 1). Herbage production increased by about 1,500 kg/hectare on cleared, unfertilized areas and about 2,200 kg/hectare on cleared, fertilized areas.

Apparently cattle concentrated grazing on the cleared areas and neglected uncleared areas with overstory canopy present. Utilization of plants of all herbaceous species classes was very heavy and generally exceeded 90%. All species found on the small grazed areas were at least partially grazed (Fig. 2).

Most (88%) of the stumps in each cleared area produced sprouts soon after being cut in May. Sprouts on both fertilized and unfertilized cleared areas were heavily browsed by cattle (Fig. 3). The average sprout length at the end of the 1973 growing season in the ungrazed area was 22 cm for unfertilized areas and 27 cm for fertilized areas. However, average sprout length at the end of the 1973 growing season in the grazed area was 5.5 cm and 4.8 cm for unfertilized and fertilized areas, respectively. Similar grazing during the growing season in 1974 and 1975 resulted in the death of all sprouts on all cleared and grazed areas by the end of the 1975 growing season. The average height of the tallest sprouts in the ungrazed area in October 1975 was about 50 cm. There was no apparent decline in vigor of sprouts in the ungrazed area between 1973 and 1975.

Our results agree with those of Reynolds (1962) and McEwen and Dietz (1965), who found that cattle prefer forage from open areas over forage beneath the canopy of trees. The removal of overstory tree cover not only increased production of herbaceous vegetation, but also increased utilization of available forage and browse. Very little browsing of elm twig tips by deer (George and Powell 1977) or by cattle was detected on uncut trees in the control areas.

Small cleared areas could be used in a management program of mechanical-biological control of American elm. If continued production of sprouts is desired, larger cleared areas would reduce the likelihood of the sprouting stumps being killed by continued heavy browsing by animals concentrating on small areas. The optimum combination of cleared area and grazing pressure will need to be determined to maximize herbage production and optimize sprout regrowth under grazing.

Literature Cited

Dalrymple, R.L., D.D. Dwyer, and J.E. Webster. 1965. Cattle utilization and chemical content of winged elm browse. J. Range Manage. 18:126-128.

Dwyer, D.D. 1961. Activities and grazing preferences of cows with calves in northern Osage County, Oklahoma. Okla. Agr. Exp. Sta. Bull. 588. 61 p.

George, J.F., and J. Powell. 1977. Deer browsing and browse production of fertilized American elm sprouts. J. Range Manage. 30:357-360.

Halls, L.K., and E.A. Epps, Jr. 1969. Browse quality influenced by tree overstory in the south. J. Wildl. Manage. 33:1028-1031.

McEwen, L.C., and D.R. Dietz. 1965. Shade effects on chemical composition of herbage in the Black Hills. J. Range Manage. 18:184-190.

Reynolds, H.G. 1962. Use of natural openings in a ponderosa pine forest of Arizona by deer, elk, and cattle. U.S. Forest Serv., Res. Note RM-78. 4 p.

Rice, E.L., and W.T. Penfound. 1959. The upland forest of Oklahoma. Ecology 40:593-608.

Steele, R.G.D., and J.H. Torrie. 1960. Principles and Procedures of Statistics. McGraw-Hill Book Company, Inc., New York. 481 p.

Welton, F.A., and V.H. Morris. 1928. Woodland pasture. J. For. 26:794-796.

BOOK REVIEWS

Tropical Pasture and Fodder Plants-Grasses and Legumes By A.V. Bogdan. Longman, Inc., London, New York. 1977. 475 p. $40.00.

This reference book, one of 18 titles in Longman's Tropical Agriculture Series, is divided into two main sections, the grasses and the legumes. More important species and cultivars of tropical forage plants are described in detail. The morphology of each taxon, its environment, flowering, reproductive methods, and seed production are presented. Work on introduction trials with results, possible methods of establishment, requirements and responses to fertilization, proper grazing and harvesting methods, and grass-legume associations are summarized for each. Herbage yields, methods of conserving forage, and chemical composition and nutritive value of each are reviewed.

In comprehensive introductions which precede each section, Bogdan explains the relation of day length, light intensity, temperature, rainfall, and soils to certain aspects of grass physiology. He shows the basic structure of grass and legume plants and presents general information about their establishment, management, herbage yield patterns, and association together. Background information for understanding comparative nutritive values of forage species and how to conserve such are included. Modes of reproduction, methods of breeding and introducing forage taxa, and seed production and germination information are summarized.

Treatment of the geographic, and not climatic, Tropics gives the book wide application. All parts of some 89 countries of the world between 23°27′ north and south latitudes have been included. Over 300 species are treated in this exhaustive review. The species are described in alphabetic order and the space given to each is in approximate proportion to its importance. *Cynodom dactylon*, for example, and its hybrids and cultivars take up 7 pages of text, while marginal species in the Tropics, like *Lotus corniculatus,* are briefed in a short paragraph. Plants are indexed separately by common and scientific names. Bogdan has included only grasses and leguminous herbs, which are the major source of feed for livestock. In the potentially yearlong tropical growing season, these are green for variable, often major, parts of the year and provide almost all of the essential nutrients for herbivores. Still, inclusion of leguminous shrubs would have produced an almost all-inclusive forages reference or source book for all secondary producers in tropical ecosystems, including browsing livestock and wildlife.

The book is an admirable synthesis from the author's knowledge and experiences and from his extensive use of the literature concerning tropical forages, over 700 items of which are included in his references section. Bogdan is a recognized authority on tropical pastures and fodder plants having served as a pasture research officer for 19 years in Kenya. He has contributed numerous technical articles to both East African and British journals, has a perennial *Dactyloctenium* named after him, and is a Fellow of the Linnean Society of London.

Fodder and pasture plants are gaining in importance over the world and especially in the tropics. They promise to alleviate too great a dependence upon grains for meat production—grains more urgently required for feeding the starving millions. Improved pasture and fodder plants are needed to improve herbivore-forage producing ecosystems, which are deplorably inefficient in developing countries and tropical areas. From Bogdan's descriptions, it will be much easier than before to select the more promising species for introduction trials or for specific uses. Also, many costly mistakes may be avoided by adopting proven methods of establishment, use, and management of the selected species, all pertinent facts which he details.

Southern U.S. pasture and forage users and resource people stand to gain much from the comprehensive, transnational reviews about Bermudagrass, St. Augustine grass, dallis grass, and sorghums. Subtropical resource users and managers will find many helpful tips concerning the seeding, management, and use of several widely used introductions, especially *Cenchrus ciliaris*; *Panicum antidotale* and *P. coloratum*—the latter currently popular across Texas; *Eragrostis curvula* and *E. lehmanniana;* and *Sorghum almum.* Arid-land resource managers may be surprised to note that several weedy annuals, e.g., *Aristida adscensionis* and *Eragrostis cilianensis,* have utility and may be seeded in arid tropical areas. As temperate zone readers might expect, there are no species of *Agropyron* or *Poa* treated and only one *Bromus, B. uniloides,* and one *Festuca, F. arundinacea,* included. Similarly, while a wealth of information concerning strictly tropical origin legumes, e.g. *Leucaena ssp., Desmodium ssp., Indigofera spp., Stylosanthes spp.* and others are summarized. Limited information naturally appears concerning temperate legumes, although brief mention is made about alfalfa and both red and white clovers, with greater attention given to Egyptian and other *Trifolium* spp.

Those seeking a source book of information concerning tropical pasture and forage plants will find this reference informative and helpful.—Reviewed by *S. Magsood Khan* under advice of *C.H. Wasser,* Fort Collins, Colo.

SYMPOSIA AND REPORTS

Plant Relations in Pastures. Edited by John R. Wilson. Commonwealth Scientific and Industrial Research Organization, 372 Albert Street, East Melbourne, Australia 3002. 1978. 425 p. $25.00.

This book contains the proceedings of a symposium for pasture agronomists, physiologists, and ecologists held in Brisbane in May 1976. It seeks to improve inderstanding of the mechanisms underlying productive pastures through knowledge of the comparative physiology of Individual plants, analysis of competitive influences, and close examination of the ecology of legume-based pastures in particular.

Pastures usually comprise a mixture of species, each of which may respond differently to the aerial, soil, and biotic environment. These species compete and interact with each other and with the grazing animal to produce a complex ecosystem. A major aim for the future to emerge from the symposim is the need to integrate and apply knowledge acquired in each of the different areas of research.

You are cordially invited to join the Society for Range Management

the Society

. . .(founded in 1948) is a private, nonprofit, professional association dedicated to advancing a comprehensive understanding of range ecosystems and the intelligent use of all range resources. The Society assists all who work with rangelands to keep abreast of new findings and applications in range management and strives to create a public appreciation of the benefits to be derived from proper range use.

Membership

. . . in the Society is open to anyone engaged in or interested in the study, management, or use of range ecosystems. Members—from more than 35 countries—include research scientists, ranchers, governmental agency administrators, advisory and technical assistance personnel, teachers, students, and people from the business community.

•

Meetings

. . . held on a regular basis by the Society and each Section, provide for a face-to-face exchange of technical information, ideas, and philosophies. The Society holds a major meeting each year in February, and Section meetings afford members an opportunity to examine applied range management methods and to discuss matters of immediate and local interest.

•

Publications

. . .include two bimonthly periodicals—*Journal of Range Management* and *Rangelands*—as well as special publications that are issued from time to time. Through these publications (which feature timely articles of general interest, research reports, management notes, viewpoints, book reviews, and news about Society members and activities) members are kept current on information pertinent to rangeland management and use.

. . . For information, write to the **Society for Range Management, 2760 West Fifth Avenue, Denver, Colorado 80204. Phone (303) 571-0174.**