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Proceedings—Symposium on Plant-Herbivore Interactions

Snowbird, Utah, August 7-9, 1985

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INTRODUCTION: PLANT-HERBIVORE INTERACTIONS

Frederick D. Provenza, Jerran T. Flinders, and E. Durant McArthur

This proceedings is the fourth in a series on the biology and management of shrubs. Earlier accounts provide information on Purshia, Cowania, and related rosaceous species, on Atriplex and related chenopods, and on Artemisia and Chrysothamnus (Tiedemann and Johnson 1983; Tiedemann and others 1984; McArthur and Welch 1986). All four proceedings have been published by the Intermountain Research Station. The Shrub Research Consortium, whose members are listed inside the front cover of this proceedings, has the continuing role of sponsoring periodic symposia and workshops on shrub biology and management. The symposium described in this volume dealt with plant-animal interactions with emphasis on woody plants and mammalian herbivores.

Plants have typically been considered passive participants in interactions with herbivores. Growing evidence, highlighted in this symposium, suggests that plants play an active role in these interactions, and may deter herbivores through changes in chemistry and morphology. Furthermore, resource availability apparently influences evolution of plant chemical and morphological responses to herbivory, and nutrient availability and light influence their phenotypic expression.

Herbivores, on the other hand, have been viewed as active participants in interactions with plants, because animals are free to select a diet from among the plant species and parts available within plant assemblages. However, people have typically considered that diet selection is genetically fixed through natural selection. The degree to which diet selection is genetically fixed is currently under question for domesticated and wild herbivores, however, and some consider that dietary experiences in early life shape the dietary habits of herbivores for life. If so, this may serve to adapt herbivores to the plant species and parts available within their environment, and may serve to counter, to some degree, the chemical and morphological defenses of plants.

This symposium proceedings addresses these general topics through text and literature citations, and is intended to provide scientists, educators, and wildland managers with current knowledge of plant-herbivore interactions. Because this is a rapidly developing field, many of the ideas presented in the symposium should be viewed as hypotheses that require further testing. We hope, however, that publications such as this will lead to further study, enhanced understanding, and ultimately better management of plants and the herbivores that feed upon them.

ACKNOWLEDGMENTS

As compilers of this symposium proceedings we thank all members of the Shrub Research Consortium for their efforts in making the symposium a success. We especially thank the session chairs: Dr. Jack Brotherson, Dr. Thomas Clausen, Dr. Lee Eddleman, Mr. Norman V. Hancock, Dr. Ron Sosabee, Dr. Darrell N. Ueckert, and Dr. Bruce Welch. Several other individuals also gave extra effort to ensure the success of the symposium and quality of the proceedings. In this regard we note especially Debbie F. Brunson, Roberta L. Powell, Mical Walker, and Tamara D. Smith.

Finally, Brigham Young University Conferences and Workshops personnel were excellent symposium hosts.

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Section 1. Plant Chemistry

EFFECT OF RESOURCE AVAILABILITY ON WOODY PLANT-MAMMAL INTERACTION

John P. Bryant, F. S. Chapin III, T. P. Clausen and P. R. Reichardt

ABSTRACT: The availability of nutrients, light, and water in the environment determine plant resistance to herbivory. Plant carbon/nutrient balance controls the expression of plant chemical defenses. Nutrient stresses cause an increase in carbon-containing defenses such as phenolics, and a decline in nitrogen-containing toxins and deterrents such as alkaloids and nitrates. Light stresses result in the opposite: carbon-based defenses decrease, and as the growth rate is reduced, nitrogen-containing deterrents increase. Fertilization may increase nitrate concentrations, thus decreasing palatability.

INTRODUCTION

A significant recent advance in plant antiherbivore defense theory is the recognition that the availability of resources (mineral nutrients, light, water) in the environment controls plant resistance to herbivory (Janzen 1974; Bryant and others 1983; Coley and others 1985). In ecosystems as diverse as tropical rainforests (Janzen 1974; McKey and others 1981; Coley 1983), subtropical savannas (Cooper and Owen-Smith 1985; Owen-Smith and Cooper, this proceedings), temperate deciduous forests (Rathke 1985), boreal forests (Bryant and Kuropat 1980; Bryant and others 1983), and arctic shrub tundra (Batzli and Jung 1980; Kuropat 1984; MacLean and Jensen 1984) rapidly growing woody plants (often deciduous species) are much more severely grazed than slowing growing woody plants (often evergreen species) (Coley and others 1985, this proceedings).

This relationship between the availability of resources in the environment and plant susceptability to herbivory is the consequence of two levels of plant response to resource availability. On an ultimate or evolutionary scale, adaptation to low resource levels, resulting in slow intrinsic growth rates (Grime 1977; Chapin 1980), favors selection of strong constitutive defenses in plants. Growth in high resource environments does not (Bryant and Kuropat 1980; Bryant and others 1983; Coley 1983; Coley and others 1985; Coley, this proceedings). On an ecological scale, phenotypic responses of plants to nutrient or carbon limitation control a plant's genetic potential to express antiherbivore defense (Bryant and others 1983).

The evolution of plant antiherbivore defense is considered in detail elsewhere in this proceedings (see Coley, this proceedings). Here we discuss the physiological mechanisims whereby woody plant carbon/nutrient balance controls phenotypic expression of plant chemical defenses against herbivory. Although we rely heavily on our own work with the woody plant-snowshoe hare interaction in interior Alaskan boreal forests, we predict that the generalizations we arrive at are common to all woody plant-herbivore interactions.

PHENOTYPIC RESPONSE TO NUTRIENT OR CARBON LIMITATION

Bryant and others (1983) suggested that the response of all plants to reduced nutrient availability is qualitatively similar (fig. 1). When nutrients are less available in the soil, less nutrients are absorbed. A reduction in nutrient concentration reduces photosynthetic rate directly by reducing RuBP carboxylase, chlorophyll, and phospholipid contents and indirectly by increasing leaf longevity; older leaves tend to have reduced photosynthetic rates (Moony 1972; Chapin 1980; Mooney and Gulmon 1982).

Growth is the process most strongly affected by nutrient stress (Chapin 1980). The decline in growth with nutrient stress is generally greater than the decline in photosynthesis; therefore carbohydrates and carbon-based secondary metabolites such as phenols accumulate (Shigo 1973; Wong 1973; McKey 1979). Under conditions of nutrient limitation carbon is relatively "cheap," and the nutrients in leaves are difficult to replace (Bryant and others 1983; Coley and others 1985). Therefore, it is not surprising to see carbon-based defenses such as phenolics increase in woody plant tissues under conditions of nutrient limitation, whereas nitrogen-containing feeding deterrents and toxins such as alkaloids and nitrate decline (Wilde and others 1948; Shigo 1973; McKey and others 1978; Gartlan and others 1980; Waring and others 1985).

The plant phenotypic response to carbon stress due to insufficient light is essentially the reverse of that described above (fig. 1). Photosynthesis and carbohydrate concentrations decline. Growth rate is reduced more severely than nutrient absorption, so that tissue nutrient

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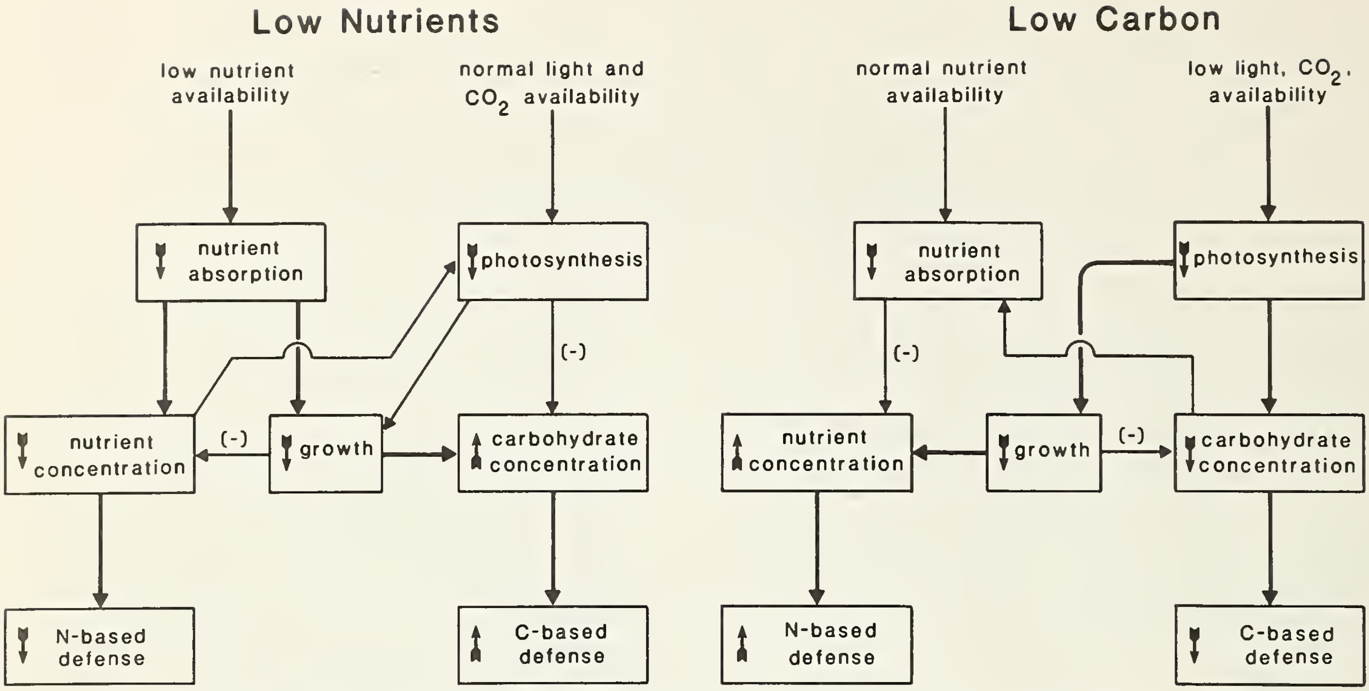

Figure 1.--Effect of suboptimal nutrient or light availability on carbon-nutrient relationships of plants and on concentrations of nitrogen and carbon-based defenses. Vertical arrows within boxes indicate increase or decrease in the parameter. Arrows between boxes indicate positive effect unless otherwise indicated(-). Thickness of arrow indicates magnitude of effect. From Bryant and others (1983).

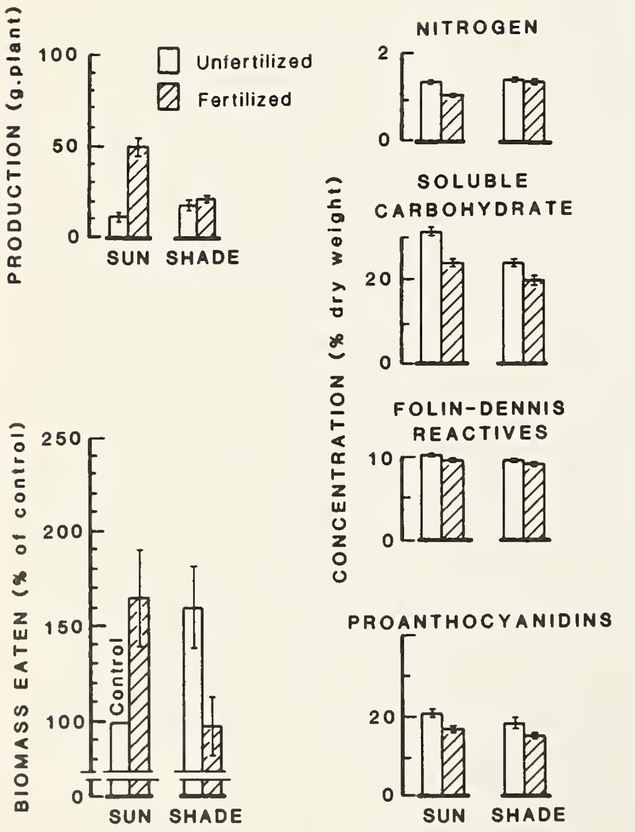

Figure 2.--Effects of fertilization and shading on *S. alaxensis* growth, chemistry, and palatabilty to snowshoe hares. Mean 1 ± SE presented, N = 30 plants or 10 hares.

concentrations accumulate above levels necessary to support growth. Under such circumstances one finds a reduction in carbon-based defenses such as phenolics and terpenes (Waring and others 1985; figs. 2,3) and in some plants a rise in nitrogen-containing feeding deterrents or toxins (fig. 1) such as nitrate (Deeb and Sloan 1975; Waring and others 1985).

Similarly, following heavy fertilization, tissue nutrient concentrations increase, and growth is stimulated more strongly than photosynthesis; therefore, concentrations of carbohydrates and carbon-based defenses decline and nitrogen-containing feeding deterrents or toxins increase (Cullvenor 1973; Deeb and Sloan 1975; Waring and others 1985).

EFFECTS OF CARBON/NUTRIENT BALANCE ON MAMMAL-WOODY PLANT INTERACTIONS IN BOREAL FORESTS

The palatability of woody plants to browsing mammals is highly sensitive to plant carbon/nutrient balance. For example, fertilization resulted in increased barking and browsing of lodgepole pine (*Pinus contorta*) by snowshoe hares (*Lepus americanus*) and red squirrels (*Tamisciurus hudsonicus*) in British Columbia (Sullivan and Sullivan 1982), snowshoe hare browsing of red pine (*P. resinosa*) in the eastern boreal forest of North America (Heiberg and White 1951), and Scots pine (*P. sylvestris*) by mountain hare (*L. timidus*) in Finland (Rousi 1983). Similarly, fertilization of Scots pine resulted in increased browsing by moose (*Alces alces*) in Finland (Loyttynieme 1981). The

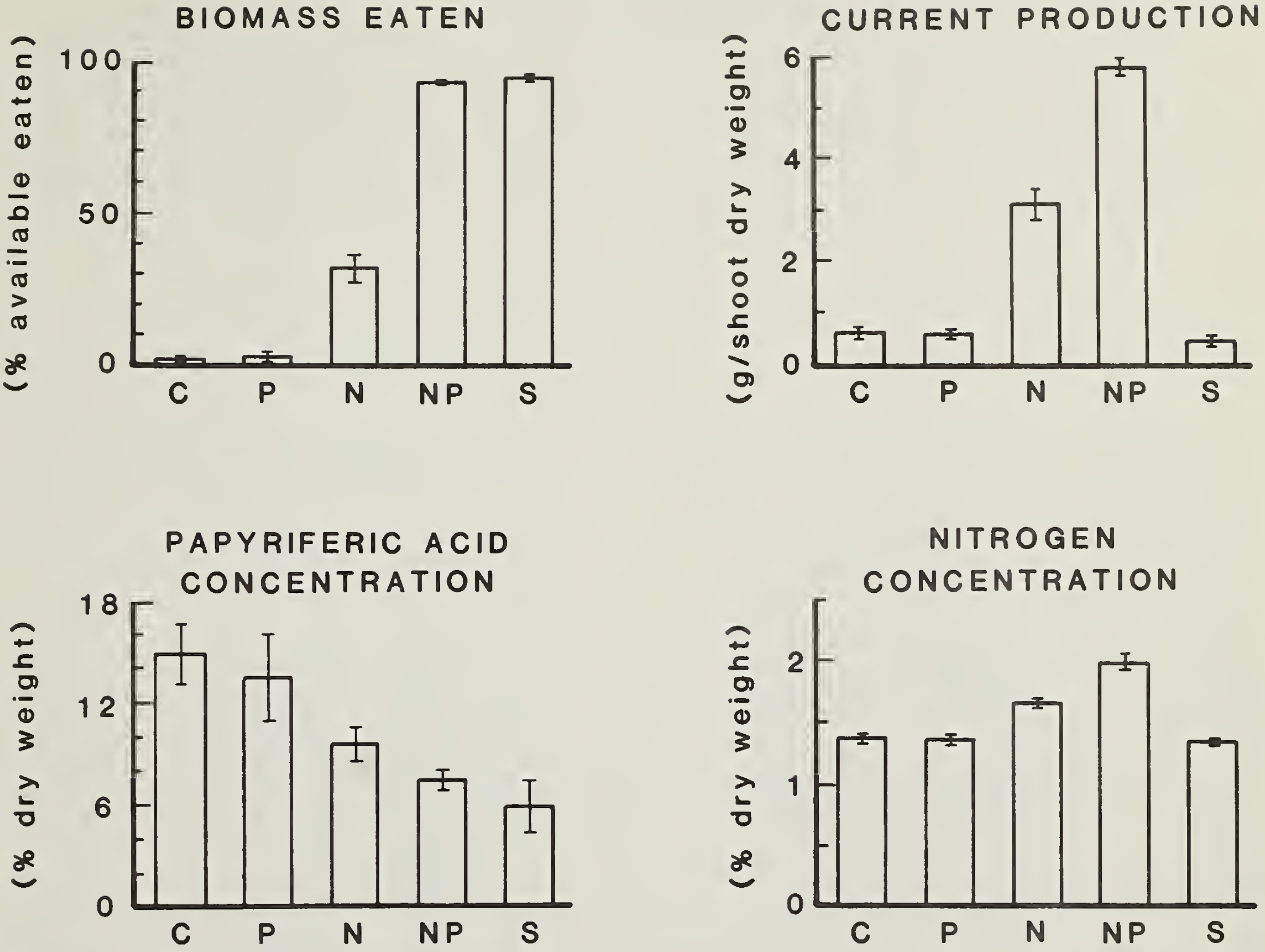

Figure 3.--Effects of fertilization and shading on B. resinifera growth, twig nitrogen concentration, papyriferic acid concentration and palatability to snowshoe hares. C = control plants, P = phosphorus-fertilized plants, N = nitrogen-fertilized plants, NP = nitrogen-plus-phosphorus-fertilized plants, S = shaded plants. (Bryant and others, unpublished data)

literature of wildlife ecology and forest management is repleat with similar examples of fertilization resulting in increased browsing of woody plants by mammals (see Behrend 1973).

Shading by alder resulted in increased use of a variety of woody plants by snowshoe hares in Alaska (Walker 1985). Rohleder (1985) experimentally demonstrated that Alaska feltleaf willow (Salix alaxensis) and balsam poplar (Populus balsamifera) grown in shade of alder (Alnus incana) are more palatable than S. alaxensis and P. balsamifera grown in well insolated willow thickets. Waterman and others (1984) found that black colobus monkeys (Clolobus satanus) fed preferentially on leaves of shaded Barteria fistulosa individuals and that those leaves contained lower tannin concentrations than did sun leaves. The extracts from leaves of shaded B. fistulosa individuals were also less inhibitory to in vitro digestion of cellulose than extracts from leaves of isolated individuals.

Hanley and others (this proceedings) found that black-tailed deer in southeastern Alaska fed preferentially on shaded shrubs as compared to sun-grown conspecifics. The leaves of shaded shrubs had lower tannin concentrations and higher in vitro digestibilities in deer rumin fluid than those of sun-grown shrubs.

Our experimental studies of forage selection by snowshoe hares in interior Alaska support the generalization that carbon/nutrient balance controls phenotypic expression of plant chemical defense against browsing by mammals. We have grown S. alaxensis under high and low mineral nutrition and light in a 2X2 factorial experiment. We applied 40 g N/m^2 as NH_4NO_3, 20 g P/m^2 as P_2O_5 and 20 g K/m^2 as potash in four applications from mid-May to mid-July over a 3 year period and reduced light by 50 percent with optically neutral shade cloth for one growing season. In the winter following the third year of fertilization and first year of

Table 1.--Correlations between *S. alaxensis* chemical fractions[1]

Fraction	N	P	EE	CHO	FD	PA	V	AT
N	1.00							
P	+.87	1.00						
EE	+.43	+.41	1.00					
CHO	-.24	-.03	+.03	1.00				
FD	+.12	+.21	+.22	+.79	1.00			
PA	+.12	+.22	+.18	+.74	+.91	1.00		
V	+.18	+.26	+.29	+.67	+.91	+.86	1.00	
AT	+.11	+.13	+.23	+.57	+.78	+.74	+.74	1.00

[1] n = 120, P = 0.01, 118 degrees of freedom = 0.246; N = total nitrogen, P = total phosphorus, EE = diethyl either extract, CHO = soluble carbohydrate, FD = Folin-Denis, P = proanthocyanidin, V = vanillin, AT = protein precipitating substances.

shading, we bioassayed winter dormant twigs from adult-phase plants (Kozlowski 1979) for palatability to snowshoe hares by offering them in a cafeteria style feeding trial. Twigs were assayed for several nutrient fractions such as nitrogen, soluble carbohydrates, and several phenolic fractions (Folin-Dennis reactives and proanthocyanidins). Fertilization increased growth (fig. 2), thereby indirectly creating a carbon stress that resulted in decreased twig soluble carbohydrate concentrations and phenolic concentrations (fig. 2). Shading directly caused carbon stress, thereby reducing twig soluble carbohydrate and phenolic concentrations (fig. 2). Feeding trials demonstrated that hares fed preferentially on fertilized-only and shaded-only plants ($P < 0.01$) but did not show any preference for fertilized-shaded over control (unfertilized-unshaded) plants (fig. 2).

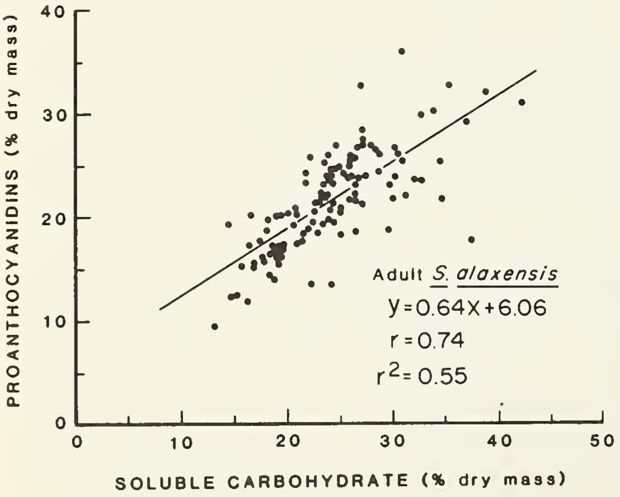

Figure 4.--Relationship between soluble carbohydrate and proanthocyanidin concentrations in winter-dormant twigs of adult-phase *S. alaxensis*. N = 120 plants. r significant at $P < 0.0001$ level of probability.

Correlation analysis of data from this experiment (table 1) demonstrated positive correlations between twig soluble carbohydrate concentrations and and concentrations of all phenolic fractions assayed. For example, results presented in figure 4 clearly indicate that a high carbohydrate status results in increased synthesis of potential hare feeding deterrents such as proanthocyanidins. Although these correlative results do not demonstrate, in the absence of preference bioassays where extracts were added to artificial diets (see paper by Reichardt and others, this proceedings), a causal link between low phenolic concentrations in shaded-only and fertilized-only plants, they are suggestive of such a link. Tahavanainen and others' (1985) and Tahvanainen's (this proceedings) demonstration that phenolics deter mountain hare use of willow support this preliminary conclusion. On the other hand, our results with *S. alaxensis* do not indicate that preferential use of *S. alaxensis* winter-dormant twigs is caused by high concentrations of potential feeding attractants such as nitrogen and soluble carbohydrate (figs. 2, 4).

In other experiments with juvenile Alaska paper birch (*Betula resinifera*) (Bryant and others, unpublished) we have arrived at a more definitive demonstration of alteration of plant defense by fertilization and shading. Fertilization increased growth and reduced twig concentrations of a known snowshoe hare feeding deterrent, papyriferic acid (Reichardt and others 1984; this proceedings). Shade reduced growth, increased palatability, and reduced twig papayriferic acid concentration. Again there was no correlation between concentrations of potential feeding attractants and hare use of winter-dormant Alaska paper birch twigs as food (fig. 3).

Results presented in figure 2 indicate that substances other than phenolics may also affect *S. alaxensis*' palatability to snowshoe hares in winter. Twigs of fertilized-shaded plants were less palatable than those of ferilized-only plants or shaded-only plants even though they had the lowest phenolic concentrations measured in our study of S. alaxensis-snowshoe hare interactions. Although our chemical analysis of S. alaxensis is still incomplete, preliminary results indicate that twigs of fertilized-shaded plants had a high nitrate concentration compared to twigs of other plants. This high nitrate concentration may be the cause of the low palatability of these twigs to snowshoe hares because nitrate is toxic to vertebrate herbivores, such as rabbits (Deeb and Sloan 1985), that are similar in physiology to hares. However, irrespective of the chemical cause of the low palatability of fertilized-shaded plants relative to fertilized-only and shaded-only plants this result further supports the generalization of Bryant and others (1983). Growth of fertilized-shaded plants was limited by light as compared to that of fertilized-only plants. And furthermore, twigs of fertilized-shaded plants had the highest nitrogen concentration measured in this study (fig. 2). Thus the conditions specified by Bryant and others (1983; see fig. 1) for accumulation of nitrogen containing feeding deterrents or toxins in plants were met.

SUMMARY

A variety of evidence exists that plant palatability to vertebrate herbivores is sensitive to carbon/nutrient balance. Thus the availability of resources in the environment not only influences plant defensive responses to herbivory on an evolutionary scale, it also affects the phenotypic expression of a plant's inherent potential for chemical defense against herbivory. Our results also indicate another aspect of chemical interactions between plants and their herbivore predators. Accumulation of substances such as nitrate that are probably not a direct evolutionary response of plants to herbivore attack may deter vertebrate herbivory. In short, some so-called plant defenses may be "exaptations" (sensu Gould and Verba 1982) rather than adaptations.

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FOREST STAND-AGE-RELATED DIFFERENCES IN APPARENT NUTRITIONAL QUALITY OF FORAGE FOR DEER IN SOUTHEASTERN ALASKA

Thomas A. Hanley, Rex G. Cates, Beatrice Van Horne, and Jay D. McKendrick

ABSTRACT: Chemical composition of Alaska blueberry (*Vaccinium alaskensis*) and bunchberry dogwood (*Cornus canadensis*) was studied during May through October along a chronosequence of five stands of Sitka spruce (*Picea sitchensis*)-western hemlock (*Tsuga heterophylla*) forest. Three young stands were open clearcuts; two older stands had well-developed overstories and understories exposed to little direct sunlight. Pronounced differences in chemical composition of blueberry and bunchberry occurred between the young and older stands. Plants in the young stands had greater astringency, concentrations of phenolics, and total nonstructural carbohydrates, but lower concentrations of nitrogen than did plants in the older stands. *In vitro* dry-matter digestibility, however, did not differ among stands. Chemical analyses of plants from a clearcut and adjacent forest at another study area indicated that concentrations of digestible nitrogen were 2.0 to 2.3 times greater in leaves from the forest than those from the clearcut. Palatability trials with three captive black-tailed deer (*Odocoileus hemionus sitkensis*) showed a consistent preference for leaves from the forest. The results indicate the carbon/nutrient balance of these plants, controlled by the relative availability of light and nutrients in their environment, has major implications for nitrogen availability to deer but may be less important for the availability of digestible energy.

INTRODUCTION

In the coastal coniferous forests of the Pacific Northwest, British Columbia, and southeastern Alaska, the theoretical linkage between deer populations and their habitat has long centered on the dramatic changes in forage quantity as stands age (Cowan 1945; Einarsen 1946a; Brown 1961; Gates 1968; Jones 1974; Wallmo and Schoen 1980; Hanley 1984). The quantity of forage is generally greatest in young, open stands, least in closed-canopy even-aged stands, and intermediate in uneven-aged, old-growth stands, depending on snow conditions. Quantity of available forage is important to habitat selection by individual deer and the numerical response of deer populations. Stand-age-related differences in the quality of forage are, however, less well understood and have generally been assumed to be less important than the differences in forage quantity. The few studies from coastal Oregon through Alaska have centered primarily on nitrogen concentration in a few key forage species and have generally indicated slightly greater concentrations of nitrogen in plants growing under forest canopies than in those growing in open clearcuts or burns (Brown 1961; Billings and Wheeler 1979; Rochelle 1980; Van Horne 1982; Ellis 1984), although Einarsen (1946b) reported the opposite. The implications of such differences have remained unclear, however, because the concentration of nitrogen is only one of several factors determining protein availability to deer. Furthermore, nitrogen is only one of many nutritional factors important to deer.

Klein's (1964, 1965) work in southeastern Alaska illustrated the importance of forage quality and nutrition to the growth rates and body sizes of individual deer and the productivity of deer populations. More recently, studies of food intake and foraging energetics of deer (Wickstrom and others 1984) and potential nutritional limitations for deer in southeastern Alaska (Hanley and McKendrick 1983, 1985) also have indicated the importance of forage quality, especially for reproductive females. To an individual mule or black-tailed deer (*Odocoileus hemionus*), the quality of available forage appears to be much more important than the quantity of forage at all but extremely low levels (<100 kg/ha) of forage availability (Wickstrom and others 1984). Although forage quantity is undoubtedly a critical factor controlling carrying capacity and potential

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population levels of deer, forage quality appears to be the more important factor affecting habitat selection and the nutrition of individual deer, at least for black-tailed deer in southeastern Alaska. The nutritional factors of greatest importance in southeastern Alaska appear to be digestible energy, nitrogen, and phosphorus (Hanley and McKendrick 1983).

In 1982-83, we conducted a study of stand-age-related differences in the chemical composition of five major understory species in southeastern Alaska. The results (in preparation) indicated some differences of potentially major significance for herbivores. The purpose of this paper is to examine a subset of those data in relation to their importance to Sitka black-tailed deer (O. h. sitkensis). The two most important species to deer, Alaska blueberry (Vaccinium alaskensis) and bunchberry dogwood (Cornus canadensis), are examined here. Of the laboratory analyses, only the neutral and acidic phenolics, astringency, total nonstructural carbohydrates (TNC), nitrogen (N), phosphorus (P), and in vitro dry-matter digestibility (IVDMD) are reported here. To relate these results to deer, we supplemented the data with detergent analyses, estimates of nitrogen digestibility, and palatability trials in 1985. The data indicate that the carbon/nutrient balance of these plants, controlled by the relative availability of light and nutrients in their environment, may determine their leaf concentrations of phenolics, total nitrogen, digestible nitrogen, and palatability to deer.

STUDY AREA AND METHODS

Study Area

The coastal forests of southeastern Alaska are dominated by western hemlock (Tsuga heterophylla) and Sitka spruce (Picea sitchensis) with much lesser amounts of western redcedar (Thuja plicata), Alaska yellow-cedar (Chamaecyparis nootkatensis), and lodgepole pine (Pinus contorta), the latter almost exclusively confined to muskegs. Chichagof and Douglas Islands (approximately 58° N. latitude, 134-135° W. longitude), where this study was conducted, are above the northern limit of the range of western redcedar. Characteristic understory species are blueberries (Vaccinium alaskensis, V. ovalifolium, V. parvifolium), rusty menziesia (Menziesia ferruginea), devilsclub (Oplopanax horridum), skunk cabbage (Lysichiton americanum), bunchberry dogwood, trailing bramble (Rubus pedatus), laceflower (Tiarella trifoliata), and associated plants (Hultén 1968). Climate is characterized by cool summers (≈ 15 °C), generally mild winters (≈ 0 °C), and precipitation year-around (≈ 150-500 cm annually). Wildfire is uncommon; windthrow and clearcut logging are the principal agents of large-scale disturbance. Secondary succession following windthrow or logging characteristically proceeds through a shrub-dominated stage during the first 20 years, to a dense, closed-canopied, even-aged forest with very depauperate understory for the next 100 or more years, to an uneven-aged old-growth condition after 200 or more years. Annual aboveground production of understory during this successional sequence ranges from as high as 5 500 kg/ha at about 20 years to as low as 0 kg/ha at 50 years (Alaback 1982).

The 1982-83 Data

Chemical composition (neutral and acidic phenolics, TNC, N, and P), astringency, and IVDMD of Alaska blueberry and bunchberry dogwood were studied along a chronosequence of five stands in the Kennel Creek drainage of Chichagof Island: a 5-year-old burned clearcut; a 5-year-old unburned clearcut; an 11-year-old unburned clearcut; an 80-year-old closed-canopy, even-aged stand; and an uneven-aged, old-growth stand (> 450 years old?). The three youngest stands were shrub-dominated, open stands, while the two oldest stands had well-developed forest overstories. On each of three dates (October 20-22, 1982, May 18-19, 1983, and July 26-28, 1983) samples of leaves were collected for analysis. Three samples of each of the two species were collected from each of the five stands. Each sample was a composite obtained from three or more individual plants. Samples were chosen to minimize phenological differences among stands at any one date. In this way, all samples of either species were close to the same phenological stage in growth and development, regardless of which stand they came from. Half of each sample was placed on dry ice immediately and kept frozen at -85 °C until analysis for phenolics and astringency. The other half was ovendried at 40 °C for 72 hours, ground in a mill with 20-mesh screen, and ovendried at 50 °C immediately preceding analysis for TNC, N, P, and IVDMD.

Neutral and acidic phenolics were measured using a Waters high pressure liquid chromatograph (HPLC). Detection was at 254 nm and 214 nm using a Model 480 LC Lambda-Max spectrophotometer and a Model 441 Spectrophotometer in series. Gradient reverse phase chromatography was performed as follows: column--Rainin Microsorb C 18, short one; solvent--(A) 2 percent acetic acid, (B) methanol/water/butanol/acetic acid (25:68:50:2); gradient--7 minutes isocratic at 30 percent B followed by 25 minutes linear gradient from 30 percent to 100 percent B; flow rate-- 1 mL/min; absorption range-- 0.2; detection--254 nm and 214 nm in series. The counts per milligram were totaled as an index of concentration of neutral and acidic phenolics for each sample.

Astringency was measured using precipitation of trypsin by tannic acid after the sample was ground under liquid nitrogen and extracted in 50 percent methanol. Protein content was determined from a 0.5-mL aliquot using the Bio-Rad assay (Bradford 1976). The assay was calibrated by precipitation of trypsin (2 mg per mL) with tannic acid (from 0.2 to 1.0 mg/mL). Data were expressed as milligrams equivalent tannic acid per gram dry weight. Details of the HPLC-phenolic and astringency methods are outlined in McElroy (1984).

Total nonstructural carbohydrates (sugars and starches) were measured using Technicon autoanalysis (Technicon Industrial Systems 1976) on reducing sugars following enzyme extraction with Mylase 100 (Smith 1969, 1979).

Nitrogen and phosphorus concentrations were measured simultaneously on a Technicon Auto Analyzer II (Isaac and Johnson 1976; Hanley and McKendrick 1983).

In vitro dry-matter digestibility was determined using the Tilley and Terry technique (Goering and Van Soest 1970). Rumen fluid was obtained from dairy cattle on high-quality grass hay. Incubation time was 48 hours.

The data were analyzed for statistical significance in a 5 (stands) by 3 (sampling dates) factorial analysis of variance (ANOVA), fixed model. An alpha level of 0.05 was used as the criterion of significance in testing the null hypotheses of no treatment or interaction effects. Each of the composite samples of each species from each stand at each date was treated as a replicate in the experiment rather than a subsample. This permitted us to use ANOVA to identify important differences between stands and dates. Our scope of inference, however, is limited to these five particular stands. Scheffe's multiple comparison procedure (Sokal and Rohlf 1981) was used for comparison of means when ANOVA indicated significant differences.

The 1985 Data

Fiber composition (detergent analysis), IVDMD, estimates of nitrogen digestibility, and relative palatability of Alaska blueberry and bunchberry dogwood were studied in an 8-year-old unburned clearcut and adjacent uneven-aged, old-growth forest on northern Douglas Island during July. Palatability trials required daily collection of forage and necessitated working near our captive deer facility in Juneau. The Kennel Creek study site was prohibitively remote.

Leaf samples of Alaska blueberry and bunchberry dogwood were collected from the clearcut and from the forest on July 5. Both samples of each species were composites, coming from more than 10 individual plants. The samples were ovendried at 40 °C for 72 hours and ground in a mill with 20-mesh screen. Sequential detergent analyses were conducted following the procedures of Goering and Van Soest (1970) as modified by Mould and Robbins (1982). IVDMD was determined with the Tilley and Terry technique (Goering and Van Soest 1970) using rumen fluid from dairy cattle on high-quality grass hay and incubating for 48 hours. Estimates of nitrogen digestibility were obtained by measuring Kjeldahl N concentration and the astringency of the plant material with bovine serum albumin (Martin and Martin 1982, with modifications): the N concentration provided an estimate of N digestibility for phenolic-free forages; and the astringency was used to correct that estimate for phenolic-rich forages by predicting the degree of depression of N digestibility (C. T. Robbins and others, in press).

Relative palatability trials for Alaska blueberry from the clearcut versus the forest were conducted with three captive, yearling Sitka black-tailed deer, (two males and one female). Leaves were collected daily and offered to each deer, housed separately, as an ad libitum supplement to their regular commercial diet, which also was offered ad libitum. Leaves were refrigerated in plastic bags overnight and weighed into feeding trays for each deer. Trays were kept filled throughout the day, emptied in late evening and contents weighed to determine daily consumption. A 5-day pretrial preceded the 6-day trial (July 1-6). Assignment of trays for each deer was determined by a flip of a coin and was maintained throughout the pretrial and trial until the last day, when the clearcut leaves were offered in the forest tray and vice versa. All data were corrected to ovendry weight (100 °C).

No statistical analyses were performed on the 1985 data because sample sizes were small and the purpose of the data was simply to aid interpretation of the earlier chemical results.

RESULTS AND DISCUSSION

Analyses of samples from the chronosequence at the Kennel Creek study area (table 1) indicated a similar pattern for both blueberry and bunchberry: concentrations of carbon-rich compounds (phenolics, astringency, TNC) tended to be greater in plants from the three young, open stands than in those from the two older, forested stands; and concentrations of nutrients tended to be greater in plants from the two older stands than in those from the three younger stands. IVDMD, however, did not vary across stands. Treatment means did not differ among plants from the three younger stands or among plants from the two older stands. The patterns of carbon-rich compounds (phenolics, astringency, and TNC) may result from differences in the availability of light. Under the low light conditions of the forest, understory plants may have reduced photosynthesis. This results in low levels of carbohydrates, growth, and production of carbon-based secondary compounds compared to plants from the open sites. Similar patterns in the production of phenolics, terpenes, and carbohydrates have been shown when light is limiting or when plants are growing under environmental stresses that limit photosynthesis (Rhoades 1979; Bryant and others 1983, this proceedings; Cates and others 1983; Waring and others 1985; Larsson and others, in press). The data for bunchberry are intermediate in this respect in the 11-year-old stand, because many of the plants were shaded by tall, dense shrubs. Similarly, samples from the old-growth stand reflected a variety of microsites differing in their exposure to sunflecks.

Table 1.--Chemical composition, astringency, and *in vitro* dry-matter digestibility (IVDMD) of *Vaccinium alaskensis* and *Cornus canadensis* leaves collected from five stands on three dates at the Kennel Creek study area

	Stand age (years)					
Variable/species/month	5 (burn)	5	11	80	>450	x̄
Neutral and acidic phenolics (counts/mg)						
V. alaskensis						[1]
May	9,807	10,151	10,685	3,323	4,523	6,566^{a}
July	9,080	10,671	10,890	750	1,439	7,195^{a}
October	9,621	10,594	10,088	798	4,873	7,698^{a}
x̄	9,503^{b}	10,472^{b}	10,555^{b}	1,624^{c}	3,612^{c}	
C. candensis						
May	23,448	15,677	14,143	1,899	4,008	11,928
July	26,189	22,794	7,415	1,265	1,976	9,665
October	13,565	23,153	5,725	2,035	3,846	11,835
x̄	21,067	20,541	9,094	1,733	3,277	***[2]
Astringency (mg/g tannic acid equivalent)						
V. alaskensis						
May	4.25	1.35	0.82	0.11	0.36	1.38^{a}
July	3.02	1.81	4.38	0.42	1.84	2.30^{a,b}
October	3.54	3.80	6.49	2.53	1.03	3.48^{b}
x̄	3.61^{c}	2.32^{c}	3.90^{c}	1.02^{c}	1.08^{c}	
C. canadensis						
May	7.76	7.56	6.67	6.94	6.44	7.07^{a,b}
July	10.77	8.36	8.16	4.96	3.95	7.24^{b}
October	6.59	9.46	4.85	2.72	3.62	5.45^{a}
x̄	8.38^{c}	8.46^{c}	6.56^{c,d}	4.87^{d}	4.67^{d}	
Total nonstructural carbohydrates (percent)						
V. alaskensis						
May	24.3	24.3	26.7	18.4	19.6	22.7^{a}
July	17.9	14.9	15.4	5.7	10.6	12.8^{b}
October	13.2	15.2	15.9	6.8	7.8	11.8^{b}
x̄	18.3^{c}	18.1^{c}	19.3^{c}	10.3^{d}	12.7^{d}	
C. canadensis						
May	8.3	10.5	9.8	5.1	6.3	8.0^{a}
July	11.7	10.7	11.5	5.4	4.7	8.8^{a}
October	8.3	10.7	9.0	4.7	6.1	7.8^{a}
x̄	9.4^{b}	10.6^{b}	10.1^{b}	5.1^{c}	5.7^{c}	
Total nitrogen (percent)						
V. alaskensis						
May	5.77	4.68	5.20	6.64	6.66	5.79
July	2.02	2.06	1.90	2.72	2.46	2.23
October	1.23	1.55	1.19	1.64	2.08	1.54
x̄	3.01	2.76	2.76	3.67	3.73	***
C. canadensis						
May	3.69	3.44	3.43	4.12	4.05	3.75^{a}
July	2.02	1.68	1.62	1.89	1.89	1.81^{b}
October	1.60	1.70	1.59	1.85	1.80	1.71^{b}
x̄	2.44^{c,d,e}	2.27^{d,e}	2.21^{e}	2.61^{c}	2.58^{c,d}	

(continued)

Table 1. Continued

Variable/species/month	Stand age (years) 5 (burn)	5	11	80	>450	$\bar{x}$
Total phosphorus (percent)						
V. alaskensis						
May	0.78	0.71	0.81	0.89	0.85	0.81^{a}
July	0.23	0.26	0.25	0.27	0.24	0.25^{b}
October	0.11	0.12	0.12	0.21	0.13	0.14^{c}
$\bar{x}$	$0.38^{d,e}$	0.37^{d}	$0.39^{d,e}$	0.46^{e}	$0.41^{d,e}$	
C. canadensis						
May	0.55	0.61	0.67	0.72	0.64	0.64
July	0.29	0.34	0.37	0.34	0.27	0.32
October	0.24	0.20	0.27	0.27	0.18	0.23
$\bar{x}$	0.36	0.38	0.44	0.44	0.36	***
IVDMD (percent)						
V. alaskensis						
May	69.0	64.3	67.3	71.1	69.1	68.1^{a}
July	46.4	41.9	43.8	41.1	43.8	43.4^{c}
October	46.1	47.9	51.2	45.6	52.1	48.6^{b}
$\bar{x}$	53.8^{d}	51.4^{d}	54.1^{d}	52.6^{d}	55.0^{d}	
C. canadensis						
May	61.2	69.0	67.6	74.4	66.5	67.8^{a}
July	69.3	62.2	57.3	62.1	55.3	61.2^{b}
October	58.4	66.1	56.9	57.5	57.2	59.2^{b}
$\bar{x}$	63.0^{c}	65.8^{c}	60.6^{c}	64.7^{c}	59.7^{c}	

[1] Means superscripted with the same letter are not significantly different at $\alpha = 0.05$.
[2] A triple asterisk in the last row, last column indicates a significant interaction at the $\alpha = 0.05$ level between month and stand.

The pattern of nitrogen concentration being greater in the forests than the clearcuts was similar to that reported by other investigators (Billings and Wheeler 1979; Van Horne 1982; Rose 1982) and appears to be consistent throughout these coastal forests. Phosphorus exhibited the same pattern with stand age as nitrogen in blueberry, but no consistent pattern in bunchberry. The relatively high concentration of nitrogen in the plants from the understory of the forests is similar to that in plants that appear to be light- or water-stressed (Rhoades 1979; Cates and others 1983, White 1984, Waring and others 1985).

The lack of between-stand differences in IVDMD was unexpected and is difficult to explain. The role of phenolics in dry-matter digestion is not well understood, but it appears that they tend to decrease *in vivo* digestibility of neutral detergent solubles (Mould and Robbins 1982). In our samples, the greater concentrations of phenolics in the leaves from the clearcuts may have been offset by the correspondingly greater concentrations of nonstructural carbohydrates that should be readily digestible.

Detergent analysis and IVDMD of the Douglas Island samples (table 2) indicated no apparent differences in fiber composition or dry-matter digestibility of bunchberry between the forest and the clearcut. Blueberry, however, appeared to have slightly higher concentrations of fiber and correspondingly lower levels of dry-matter digestibility in the leaves from the forest than in those from the clearcut. This difference in digestibility appears contrary to the results from the Kennel Creek study area but is based on a much smaller sample. The July 26-28 IVDMD values from Kennel Creek (table 1) compare favorably with the August 3 IVDMD values reported

Table 2.--Detergent fiber composition, *in vitro* dry-matter digestibility (IVDMD), crude protein, and estimated digestible protein of *Vaccinium alaskensis* and *Cornus canadensis* leaves collected from an 8-year-old unburned clearcut and adjacent old-growth forest in July at the Douglas Island study area. All values are percentage dry weight

	V. alaskensis		*C. canadensis*	
Variable	Forest	Clearcut	Forest	Clearcut
NDF[1]	41.5	35.1	23.0	24.4
ADF[2]	25.2	20.0	16.5	17.4
Cellulose	13.3	8.7	13.3	14.1
Lignin/cutin	11.4	10.9	2.1	2.6
Residual ash	0.6	0.4	1.0	0.7
IVDMD	54.7	57.8	73.3	71.0
Crude protein	17.1	12.4	15.4	11.3
Digestible protein	11.2	4.8	7.5	3.8

[1] NDF = neutral detergent fiber.

[2] ADF = acid detergent fiber.

by Hanley and McKendrick (1983) for Admiralty Island (45.8 percent for blueberry and 58.4 percent for bunchberry), though they are about 10 percentage points lower than the values for the July 5 samples from Douglas Island. The differences in IVDMD between the Kennel Creek and Douglas Island study areas probably reflect phenological differences in plant development. Regardless, the results from the Douglas Island samples (table 2) indicate that IVDMD was strongly related to fiber composition in both blueberry and bunchberry: estimates of apparent dry-matter digestibility based on fiber composition alone (equation for white-tailed deer, Mould and Robbins 1982) are 52.5 versus 55.5 percent and 79.1 versus 77.1 percent for forest versus clearcut in blueberry and bunchberry, respectively.

The differences in digestible protein concentration of the leaves from the clearcut versus the forest at the Douglas Island study area were especially pronounced (table 2). Both blueberry and bunchberry exhibited the common pattern of greater concentrations of crude protein in the forest than in the clearcut. But the combined effect of greater concentrations of crude protein along with lower concentrations of phenolics resulted in digestible protein concentrations 2.0 to 2.3 times greater in the forest leaves than the clearcut leaves for bunchberry and blueberry, respectively. These differences are especially significant in relation to a crude protein requirement of about 12 percent for a lactating doe (8 percent digestible protein, assuming a protein digestion coefficient of 0.63-0.70) (Verme and Ullrey 1972; Holter and other 1979). Leaves from the forest would meet this requirement, but leaves from the clearcut would meet only about half the requirement.

It appears, therefore, that on a dry-weight basis, dry-matter digestibility (and, consequently, concentration of digestible energy) may not differ in leaves from forests and clearcuts, but the concentration of digestible nitrogen may be twice as great in leaves from forests than in those from clearcuts. Consequently, if deer are bulk-limited (dry-weight-limited) in the amount of food they can eat and process through their rumen, they would consume equivalent amounts of digestible energy but only about half as much digestible protein by feeding in an open clearcut compared to a forest, assuming all other factors equal.

On the other hand, the specific leaf weights of blueberry and bunchberry were, respectively, 2.0 and 2.3 times greater in the clearcut than the forest (0.006 vs. 0.003 g/cm^2 for blueberry and 0.007 vs. 0.003 g/cm^2 for bunchberry, Douglas Island study area). If dry-matter intake rates of foraging deer are largely a function of bite size (Wickstrom and others 1984), then intake rates should be greater in the clearcut than the forest. Consequently, the rate of digestible energy intake would be greater in the clearcut than the forest and the rate of digestible protein intake in the clearcut may approach that in the forest. Thus, one of the critical questions is whether deer are more bulk-limited than time-limited in the amount and quality of food they can selectively harvest and process during the summer. We know that the two limitations are interrelated (Spalinger and others 1986) but do not know the precise nature of the interrelationships or which limitation is more important under a given set of environmental conditions.

In the palatability trials, all three deer distinguished between the blueberry leaves from the forest and those from the clearcut, and preferred (or at least ate more of) the leaves from the forest (fig. 1). One deer overwhelmingly preferred the leaves from the forest to those from the clearcut (4:1 ratio), while the preferences of the other two deer were less marked (ratios of 1.5:1 and 1.3:1). The pattern evident in figure 1 was consistent each of the 6 days of the feeding trial and was unaffected by switching feeding trays on the last day. The only exception was that on 1 of the days the female ate slightly more of the leaves from the clearcut than the forest. Forest leaves were preferred to clearcut leaves on all 17 of the other deer days.

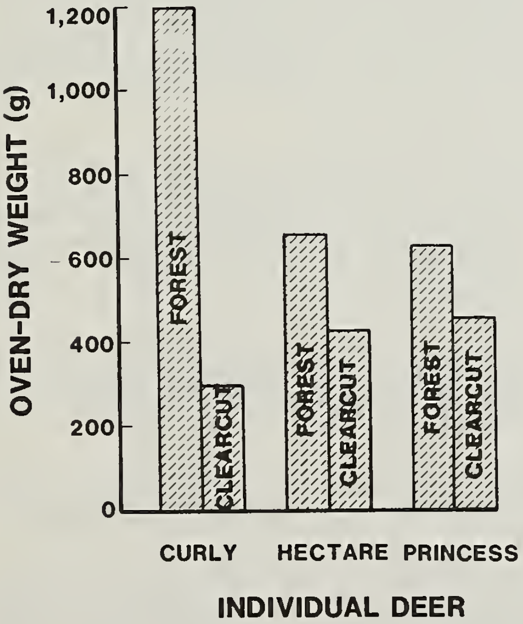

Figure 1.--Total consumption by three individual deer during a 6-day feeding trial of *Vaccinium alaskensis* leaves from an 8-year-old clearcut and adjacent old-growth forest at the Douglas Island study area.

CONCLUSIONS

Our current hypothesis is that blueberry and bunchberry plants growing in the shaded understories of forests in southeastern Alaska are essentially light-limited and allocate carbon primarily to growth and maintenance. On the other hand, blueberry and bunchberry plants growing in the open environments of young clearcuts appear to accumulate sufficient carbon for growth and maintenance as well as relatively high concentrations of carbon-rich secondary compounds such as tannins and other phenolics. We do not know whether high levels of these compounds are of use to the plant as ultraviolet light screens that transmit visible light (Lowry and others 1980), a means of tying up excess carbon, a deterrent to herbivores, or a combination of some or all of the above. In any case, plants in the open had higher concentrations of carbohydrates and phenolics and lower concentrations of nitrogen than did plants growing in the forest. The amount of solar radiation reaching the understory of forests in southeastern Alaska is typically less than 1 percent of that in the open (Alaback, unpublished data) and probably is the major environmental factor responsible for the observed differences in plant chemistry.

Our results indicate major environmentally controlled differences in forage quality for deer, with potential implications for deer productivity. Further research is needed to test the carbon/nutrient balance hypothesis under controlled conditions and to determine the relative importance of bulk- versus time-limitations for foraging deer.

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SECONDARY CHEMISTRY AMONG SYMPATRIC PLANT SPECIES AND ITS RELATIONSHIP TO INSECT HERBIVORY

Rex G. Cates and Debra Carol McElroy

ABSTRACT: Leaves of 24 sympatric plant species in an Atriplex-Artemisia grassland community were analyzed for terpene, alkaloid, cyanide, and trypsin-precipitating content. Those species that were classified as unpredictable contained higher amounts of cyanide, myrtenal, citronellyl acetate, cinnamic acid methyl ester, and water in their leaf tissues than those in the predictable category. Leaves of those species classified as predictable were higher in alpha-pinene, an unidentified sesquiterpene, and in trypsin-precipitating capacity than those in the unpredictable category. Young leaves contained significantly higher concentrations of potentially toxic or defensive secondary metabolites than mature leaves. Usually, polyphagous herbivores preferred host plants in the predictable category that were devoid of the secondary metabolites analyzed; monophagous herbivores preferred predictable species. Polyphagous herbivores preferred mature leaves while monophagous herbivores preferred young leaves. When reared on young and mature leaves of Helianthus, larval and adult parameters of the polyphagous Estigmene were higher on the mature leaves.

INTRODUCTION

Much evidence indicates the importance of secondary metabolites in biological systems. These compounds are thought to be essential to the survival of plants, and represent foci in the mediation of interaction at the plant-plant, plant-herbivore, and plant-pathogen interfaces (Rosenthal and Janzen 1979; Green and Hedin 1986). They are recognized also as major factors in plant physiological and ecosystem processes.

However, no study has examined the distribution of secondary chemistry in a community of plant species and related this distribution to herbivory in that plant community. Janzen (1973) and Cates and Rhoades (1977) have discussed the community of secondary metabolites that might be expected in leaf tissue of sympatric plant species. Unpredictable or ephemeral species were suggested to be characterized by toxin or qualitative defensive chemistry (Feeny 1976; Rhoades and Cates 1976). Predictable species were suggested to converge on the digestibility-reducing or quantitative defensive systems. Escape in space and time was thought to be an effective mecahnism in reducing herbivory especially against adapted herbivores. In general, adapted or more specialized herbivores were expected to prefer plant tissues or species that were typical of the unpredictable category while nonadapted or more generalized herbivores would prefer tissues and species that had converged upon quantitative defenses.

This paper is a synthesis of two major areas of research that we pursued from 1978 to 1984, and represents an attempt to relate the potential defensive chemistry of 24 sympatric plant species in an Atriplex-Artemisia grassland community to herbivore feeding patterns (Cates 1980, 1981; McElroy 1984; Cates and McElroy, submitted). Three classes of toxins and the trypsin-precipitating ability of leaf extracts of unpredictable and predictable plants were examined. First, we present the secondary chemistry of the plant species, and then the relationship of this chemistry to the young and mature leaves of the plant species. Finally, these data are discussed in terms of feeding patterns of monophagous-oliophagous and polyphagous herbivores.

MATERIALS AND METHODS

Site Location and Tissue Collection

The study site was located at the Petroglyph Open Space Preserve located 12 km northwest of the University of New Mexico campus, Albuquerque, NM. The site is a sandy area at the base of a volcanic escarpment; it supports a diverse plant community consisting predominantly of Artemisia filifolia, Atriplex canescens, Gutierrezia sarothrae, Dalea scoparia, and several desert annuals and grass species (table 1). This site previously had been characterized for plant density and herbivore plant and tissue preferences (Cates 1980, 1981; McElroy 1984). It has three semidistinct subsites: a sandy hill next to the escarpment, a less sandy flat area north and west of the hill, and an arroyo. The entire site measures approximately 300 m by 400 m.

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Plant tissue was collected from April 1982 to September 1982. Plants were collected along random transects to ensure that the tissue obtained was representative of the species throughout the site. A minimum of 30 individual plants per species (except for Cucurbita of which there was only one individual on the site) were collected and their young or mature leaf tissues were pooled in three groups of at least 10 plants per group. This was done to minimize intraspecific chemistry variation due to genetic or microenvironmental differences among individual plants.

Young and mature leaf tissues for each species were collected separately just prior to flowering. This was done because it had been suggested that leaves present prior to and at flowering are of the most value to a plant, and therefore, would be highly protected (Krischik and Denno 1983). All plants of a particular species were collected at dawn within a 3-day period and immediately placed on ice. Whenever possible, the entire plant was uprooted. In the case of woody perennials, large branches were collected. The collected plants or branches were taken to McElroy's home (a few minutes from the site) where the leaves were picked by hand, separated according to their relative age, packaged in aluminum foil, and labeled. The packages were stored in an ultra-cold freezer (-80 °F) until the chemical analyses were performed.

Young leaves were located at a growing apex and were fully open but had not yet grown to average leaf size. Mature leaves were of average leaf size, were not located at a growing point, and did not show any signs of senescence. Leaves damaged by herbivory, pathogens, or abiotic influences were not collected.

Determination of Plant Species Predictability

The young and mature leaf tissues of 24 sympatric plant species were tested for toxins (terpenes, cyanogenic glycosides, and alkaloids), tannins (trypsin-complexing compounds) (table 1), and percent water content. The species investigated represented a predictability continuum from unpredictable short-lived annuals to dominant, highly predictable woody perennials. Plant species predictability (following Rhoades and Cates 1976) was used as the measure of the different resource types.

Predictability was defined as the availability of plant species as a food resource but did not include the capacity of the herbivores to locate their host plants. Predictability categories were determined by plant growth form (annual, herbaceous perennial, and woody perennial) and plant density data collected from 1978 through 1982 (McElroy 1984; Cates and McElroy, submitted). Herbaceous species having a density of less than 0.10 individual/m^2 for at least 7 months (one third of the density measurements) were classified as rare. Those species with densities greater than 1.0 individual/m^2 for at least 5 months were considered common, and herbaceous species with density measurements in between were considered to be of average abundance. Variability of abundance was judged to be low if the range in density for the species did not exceed 1.0/m^2. Average variability was defined as a density range of 1.0 to 5.0/m^2, and high variability was considered to be a density range exceeding 5.0/m^2. Herbaceous species that were rare or exhibited a range of densities over the sampling years were defined as unpredictable. Woody perennial species were defined as predictable.

A total of 10 annual species representing eight families were included (table 1). Nine herbaceous perennial species from six families and five woody perennial species representing three plant families were sampled. Plant taxonomy was according to Martin and Hutchins (1980).

Greater description of the site, tissue collection, and detailed chemical methodology are found in McElroy (1984). Presented here are summaries of the chemical methods.

Water Content of Leaf Tissue

Leaf samples (1 g) were weighed on a Mettler H30 balance to within 0.1 mg. The samples were dried at 60 °C for 72 hours and reweighed. Percent water content was calculated as the ratio of weight lost to fresh tissue weight.

Alkaloid Analysis

Due to the diverse chemical nature of alkaloids, two methods were used to screen for their presence (Cates and McElroy, submitted). First, a modified Wall precipitation reaction (Cordell 1981) was used to determine if a plant produced alkaloids. Second, thin-layer chromatography was performed to determine the number of alkaloid compounds produced (McElroy 1984). Mayer's, Wagner's, Dragendorff's, and Ehrlich's reagents were used to detect alkaloids (including N-oxide alkaloids) in the above screening procedures. The thin-layer procedure also provided an estimate of the number of alkaloids present in a given tissue. In plants where alkaloids were present, high-pressure liquid chromatography (HPLC) was performed.

High-pressure liquid chromatography.--Those plants that gave positive precipitation reactions were subjected to analysis for specific types of alkaloids using high-pressure liquid chromatography. A modification of the method of Segall and Molyneux (1978) was used to test for the presence of pyrrolizidine alkaloids in Senecio longilobus. Using the method of Durbuc and others (1981) no steroidal alkaloids were found in any of the species.

Cyanogenic Glycoside Analysis

Leaf tissue samples were analyzed for the presence of cyanogenic glycosides as outlined by Mao and others (1965) using Conway microdiffusion glassware (Cates and McElroy, submitted). Color development was allowed to proceed at room temperature for 90 minutes after the addition of Chloramine T reagent, and the absorbance at 620 nm was read. The quantity of cyanide present was

Table 1.--Categories of plant species predictability and the associated secondary metabolites[1]. T = No. of terpenes, C = cyanide, A = No. of alkaloids, TP = trypsin-precipitating capacity, M = mechanical (modified after Cates and McElroy, submitted)

Category	T	C	A	TP	M
Unpredictable					
Annuals:					
Boraginaceae					
Cryptantha crassisepala	-	-	-	-	+
Capparidaceae					
Polanisia trachysperma	2	+	-	-	-
Cruciferae					
Dithyrea wislizenii	-	+	-	-	-
Euphorbiaceae					
Croton texensis	21	-	-	-	-
Hydrophyllaceae					
Nama dichotomum	1	-	-	-	-
Phacelia integrifolia	+[2]	+	-	-	-
Loasaceae					
Mentzelia laciniata	-	-	-	-	+
Herbaceous perennials:					
Compositae					
Senecio longilobus	18	+	5	-	-
Cucurbitaceae					
Cucurbita foetidissima	-	-	3	-	+
Fabaceae					
Astragalus lentiginosus	-	+	-	-	-
Dalea lanata	16	+	1	-	-
Hoffmanseggia jamesii	-	-	-	-	-
Malvaceae					
Sphaeralcea incana	-	-	-	-	-
Polygonaceae					
Rumex hymenosepalous	-	-	-	-	-
Solanaceae					
Solanum eleagnifolium	-	-	-	-	+
Predictable					
Annuals:					
Chenopodiaceae					
Salsola kali	-	-	-	-	+
Compositae					
Franseria acanthicarpa	23	-	-	+	-
Helianthus petiolaris	16	-	2	-	-
Herbaceous perennials:					
Compositae					
Machaeranthera canescens	16	-	-	+	-
Woody perennials:					
Chenopodiaceae					
Atriplex canescens	-	-	-	-	+
Compositae					
Artemisia filifolia	27	+	2	-	-
A. ludoviciana	29	+	2	+	-
Gutierrezia sarothrae	30	+	1	-	-
Fabaceae					
Dalea scoparia	15	-	-	+	-

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[1] + = secondary metabolites or mechanical properties present; - = secondary metabolites or mechanical properties not detected.

[2] Numerous unresolved terpenes.

determined by comparing the spectrophotometric reading obtained from a standard curve prepared from known amounts of potassium cyanide. Linear regression analysis was performed on the data and the linear function obtained was used to determine the concentration of HCN present in the leaf tissue.

Terpene Analysis

Leaf tissue was prepared for gas chromatographic analysis by weighing 300-mg leaf tissue to the nearest 1 mg. After extraction and filtering, 2 μL aliquot of a concentrated ether extract was injected immediately into a Perkin Elmer Sigma 2B gas chromatograph equipped with a flame ionization detector and SE-54 fused quartz capillary column (15-m by 0.02-mm ID) from Hewlett Packard. The initial temperature of 70 °C was increased from the moment of injection at a rate of 6 °C per minute until the final temperature of 200 °C was reached. The temperature remained at 200 °C for 10 minutes.

Terpene peaks were recorded and integrated on a Hewlett Packard model 3390A integrator. The concentration of each peak was calculated relative to the concentration of the internal standard. The actual concentrations per sample for the internal standards were: fenchone 118.5 μg, bornyl acetate 122.8 μg, and fenchyl alcohol 118.8 μg. Identification of the terpenes was achieved by comparing retention times of the terpene peaks to the retention times of known terpene standards, by spiking the peaks with standard terpene solutions, and by GC/MS on a Finnigan Quadrupole EICI instrument. The concentrations of all identified or numbered unknown terpenes were calculated to micrograms of terpene per gram dry weight of leaf tissue.

Determination of Protein-Complexing Compounds

Protein-complexing compounds (presumed to be hydrolyzable tannins) were analyzed using a modification of the method of Hagerman and Butler (1978) (McElroy 1984). To prevent oxidation of tannins, nitrogen gas was passed over the sample during the extraction and evaporation periods (Cates and McElroy, submitted). The absorbance of the supernatant, read at 595 nm, was compared to the standard curve of unprecipitated trypsin and converted to milligrams tannic acid equivalents per gram dry weight of leaf tissue.

Herbivore Feeding Preferences

The relationship between species predictability, secondary metabolites, and herbivory was examined. The methodology for sampling and determining leaf tissue and plant species preference is outlined in Cates (1980, 1981). For determining host plant preference, herbivores were visually sampled weekly during the 1977 through 1979 field seasons. A preference ranking that included the abundance of the plant species as well as the number of herbivores feeding on each plant species was calculated (Cates 1981).

Leaf tissue preference of each herbivore was determined by a relative tissue preference index that was based on the number of herbivores observed feeding on a plant and on the abundance of each leaf tissue type for each host plant (Cates 1980). At the same time the plant species abundances were determined, the plants were examined visually for leaf-chewing herbivores. Relative tissue preference (RTP) was calculated by dividing the number of feeding observations per tissue type per plant species by the amount of tissue available. The tissue with the highest value (the preferred tissue) was assigned a value of 100; the value for the less-preferred tissues was then normalized by dividing this number by the highest of the two and multiplying by 100.

To determine the effect of young and mature leaf tissues on larval growth rate, adult dry weight production, and egg mass production, larvae of Estigmene acraea (Arctiidae) were reared on leaf tissue of Helianthus petiolaris in a controlled environmental chamber. Fifty newly emerged, first-instar larvae were placed on either young (25 larvae) or mature (25 larvae) leaf tissues enclosed in glass petri dishes. Leaf tissue was replaced every 24 h to prevent drying and changes in the leaf tissue while the larvae were in the early instars, and every 12 h during the fifth and sixth instars. Larval growth rate was determined by subtracting the initial weight from the ending weight (pupal weight) and dividing this value by the number of days to reach pupation. As the female adults emerged, half were sacrificed to determine egg-mass production; the other half were sacrificed to determine adult dry weight production.

RESULTS

On the basis of the criteria used to determine the level of predictability of a given plant species, seven annuals in six families and eight herbaceous perennials in six families were designated as unpredictable (table 1). No woody perennials were deemed unpredictable resources. Predictable species included three annual species from two families, one herbaceous perennial (Compositae), and five woody perennials from three families. All annuals in the unpredictable category were short-lived and highly variable in abundance. This was epitomized by Cryptantha, Croton, and Nama. Most of the herbaceous perennials were relegated to this category because of their rarity. Rumex hymenosepalous emerged early in the spring (the end of February on occasion, but commonly around March 10-15) and completed flowering and seed production by the end of April or early May. Rumex is a species that generally escapes from herbivores at the study site due to its early emergence.

Three annuals were included in the predictable category because they were long-lived, often emerging in June and remaining in the community until September. None of the annuals in the unpredictable category were as long-lived. In terms of longevity, Machaeranthera appeared in late May and remained until October; during this time individuals were continually producing new leaf tissue, flowering, and producing seed. Relative to the growing season, it behaved much like the woody perennials.

Much variation was found within and between predictability categories in the levels of the terpene, cyanide, alkaloid, and trypsin-precipitating secondary metabolites. Species in the unpredictable category averaged one class of compound in the leaf tissue (table 1). Exceptions were Senecio longilobus and Dalea lanata, both of which had three classes of compounds in their leaf tissues. Cryptantha, Nama, Mentzelia, Cucurbita, Astragalus, Hoffmanseggia, Sphaeralcea, Rumex, and Solanum (all assigned to the unpredictable category) were depauperate in the secondary chemicals analyzed. Of these, four were associated with potential mechanical defenses; one (Rumex) appears early in the growing season, and Nama is short-lived with little biomass per individual relative to the other species.

Species in the predictable group averaged 2.3 classes of compounds in their foliage, which is significantly different from the average of one in the unpredictable species ($p<0.02$) (table 1). For terpenes, unpredictable species produced an average of 4.2 terpenes while predictable species produced 17.3 terpenes ($p<0.01$). However, three unpredictable species (Croton, Senecio, and Dalea) produced 21, 18, and 16 individual terpenes, respectively.

To test the hypothesis that predictable species do not differ in qualitative or quantitative production of secondary metabolites relative to unpredictable species, stepwise discriminant analysis was performed (Neff and Marcus 1980; Dixon 1983). An eight-variable model was generated from the 77 variables incorporated in the analysis showing a significant difference between the two predictability categories (table 2). Figure 1 shows the separation of the predictability groups, with the species in the predictable category having a mean discriminant score of 1.52 and those in the unpredictable category having a discriminant mean of -0.98. The species in the predictable category were characterized by higher levels of tannic acid equivalents, alpha-pinene, and unknown sesquiterpene number 12 than the unpredictable category (table 2). The unpredictable category was higher in water, cyanide, myrtenal, citronellyl acetate, and cinnamic acid methyl ester content than the predictable category.

Table 3 delineates the species that produce unique toxin or qualitative secondary metabolites as defined by terpenes. The five species in the predictable category produced more unique compounds than did the three in the unpredictable category. Sesquiterpenes were important in the delineation of these categories.

To test for quantitative differences in secondary metabolites between young and mature leaves, a Willcoxon signed rank analysis was done on the t values generated from t-tests that compared the mean concentrations of the compounds assayed in the young and mature leaves for each species (Zar 1974). The 14 species that produced four or fewer secondary metabolites were not subjected to this analysis because a significant result could not be obtained due to limitations of the analysis (DeVore 1982; McElroy 1984). Of the 10 species tested, nine had significant t values, indicating significantly higher concentrations of secondary metabolites in young leaves than mature leaves (table 4).

Table 2.--Discriminant analysis for the classification of predictable and unpredictable species based on water and secondary metabolite content of leaves (d.f.=8, 129; $p<0.0005$) (modified after Cates and McElroy, submitted)

Variable	Standardized coefficient
Percent water content	-0.4309
HCN	- .0036
Tannic acid equivalents	1.1461
Alpha-pinene	.0139
Myrtenal	- .1058
Citronellyl acetate	- .1945
Unknown sesquiterpene #12	.0678
Cinnamic acid methyl ester	- .2290

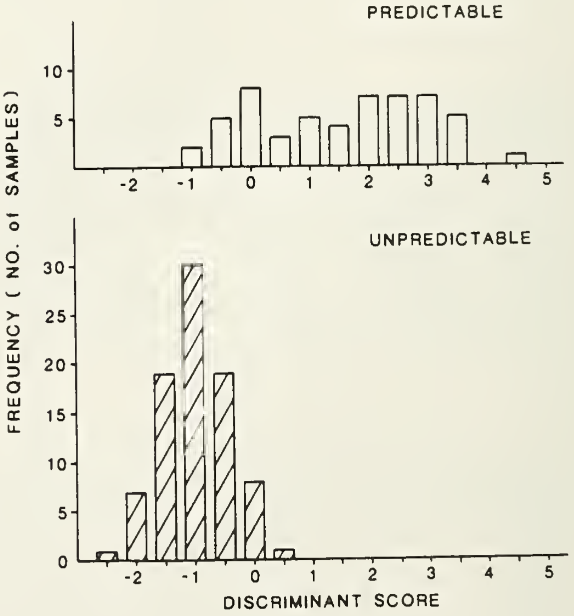

Figure 1.--Plot of the discriminant scores of leaf tissue samples of 23 species. Discriminant scores were calculated using an 8-chemical variable discriminant model.

Table 3.--Plant species producing unique toxin or qualitative secondary metabolites (after Cates and McElroy, submitted)

Species	P/U[1]	Compound
Artemisia filifolia	P	Unknown alcohol #1 Unknown sesquiterpene #21 Unknown sesquiterpene #22
Artemisia ludoviciana	P	Artemisia ketone Artemisia alcohol Sabinol Sabinyl acetate Sabinyl hydrate Thymol Unknown sesquiterpene #27 Unknown sesquiterpene #28
Croton texensis	U	Cinnamic acid methyl ester
Dalea lanata	U	Citronellal Citronellyl acetate Neryl acetate Unknown sesquiterpene #18 Unknown sesquiterpene #19 Unknown sesquiterpene #20
Dalea scoparia	P	Unknown sesquiterpene #26
Franseria acanthicarpa	P	Camphene hydrate Geraniol Beta-fenchene Beta-bisabolol Unknown sesquiterpene #13 Beta-farnesene Unknown sesquiterpene #16 Unknown sesquiterpene #17
Gutierrezia sarothrae	P	Trans-pinocarveol Alpha-camphene aldehyde Carvone Eucarvone Beta-eudesmol Unknown sesquiterpene #23 Unknown sesquiterpene #24 Unknown sesquiterpene #25 Verbenone Umbellulone Alpha-pinene oxide
Senecio longilobus	U	Unknown sesquiterpene #15 Alpha-farnesene

[1] P = predictable resource, U = unpredictable resource.

Table 4.--Significant Willcoxon signed-rank statistics calculated on the *t* value comparing young and mature leaf tissues within each species. A negative sign on the z value indicates a higher concentration of potential toxin or qualitative chemistry in young leaves (after Cates and McElroy, submitted)

Species	Z-values	*P*
Artemisia filifolia	-4.144	0.0004
A. ludoviciana	-3.618	.0004
Croton texensis	-2.354	.0186
Dalea lanata	-2.025	.0440
D. scoparia	-2.959	.0031
Franseria acanthicarpa	-4.029	.0004
Gutierrezia sarothrae	-2.403	.0164
Machaeranthera canescens	-3.593	.0004
Senecio longilobus	-2.651	.0008

Of the six host plants observed fed on by the polyphagous lepidopteran *Estigmene*, *Rumex* was preferred in March and April, while *Atriplex* was preferred in July and August. Both species were devoid of the secondary metabolites that we analyzed (table 5). *Senecio* is an unpreferred host in March and April, but is second in preference in July and August. *Hyles* and *Vanessa*, both lepidopterans, prefer *Rumex* and *Lupinus*, respectively. (*Lupinus* was not present on the site the year secondary chemistry was measured.) *Diapheromera*, a walkingstick, preferred two predictable species (*Atriplex* and *Dalea scoparia*). The monophagous herbivores preferred *Helianthus* (a long-lived annual), *Machaeranthera* (a long-lived herbaceous perennial), and *Artemisia filifolia* (a woody perennial).

When comparing the feeding patterns of polyphagous and monophagous-oliophagous herbivores on young and mature leaf tissues, all three of the more generalized herbivores preferred mature leaf tissues of plants assigned to both predictability categories (table 6). Alternatively, both monophagous herbivores preferred young leaves of plant species of the predictable resource category.

Larvae of *Estigmene*, a lepidopteran with a host plant list of six species (Cates 1981), preferred mature leaves over young leaves of *H. petiolaris* (table 7). Larval growth rates, adult dry weight production, and egg mass production were significantly lower when larvae were reared on young leaves as compared to mature leaves.

CONCLUSIONS

Feeny (1976), Rhoades and Cates (1976), Cates and Rhoades (1977) and McKey (1979) hypothesized that ephemeral, unpredictable, young leaf tissues would be characterized primarily by low molecular weight toxin or qualitative defenses, and that predictable, mature leaf tissues would contain higher concentrations of digestibility-reducing or quantitative defenses. Patterns in the production of secondary metabolites among the sympatric species at the *Atriplex*-*Artemisia* site support these ideas. The leaf tissues of the predictable species contained higher concentrations of trypsin-binding compounds and had higher concentrations of the higher molecular weight sesquiterpenes than the leaf tissues of the unpredictable species (tables 2 and 3). Alternatively, leaves of the unpredictable species did not contain tannins, but had higher concentrations of cyanide and the lower molecular weight terpenes than the predictable species (tables 2 and 3). Furthermore, young leaf tissues of 9 of the 10 species analyzed had higher concentrations of toxin or qualitative compounds than the mature leaves.

Cates and Rhoades (1977) predicted that selection by herbivores and pathogens would favor divergence in the production of toxins in leaf tissues of sympatric species, and convergence in the production of digestibility-reducing systems. This was supported by the terpenoid and trypsin-precipitating analyses. On the basis of terpenoids alone, eight of the species produced a total of 37 unique terpenes (table 3). Based on rf values, all of the alkaloids in the seven species that contained alkaloids were different. For example, in *Senecio* five pyrollizidine alkaloids were identified (McElroy 1984). None of the other species contained this type of alkaloid, even though *Cryptantha* was a candidate for pyrollizidine alkaloids since they are reported in the Boraginaceae.

Alternatively, all of the species producing trypsin-precipitating compounds were in the predictable category, and none of the unpredictable species were found to produce these compounds. However, only four of the nine species (44 percent) in the predictable category were shown to precipitate trypsin. A more rigorous test would be to measure binding capacity using a wide variety of proteins (such as hemoglobin, ribulose carboxylase, and proteins natural to the leaf tissues) since some secondary metabolites may not bind with trypsin but might with other proteins.

The question arises as to the accuracy, based on the secondary metabolites produced, of assigning plant species to the predictable and unpredictable categories based on growth form and abundance. Perhaps at other sites, some of the herbaceous perennials that were classified as unpredictable might be relegated to the predictable category. Several of the herbaceous perennials were classified as unpredictable species based on rarity at the site. Senecio and Dalea lanata reflect more of the predictable mode. These two species are characteristic of three of the five woody perennials in that they have at least three classes of compounds produced in the leaf tissues. In terms of the overall patterns, moving these two species to the predictable category would only enhance the differences already found in the distribution of toxins and digestibility-reducing secondary metabolites between the two categories. Based on rarity, Sphaeralcea is typical of other species in the unpredictable category. But this species is present during the entire growing season from June to October. In other communities Sphaeralcea may be abundant and more typical of the predictable category. However, no terpenoids, cyanide, alkaloids, or trypsin-precipitating compounds were found in its leaf tissues.

Several species were found to produce little if any of the secondary metabolites that were analyzed. The unpredictable species, Cryptantha, Nama, Mentzelia, Hoffmanseggia, Sphaeralcea, Rumex, and Solanum, and the predictable species, Salsola and Atriplex, may produce other compounds that were not analyzed in this study. For example, Atriplex may contain saponins (see McArthur, this proceedings). If species without any of the secondary metabolites we analyzed for were shown to contain other types of secondary metabolites, this would only increase the diversity of compounds, adding credence to the hypothesis that large chemical diversity exists among sympatric plant species. An obvious group to have included in this study is the monomeric phenolics.

Feeny (1976), Rhoades and Cates (1976), and Cates and Rhoades (1977) suggested that, in general, monophagous-oliophagous or adapted herbivores have evolved a preference for ephemeral or unpredictable species while polyphagous or less-adapted herbivores would prefer predictable or apparent species. Larvae of Estigmene, which is a polyphagous, bivoltine herbivore, preferred Rumex in the March and April sampling, and Atriplex in the July and August sampling (table 5). Both of these species were devoid of the secondary metabolites analyzed (table 1). In the July and August sampling, however, Senecio was important as a host plant in terms of the number of larvae feeding on it as was Atriplex (Cates 1981). Based on the three classes of secondary metabolites produced by Senecio (table 1), this would not be suspected; generally, the larvae selected other plants that were devoid of secondary metabolites (tables 1 and 5). However, it is known that alkaloids in Senecio decrease 40 to 60 percent when leaves begin to wilt. It may be that in July and August the defenses of Senecio are less effective resulting in its increased use as a host plant. The feeding pattern of Estigmene appears to support the hypothesis that polyphagous or nonadapted herbivores prefer host plant tissues low in toxin defensive systems.

Hyles, Vanessa, and Diapheromera are less generalized in their diet (Cates 1981) but show a similar pattern to Estigmene; they prefer plants devoid of secondary metabolites (Rumex, Cryptantha, and Atriplex) (tables 1 and 5). Hyles and Vanessa at the species level have been shown to have large host plant lists. However, at the population level they appear less generalized in their diet than Estigmene (Cates 1981). Diapheromera prefers Dalea, which is known to have three classes of secondary metabolites, to Atriplex (table 5) but this may be due in part to its feeding on the young stem growth instead of leaf tissue. Analysis of young stem tissue may show it to be low in toxins and high in digestibility-reducing capacity.

The monophagous herbivores preferred predictable species: Helianthus which is a long-lived annual; Machaeranthera, an herbaceous perennial; and Artemisia filifolia, a woody perennial (table 5). These data are not supportive of the contention that specialists have evolved a preference for ephemeral and unpredictable species.

In every case, leaf tissue preferences of monophagous and polyphagous herbivores are consistent with the hypothesis that more specialized herbivores prefer ephemeral, unpredictable tissues, and generalized herbivores prefer the predictable, mature leaf tissues (table 6). For nonadapted herbivores, mature leaves are significantly preferred over ephemeral leaves, while adapted herbivores prefer significantly the young leaf tissues over the mature tissues. Young leaves are high in toxin or qualitative defenses while mature leaves are high in digestibility-reducing or quantitative defenses (tables 2 and 4, figure 1). Furthermore, it appears that young leaves of predictable species, as well as young leaves of some of the unpredictable species, are very diverse in terpenoid chemistry (table 3) adding to the contention that young leaves represent well the toxin mode of defense. Clearly, when Estigmene is reared on young or mature leaves, larval growth rate, adult biomass production, and egg mass production are greatest on the mature leaf tissues of Helianthus (table 7).

Growth rates were not measured for any of the plant species, so direct assessment of Bryant and others (1983) and Coley and others (1985) cannot be made. However, if we assume that predictable resources in general represent species with slower growth rates as compared to species in the unpredictable category, some preliminary comparisons can be made (Cates and McElroy, submitted). Predictable species are higher in carbon-based defenses than unpredictable species. Unpredictable species are higher in cyanide content than the predictable ones. However, six of the 15 (40 percent) and three of the 15 (20 percent) unpredictable resources produced

Table 5.--Plant species preferences of polyphagous and monophagous insect herbivores on annuals and herbaceous perennials (modified after Cates 1981)

Herbivore species	Plant species	Pref. ranking (PR)
Polyphagous herbivores:		
Estigmene acraea[1]	Chenopodiaceae[2]	
	Atriplex canescens	2
	Salsola kali	1
	Compositae[2]	
	Guiterrezia sarothrae	0
	Senecio longilobus	1
	Fabaceae[2]	
	Dalea scoparia	1
	Polygonaceae[2]	
	Rumex hymenosepalus	100
	Chenopodiaceae[3]	
	Atriplex canescens	100
	Salsola kali	1
	Compositae[3]	
	Helianthus petiolaris	5
	Senecio longilobus	84
	Fabaceae[3]	
	Dalea scoparia	5
Hyles lineata	Polygonaceae	
	Rumex hymenosepalus	100
Vanessa cardui	Boraginaceae	
	Cryptantha crassisepala	1
	Fabaceae	
	Lupinus pusillus	100
Diapheromera velii	Chenopodiaceae	
	Atriplex canescens	79
	Fabaceae	
	Dalea scoparia	100
Monophagous herbivores:		
Chlosyne lacinia	Compositae	
	Helianthus petiolaris	100
Stiria rugifrons	Compositae	
	Helianthus petiolaris	100
Chlosyne acastus	Compositae	
	Machaeranthera canescens	100
Hemileuca hera magnifica	Compositae	
	Artemisia filifolia	100

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[1] Adults of *Estigmene* lay eggs twice/year.

[2] Eggs laid in March and April.

[3] Eggs laid in July and August.

Table 6.--Leaf tissue preferences of monophagous and polyphagous herbivores on annuals and herbaceous perennials (modified after Cates 1980)

Herbivore species	Plant species	Young	(N)	Mature	(N)
Polyphagous herbivores:					
Estigmene acraea[1]	Chenopodiaceae[2]				
	Atriplex canescens	4	(5)	100	(71)
	Salsola kali	10	(3)	100	(34)
	Compositae[2]				
	Senecio longilobus	0	(0)	100	(75)
	Fabaceae[2]				
	Dalea scoparia	0	(0)	100	(26)
	Polygonaceae[2]				
	Rumex hymenosepalus	10	(156)	100	(1984)
	Chenopodiaceae[2]				
	Atriplex canescens	4	(5)	100	(69)
	Compositae[2]				
	Helianthus petiolaris	0	(0)	100	(527)
	Senecio longilobus	19	(3)	100	(75)
	Fabaceae[2]				
	Dalea scoparia	0	(0)	100	(26)
Hyles lineata	Polygonaceae				
	Rumex hymenosepalus	84	(11)	100	(123)
Vanessa cardui	Boraginaceae				
	Cryptantha crassisepala	0	(0)	100	(508)
	Fabaceae				
	Lupinus pusillus	0	(0)	100	(71)
Monophagous herbivores:					
Chlosyne acastus	Compositae				
	Machaeranthera canescens	100	(78)	0	(0)
Hemileuca hera magnifica	Compositae				
	Artemisia filifolia	100	(335)	0	(0)

[1] Adults of *Estigmene* lay eggs twice/year.

[2] Eggs laid in March and April.

Table 7.--The effect of leaf tissue type of *Helianthus petiolaris* on the generalized *Estigmene acraea*. Data are mean ± 1 SD

Parameters	Leaf tissue type	
	Young	Mature
Larval growth rate (mg)	17.6 ± 1.8	[1]21.7 ± 4
Adult dry weight (mg)	61.0 ± 9.7	[1]84.0 ± 18
Egg mass (dry wt)	61.0 ± 8.5	[1]87.0 ± 20

[1] $P<0.003$ for comparison of horizontal means.

cyanide and alkaloids, respectively, while three of the nine (33 percent) and four of the nine (44 percent) predictable species produced cyanide and alkaloids, respectively, indicating little difference if any in nitrogen-based secondary metabolites. Should *Senecio* and *Dalea lanata* be shifted to the predictable category, as the chemical evidence suggests, then the data do not support the growth rate hypothesis. If this were the case, then four of the 15 (27 percent) and one of the 15 (7 percent) of the unpredictable resources would produce cyanide and alkaloids, respectively, while five of the nine (57 percent) and six of the nine (67 percent) of the predictable species would produce cyanide and alkaloids, respectively. Furthermore, a greater diversity of terpenoids is found in the predictable species than the unpredictable ones (table 3). A knowledge of the availability and use of nutrients and moisture by the plant species would be useful in interpreting the patterns in the production of secondary metabolites.

The greater diversity of terpenoids in the predictable species suggests that biotic interactions such as those dealing with plants and herbivores, plants and pathogens, and plants versus plants are major influences in the production of secondary metabolites among sympatric plant species. Theories of the evolution of plant defenses must deal with variation in secondary metabolites among sympatric species having similar growth rates, since variation among and within sympatric plant species is now recognized as an important influence in the dynamics of herbivores (Denno and McClure 1983; Cates and Redak 1986).

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BETWEEN-SPECIES DIFFERENCES IN LEAF DEFENSES OF TROPICAL TREES

Phyllis D. Coley

ABSTRACT: Rates of herbivory and patterns of leaf defense are presented for light-demanding and shade-tolerant tree species growing in a lowland rainforest in Panama. More than 85 percent of the annual leaf damage is due to grazing by insects. There are over three orders of magnitude difference between species in the rates of herbivory on mature leaves. More than 70 percent of this variation can be statistically explained by measured defenses. Species with little herbivore damage have tough, fibrous leaves with low concentrations of nitrogen and water. Tannin levels are not significantly correlated with herbivory. Shade-tolerant species have higher levels of defense and suffer less herbivory than species that require light gaps for establishment. This may be due to differences in inherent growth rates between species, with slow-growing species being better defended. Evidence is also presented showing a correlation between leaf lifetime and type of defense. Comparisons of general patterns of herbivory and plant defense are made between temperate and tropical forests.

INTRODUCTION

In this paper, I present patterns of herbivory and plant defenses observed in a lowland tropical forest, in an attempt to explain why some species are better defended than others. Initially, I will describe various plant characteristics that make leaves palatable to herbivores, and then present evolutionary arguments for why we might see differences in both type and amount of defense.

TROPIC/TEMPERATE COMPARISONS

Research was carried out in a lowland tropical rainforest on Barro Colorado Island (BCI) in Panama. The site is administrated by the Republic of Panama and the Smithsonian Institution, and has been protected from poachers and tree cutters since the 1920's. Most of the forest is at least 200 years old (Foster and Brokaw 1982).

Climate

Several aspects of the climate and forest are noteworthy since they contrast sharply with many temperate systems. First, seasonality is much less dramatic on BCI (Croat 1978; Leigh and others 1982). Temperatures average 25 °C year round, with much of the variation being diurnal. Annual rainfall is high (250 cm/yr), but includes a distinct 4-month dry season. The dry season is clearly important in the annual rhythms of both plants and animals; however, only a few tree species are completely deciduous, and insect abundances remain relatively high (Wolda 1978). In northern systems that experience much greater seasonal severity, environmental constraints on evergreenness and insect life cycles may play a much more dominant role in plant/herbivore interactions.

Light

In contrast to many shrub-dominated areas in the Western United States, light may be the most limiting and variable resource in the forest on BCI. The canopy is 30 to 40 m tall, reducing light levels at the forest floor to only 1 to 5 percent of full sunlight (Chazdon and Fetcher 1984). In comparison, light levels in gaps created by fallen trees can be dramatically higher. although light gaps comprise only about 5 percent of the area, the increased light levels make them important areas of productivity (Hubbell and Foster in press). Smaller breaks in the canopy create light flecks which can be the major source of carbon gain for plants below (Bjorkman and others 1972; Pearcy and Calkin 1983).

Accompanying the wide range of light conditions at the forest floor is a continuum in shade tolerance among different tree species (Whitmore 1978; Denslow 1980; Hartshorn 1980; Brokaw 1985). At one extreme are species found only in light gaps that rely on rapid germination and establishment once a gap is formed. At the other extreme are highly shade-tolerant species, that can persist for many years in the understory.

Diversity

Another important feature of the forest on BCI relative to temperate communities is its high species diversity. Per hectare, there is an average of 60 tree species with greater than 20 cm d.b.h. (Leigh 1982). This diversity has several interesting implications for herbivory. First, one might predict that there would be fewer specialist herbivores than in a less diverse community. Although there are no data with which to test this, my personal observations suggest the contrary: most leaf damage on BCI is done by relatively specialized insects. Another consequence of

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tropical forest diversity is that one cannot understand general defense patterns and effects on herbivory by studying the dominant few species in the community. There simply aren't a few dominant species. However, working in a diverse community helps avoid the problem that general patterns may simply be a consequence of phylogenetic constraints on the dominant species. If large numbers of unrelated species have converged on a particular set of effective defenses, this can be a strong argument for the effectiveness of those defenses.

Herbivores

In neotropical forests, the vast majority of leaf tissue is eaten by insect rather than vertebrate herbivores. On BCI, 85 percent of the leaf area eaten annually is consumed by insects (Leigh and Smythe 1978). Vertebrate herbivores, notably sloths, iguanas, howler monkeys, and tapirs are conspicuous, but consume relatively little leaf material. I would argue that in neotropical forests the major selective pressure for the evolution of plant defenses is, therefore, due to grazing by insects.

HERBIVORY AND DEFENSES

To document general community-wide patterns, I measured herbivory and defenses for 47 of the most common canopy tree species on BCI (Coley 1983). These species represented a range of shade tolerance, from species that were gap specialists to those that could tolerate deep shade. To facilitate measurements, I worked with saplings. All individuals were studied in gaps to control for environmental influences and the availability of herbivores.

Patterns of Herbivory

Patterns of herbivory were quantified as the rate of damage to mature leaves. Over 400 saplings and approximately 10,000 leaves were marked and rates of herbivory measured during 6-week periods in each of the early wet, late wet, and dry seasons (Coley 1983). I emphasize the importance of measuring herbivory as a rate: the percentage of leaf area removed per unit of time. Because leaf lifetimes for different species vary by orders of magnitude, leaves are available to herbivores for different amounts of time. Single measurements of the amount of standing crop damage would therefore be misleading.

Average rates of herbivory differed enormously between the 47 study species (fig. 1). The least susceptible species lost an average of 0.0003 percent of its leaf area per day compared to 0.85 percent for the most damaged species (Coley 1983). This is a difference among species of over three orders of magnitude, despite the fact that study individuals were growing as neighbors in the same microhabitat, and were susceptible to the same herbivores.

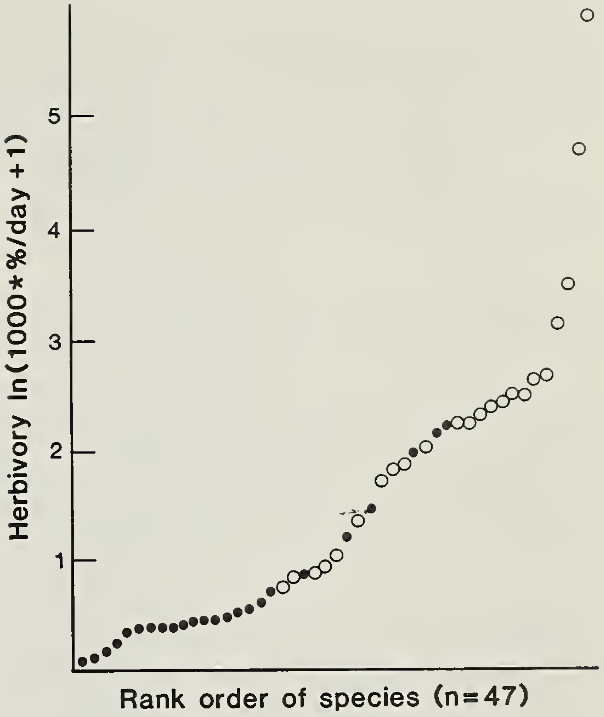

Figure 1.--Average annual rates of herbivory for mature leaves of 47 tree species on Barro Colorado Island, Panama. Herbivory measures are expressed as the natural log transformation of the percentage of leaf area consumed per day. Solid circles indicate shade-tolerant species, open circles indicate light-gap specialists.

Plant Defenses

Why are herbivores showing such strong preferences for certain species over others? To answer this, I measured leaf and plant properties that might influence rates of herbivory (Coley 1983) (table 1). Because it is impossible to measure all the secondary metabolites, I focused on a single widespread group: condensed tannins. There is considerable controversy surrounding the mode of action of tannins, but it is fairly well accepted that they serve some defensive function (Feeny 1970, 1976; Swain 1979; Bernays 1981; Martin and Martin 1982; Zucker 1983). I measured two forms of condensed tannins using the vanillin (VAN) and proanthocyanidin/BuOH (PRO) assays. Various components of fiber were also quantified (cellulose, acid-detergent fiber, neutral-detergent fiber, and lignin). Fiber provides structural support for the leaf, but it also reduces leaf digestibility for vertebrate and presumably invertebrate herbivores (Van Soest 1975; Milton 1979). Another measure related to fiber content is leaf toughness. This was measured as the amount of weight needed to punch a 3-mm rod through the leaf. Leaf pubescence was quantified as the density of hairs on the lower leaf surface. In addition to measuring potentially defensive properties, leaf nutritional value was estimated as the percentage of nitrogen and water.

Table 1.--Correlation coefficients for mature leaf characteristics and rates of herbivory for 47 canopy tree species on Barro Colorado Island, Panama. Values are the mean of several individuals for each species. Herbivory rates were measured throughout the year (Coley 1983)

Leaf characteristic	Correlation with herbivory
Tannin (VAN) % dw	-0.112
Tannin (PRO) % dw	-0.128
Fiber (NDF) % dw	-0.278 *
Fiber (ADF) % dw	-0.424 *
Lignin % dw	-0.223
Cellulose % dw	-0.473 *
Toughness (grams)	-0.515 *
Pubescence #/mm2	0.635 *
Water %	0.507 *
Nitrogen % dw	0.287 *

* Significant at P<0.05.

Table 1 correlates each leaf characteristic with herbivory. The magnitude of the correlation coefficient indicates the relative importance or effectiveness of each characteristic against herbivory. Water and nitrogen content were significantly positively correlated with herbivory. The various fiber components and the related toughness measure were all highly negatively correlated with herbivory. Tannin levels, however, showed no significant relationship to herbivory, and tannin/protein ratios were similarly uncorrelated. Pubescence was the only characteristic positively correlated with herbivory. This, along with its inverse relationship to other defenses, suggests that hairs may provide a simple way of identifying poorly defended species.

The results presented in table 1 show that species with tough, fibrous leaves of low nutritional value suffer the least amount of herbivory. Are these, however, the major leaf characteristics responsible for deterring herbivores? To examine this, I ran a multiple regression of herbivory as a function of the leaf characteristics mentioned above (Coley 1983). More than 70 percent of the variation in herbivory among species was statistically accounted for by differences in these leaf properties (r=0.84, p<0.001). This is an enormous amount of variation to explain for a natural system and suggests that nutritional and fiber contents are extremely important determinants of herbivory. Species not well defended by these measures are not escaping damage by other means (Rhoades and Cates 1976; Feeny 1976), but in fact are suffering high levels of herbivory.

BETWEEN-SPECIES DIFFERENCES IN DEFENSES

Defenses and Shade Tolerance

There is considerable variation among species in the extent of their defenses and in the resulting rates of herbivory. Are there any general defensive patterns, with certain groups of species tending to be better defended? For the species I studied on BCI, there were dramatic defensive differences related to the ability of each species to tolerate shade. In table 2, the 47 study species are divided into two categories based on their degree of shade tolerance. On average, species that were found only in light gaps were eaten six times more rapidly than shade-tolerant species. They had significantly lower concentrations of tannins, were less fibrous by all four measures, and only half as tough. In addition to being less well-defended, gap species had a higher nutritional value as measured by water and nitrogen contents.

Defenses and Growth Rate

The defensive differences between gap and shade-tolerant species (table 2) may be due to differences in inherent growth rates. Under the same microclimatic conditions, gap species grow more than twice as fast as shade-tolerant species (Coley 1983). Does the inherent growth rate of a species therefore show a relationship to the level of defense? For the 47 study species, there was a significant positive relationship between growth rate (annual height increase) and herbivory (r=0.52, p<0.001). This relationship was the same using other growth measurements such as annual leaf

Table 2.--Comparisons of mature leaf characteristics and rates of herbivory for 23 light-gap specialists and 24 shade-tolerant tree species on Barro Colorado Island, Panama. Values are the means for each species

Leaf characteristic	Light-gap specialist	Shade tolerant
Herbivory %/day	0.24	0.04 **
Tannin (VAN) % dw	0.8	2.4 *
Tannin (PRO) % dw	1.7	4.8 *
Fiber (NDF) % dw	41.3	51.1 *
Fiber (ADF) % dw	29.2	37.2 *
Lignin % dw	10.3	12.1
Cellulose % dw	17.4	23.4 *
Toughness (grams)	392	622 **
Water %	72	63 **
Nitrogen % dw	2.5	2.2 *

* significant at P<0.05
** significant at P<0.01

area production or maximum growth rate measured for an individual. There was also a significant negative relationship between growth rates and a linear combination of defenses ($r=0.72$, $p<0.001$). This indicated that the degree of investment in defenses was a function of inherent growth rate.

Conclusions

The general pattern that emerged from these data is that inherently slow-growing species show much higher investments in defense and consequently suffer much less herbivore damage. I and others argue that inherently slow growth rates select for high defense levels because the cost of defense is smaller and the impact of herbivory is potentially greater than for fast-growing species (Coley and others 1985; Gulmon and Mooney 1985). Inherent growth rates are determined evolutionarily by resource availability in the habitat to which a species is best adapted (Grime 1979; Chapin 1980). In my study, it was the shade-tolerant species that existed in resource-limited microhabitats and therefore had the slowest growth rates. Consequently they were also the best defended. This pattern of slow growers being better defended is also seen in areas where growth is limited by other resources such as water or nutrients (Brunig 1969; Janzen 1974; McKey and others 1978; Grime 1979; Bryant and Kuropat 1980; Bryant and others 1983; Coley and others 1985).

TYPE OF DEFENSE

The evidence presented above shows that slow-growing species tend to have greater amounts of defense, but makes no predictions concerning the type of defense. The diversity of plant secondary metabolites is enormous. Why are some species defended by tannins and others by alkaloids? What factors influence the type of chemical defense that will be used by different species? Part of the answer may be found by examining costs of different defenses under different conditions (McKey 1979, 1984; Coley and others 1985).

Traditionally, secondary compounds were considered inexpensive if they were present in low concentrations, and expensive if they occurred at high concentrations (Rhoades and Cates 1976; Feeny 1976). This ignores the potentially high cost associated with turnover (Coley and others 1985). Metabolically active compounds, such as alkaloids, cardiac glycosides, and mono- and di-terpenes can have half-lives on the order of hours or days (Robinson 1974; Waller and Nowacki 1978; Croteau and Johnson 1984). Although the pool size of these compounds is typically small, they have high rates of turnover. In other words, the plant must continually synthesize more compound to maintain the same concentration in the leaves. The cost of defense by these "mobile" compounds is therefore accumulated throughout the leaf life. This contrasts to "immobile" compounds such as fiber and tannins. There is an initial construction cost that can be high since they tend to be present in large concentrations. However, they are metabolically inactive, so there are essentially no continued costs associated with turnover (Walker 1975; Swain 1979). Because of their metabolic inactivity, immobile compounds cannot be withdrawn from the leaf at senescence (Mckey 1979). For leaves with short leaf life, the cost of defending with mobile defenses is likely to be less than the cost of immobile ones (McKey 1984; Coley and others 1985). As leaf life time increases, the costs of defense by immobile compounds are expected to be less.

The above predictions are supported by data I obtained on BCI. Leaf life times were measured on 46 species, and ranged from an average of 4 months to over 3 years (Coley 1981). There is a significant positive correlation between the condensed tannin content and average leaf life of each species ($r=0.46$, $p<0.005$). There is also a significant positive correlation between total fiber content and leaf life ($r=0.62$, $p<0.001$). This suggests that species with longer lived leaves have higher investments in immobile defenses.

The distribution of immobile defenses observed for the BCI trees is what would be predicted based on cost/benefit analyses. What other constraints besides costs could influence the advantage of one type of defense over the other? Are there conditions under which we would expect to find mobile defenses in long-lived mature leaves, and how might these vary between the temperate and tropical zones? Unfortunately there are few data with which to test this, particularly from the tropics. Studies of temperate trees have shown that insect damage or environmental stress can induce short-term production of several classes of secondary compounds (Haukioja and Niemela 1979; Baldwin and Shultz 1983; Rhoades 1985). Most often these seem to be mobile compounds such as simple phenols and monoterpenes. Their production, even in species with long-lived leaves, would be effective against temporary outbreaks of herbivores. Once the outbreak passed, the resources contained in the mobile defenses could be reallocated to other functions. The cost would therefore only be incurred for a short period. Hypothetically then, if short-term induction is a response to herbivory, and if insect outbreaks are more common in the temperate zone compared to the aseasonal tropics, one might expect induction of defenses to also be more common in the temperate zone.

Another condition that might favor mobile defenses in mature long-lived leaves is a strong seasonality of herbivore populations. Variation in the types and numbers of herbivores could make different defenses advantageous at different times of the year. Many temperate evergreen trees suffer primarily from insect herbivores in the summer and vertebrate grazers in the winter. This type of seasonality in herbivores is not generally as pronounced in the humid neotropics.

A final condition likely to favor mobile defenses is seasonality in nutrient availability. If nutrients are primarily taken up at a time of year when growth demands are low, they must be temporarily stored. Mobile defenses would be a good form of storage (Mooney and others 1983).

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Section 2. Palatability

PLANT SECONDARY METABOLITES AS FEEDING DETERRENTS TO VERTEBRATE HERBIVORES

P. Reichardt, T. Clausen and J. Bryant

ABSTRACT: The effects of specific phytochemicals on plant palatability to hares have been determined in feeding trials utilizing purified compounds in concert with quantification of deterrent substances in plant tissues having a range of palatabilities. These studies suggest that: plant chemical defenses rely on the properties of individual compounds, unpalatability is closely tied to exact molecular structure, and no broad class of secondary metabolites contains individual compounds with uniform deterrent properties.

INTRODUCTION

Limited understanding of the factors governing diet selection by herbivores has prompted numerous studies that demonstrate a relationship between an herbivore's feeding behavior toward some plant and certain physical or chemical properties of the plant. Palatabilities of plants have been claimed to be inversely related to levels of secondary metabolites (such as phenols, tannins, monoterpenes, and alkaloids) and physical properties (such as leaf toughness and twig diameter) and directly related to levels of nutrients (such as total carbohydrates and nitrogen). While data from various studies support such relationships, seldom do they support the assertion that the relationships are causative. While there are documented cases of plant unpalatability being correlated with total tannin content, we know of no case where it has been clearly demonstrated that tannin level is the governing factor leading to unpalatability. The purpose of this article is to present some conceptual and empirical approaches to critically testing the causative nature of the relationship between plant properties and palatability to herbivores.

Following the observations of Bryant and Kuropat (1980) that highly resinous plants and plant parts are generally associated with unpalatability to boreal forest vertebrate herbivores, we are studying the role of secondary plant metabolites in diet selection by the snowshoe hare (Lepus americanus). While this study of snowshoe hare/woody plant interaction is important in its own right because of the impact of browsing by hares on boreal ecosystems (Cook and Robeson 1945; Bryant and Chapin, in press), we take this opportunity to present a more general discussion of phytochemical mediation of diet selection by a generalist herbivore.

In this context we will address two questions: How can the contention that phytochemicals play a role in diet selection by an herbivore be empirically substantiated? If diet selection is--at least in part--determined by phytochemicals, what can be said about the structure/activity relationships of phytochemicals?

Before exploring these questions, several points about unpalatable plants must be clarified. There must be some underlying reason for unpalatability (such as low nutrient status, undigestibility, toxicity, or simply bad taste). There must be some plant attribute that allows detection or recognition by an herbivore (such as morphology, color, taste, smell). Furthermore, these two attributes may or may not have their basis in a single plant property or substance (see for example Camazine 1985). These ideas are not new (Eisner and Grant 1981), but they are often forgotten.

The snowshoe hare is an excellent test animal for investigation of plant/vertebrate herbivore interactions. Hares are relatively abundant in the boreal forest; they can have a significant impact on their environment; and they show dramatic dietary preferences, both among plant species and among plant parts. Furthermore they can, with a bit of care, be maintained in captivity.

THE ROLE OF SECONDARY PLANT METABOLITES IN DIET SELECTION BY A VERTEBRATE HERBIVORE

Initially our work focused on developing empirical methods for investigating the hypothesis that secondary plant metabolites play a role in diet selection by the snowshoe hare. Palatability has been observed to be inversely proportional to resin (ether-extractables) content (Bryant 1981). Based on Bryant's observations that snowshoe hares generally avoid resinous plants (Bryant and Kuropat 1980) and that application of ether extracts of some boreal plants to either preferred

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browse or commercial food reduced their palatabilities (Bryant 1981), we chose to test this hypothesis utilizing Betula species. This genus includes species and growth stages that run the gamut from highly palatable to unpalatable.

It has been known for some time that hares find internodes of mature Alaska paper birch (Betula papyrifera var. neoalaskana) (Viereck and Little 1972) highly palatable, but that they reject juvenile internodes (Klein 1977) as well as buds and catkins of both growth stages (Bryant and Kuropat 1980). We were able to demonstrate very quickly that juvenile internodes of paper birch contained substantial quantities of a single substance that was essentially absent in mature internodes. Subsequent work revealed this substance to be a triterpene, papyriferic acid (Reichardt 1981), and that its addition to food offered to our colony of snowshoe hares reduced the food's palatability (Reichardt and others 1984).

Once we had identified a single substance that deterred hare feeding, our next step was to quantify levels of papyriferic acid in plant parts and correlate these levels both with palatability and deterrent potency. In a study designed to minimize the genetic variations between plants, we determined the levels of papyriferic acid in ramets of five highly palatable mature paper birch trees and in their respective unpalatable juvenile adventitious shoots. We found that papyriferic acid represented an astounding 11 percent of the dry weight of juvenile birch but less than 0.5 percent of the dry weight of genetically identical adults (Reichardt and others 1984). Palatability of paper birch to the snowshoe hare is directly related to levels of this single substance. We have come to accept this type of result--documentation of a deterrent substance and verification of its abundance in unpalatable plant material at active concentrations--as the minimum criteria needed to substantiate the claim of chemically mediated deterrence.

We have, however, carried out other types of experiments that provide alternative evidence that this substance deters hare feeding. In a study designed to probe the ecological effects of plant carbon/ nutrient balance (Bryant and others 1983a), we carried out a series of fertilization and shading experiments with a plot of sapling paper birches. Fertilization and shading allowed us to manipulate plant growth rate, and we found that both plant palatability and papyriferic acid levels were altered (fig. 1). The reasons behind these changes are beyond the scope of this paper (see Bryant and others, this proceedings), except to note that in the altered plants palatability consistently related to papyriferic acid levels in the expected manner while it did not consistently correlate with nutrient levels (such as nitrogen).

Another insight into a similar system was unexpectedly obtained in a 1984 field trip to the Kevo and Pakatti Gardens in northern Finland.

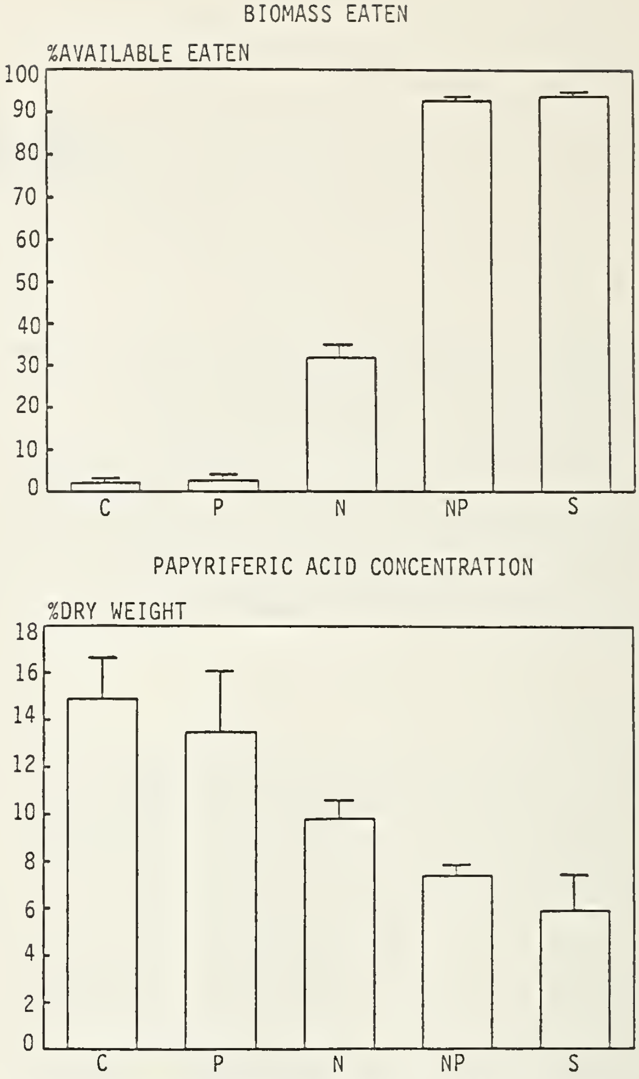


Figure 1.--Relationship between levels of papyriferic acid in B. papyrifera var. neoalaskana and palatability to snowshoe hares. Plant treatments are: control (C), nitrogen-fertilized (N), phosphorus-fertilized (P), nitrogen and phosphorus-fertilized (NP), and shaded (S). Standard errors are shown.

During the winter of 1982-83, mountain hares (Lepus timidus) broached the fences surrounding plots of birches maintained by Dr. Matti Sulkinoja of the University of Turku. Among the birches in these plots were B. pendula (a resinous, unpalatable birch), B. pubescens (a nonresinous, palatable birch), and some highly palatable hybrids of the two. Analyses of these plants (table 1) showed that browsing by mountain hares was inversely related to levels of papyriferic acid. However, more interesting is the apparent loss of chemical defense in the hybrid. Perhaps this signifies that birch's chemical defense against herbivores is a recessive trait held in a plant population only by browsing pressures.

All of these experiments dealt with the signaling aspect of plant palatability. We have not dealt with the other aspect of plant palatability--

underlying reasons--but we have initiated collaborative efforts with others who are beginning to investigate this aspect. Risenhoover and others (1985) demonstrated the ability of papyriferic acid to inhibit cellulose digestion in their in vitro assay with elk rumen fluid. Although these experiments may not be relevent to the hare studies, they do represent an empirical approach to investigations of the role that secondary plant metabolites can play in actually determining the food value of plants.

Table 1.--Relationships between level of papyriferic acid and palatability for three birch genotypes

Genotype	Papyriferic Acid (dry weight basis)	Plants Browsed in Kevo Garden	Plants Browsed in Pakatti Garden
	Percent	Percent	Percent
Betula pubsecens	<0.06	10	8
Betula pendula	.8	2	2
Betula pubsecens x *pendula*	<.04	30	50

MOLECULAR SPECIFICITY AND PALATABILITY

The literature of chemical ecology is full of reports of chemically mediated plant/herbivore interactions, but many of them focus on correlations of levels of certain classes of partially characterized substances (such as phenols, tannins, monoterpenes, alkaloids) with feeding behavior. Although there are good reasons to suspect that these classes of substances may have negative effects on plant palatability, the signals and underlying reasons for unpalatability must reside in discrete molecular interactions (Arnold and Hill 1972).

While the studies described in the previous section demonstrate empirical methods capable of documenting the roles secondary metabolites can play in plant palatability and suggest that these compounds can affect the food value of plants, they deal with a single substance and thus do not allow evaluation of the specificity of the relationship between structure and biological activity. Probing this question requires determining the palatabilities of a variety of phytochemicals present in browse or the palatabilities of structural analogues of nonpalatable substances. Our efforts have, to this point, concentrated on the first approach, although we have done a bit of work with analogues. Using the snowshoe hare as an herbivore, we have tested the effects of a variety of metabolites from Alaskan paper birch, American green alder (*Alnus crispa*), and balsam poplar (*Populus balsamifera*) on palatability.

Even at this early stage of our investigations it is clear that a wide variety of structural types have negative effects on plant palatability to hares. The structures of several such phytochemicals are given in figure 2. In addition to papyriferic acid, we have found palatability-reducing phenols (pinosylvin), monoterpenes (cineol), sesquiterpenes (bisabolol), and one metabolite (6-hydroxycyclohexenone) that does not neatly fit into any of the standard biogenetic classifications. Thus we believe that the signaling aspect of plant chemical defense against the snowshoe hare relies on specific receptor-substrate interactions (Chapman and Blaney 1979) and not on physiochemical properties associated with general structural type.

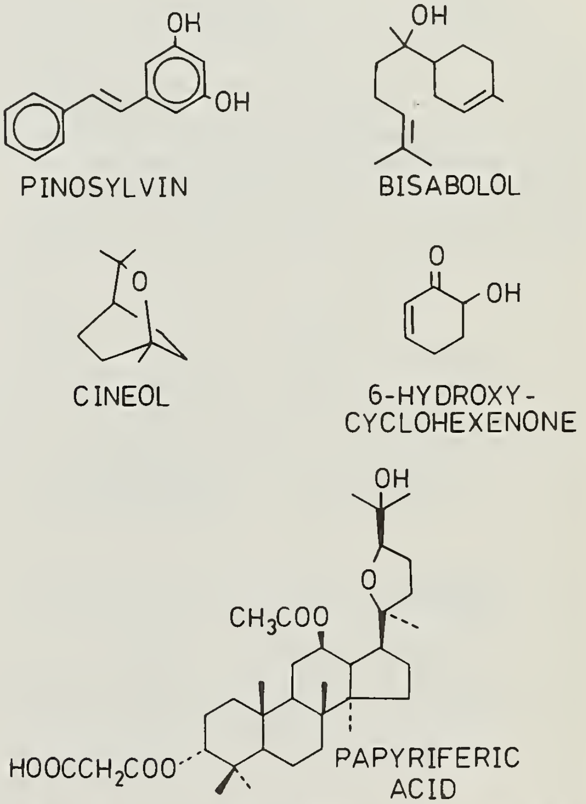


Figure 2.--Structures of several phytochemicals that deter feeding by snowshoe hares.

This idea is further substantiated by our discovery that no class of secondary plant metabolites contains uniformly active substances. Monoterpenes with widely varying potencies have been encountered (fig. 3), although we have yet to find a highly active monoterpene hydrocarbon. We have tested plant-derived phenols that vary in activity from highly deterrent to nearly benign (fig. 4), and we have preliminary evidence to indicate that the prototype--phenol itself--may even have attractive properties. In some cases, slight structural modifications have little effect on deterrent potency while in others large differences are seen (fig. 5). In general one is left with the impression that the deterrent properties of a given substance are dependent on its detailed structure.

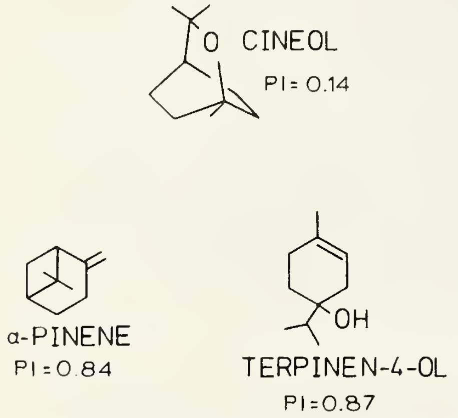


Figure 3.--Monoterpenes from P. balsamifera and their effects on feeding by snowshoe hares in bioassay experiments. Deterrent effects are given by preference index (PI) = percent treatment eaten ÷ percent control eaten for compounds applied to food at 1.0 percent (dry weight basis).

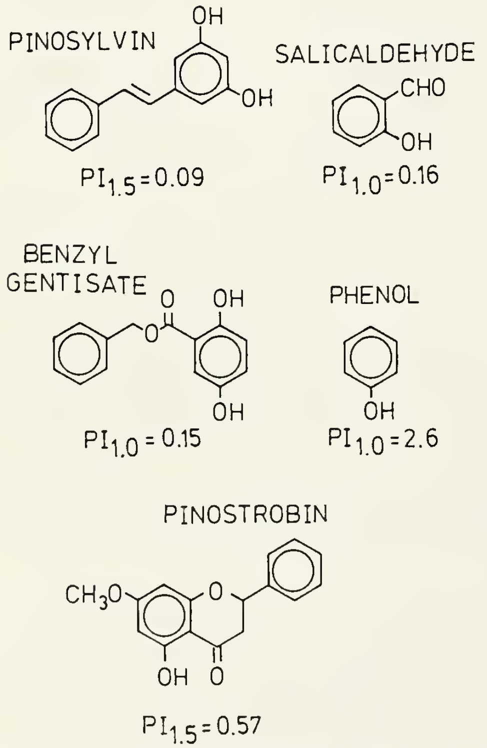
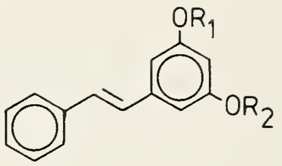


Figure 4.--Effects of selected phenols on feeding by snowshoe hares in bioassay experiments. Deterrent effects for samples applied to food at indicated percentages (dry weight basis) are given by preference index (PI) = percent treatment eaten ÷ percent control eaten.



R_1	R_2	PI
H	H	0.09
H	CH_3	0.12
CH_3	CH_3	0.63

Figure 5.--Relationship between structure of stilbene derivatives and effect on snowshoe hare feeding in bioassay experiments. Deterrent effects are given by preference index (PI) = percent treatment eaten ÷ percent control eaten for compounds applied to food at 1.5 percent (dry weight basis).

Another interesting aspect of this specificity concerns the breadth of biological activity associated with a compound found to have activity in a single bioassay. In general it appears that a substance biologically active in one system (hare deterrence for example) has a broad spectrum of activity. Table 2 gives partial listings of biological properties ascribed in the literature to two compounds that we have found to function as deterrents to hare feeding. However, it is difficult to make strong arguments from data of this type because the reported biological activities of molecules are, in part, a function of how intensively they have been investigated.

Table 2.--Reported properties of two phytochemical defensive substances

Substance	Property	Reference
Pinosylvin methyl ether	feeding deterrent to hares	Bryant and others 1983b
	toxicity to mice	Frykholm 1945
	fungicidal	Lyr 1962
	bacteriocidal	Frykholm 1945
	insecticidal	Wolcott 1972
Bisabolol	feeding deterrent to mice	Henttonen and others in prep
	bacteriocidal	Dull and others 1956-57
	fungicidal	Szalonkai and others 1976
	insecticidal	Bar-Zeev 1980
	antiinflamatory agent	Jakovlev and others 1979
	toxicity to mammals	Habersang and others 1979
	ulcer inhibitor	Szelenyi and others 1979

Some of the compounds mentioned here have, to our knowledge, only been studied in our laboratory; our knowledge of them is limited due to experimental neglect. On the other hand bisabolol has been extensively investigated because of its occurrence in camomile, a plant used for medicinal purposes since antiquity. Nevertheless, it appears that nature's defense of plants relies on highly specialized molecules that are rather versatile in their roles as defensive agents.

CONCLUSIONS

Two hypotheses emerge from our studies at this point, and they both suggest productive lines for future experimentation.

Hypothesis 1: Nature operates on a molecular basis, and the ability of any phytochemical to serve as a defensive signaling substance requires only that the herbivore have a proper receptor.

Hypothesis 2: Molecular diversity is part of the chemical defense strategy of the plant kingdom against generalist herbivores, a situation suggesting toxin-based defenses.

Testing of hypothesis 1 requires more extensive investigation of structure/activity relationships of potential signaling substances utilizing both phytochemicals and synthetic analogues. A second, more exciting, area is that of signal/ receptor interactions. Tests of hypothesis 2 must rely on extensions of in vitro studies like that of Risenhoover and others (1985) that can probe the differences between toxicity and digestion-inhibition. Although experimentally fraught with difficulty, such studies are crucial to our understanding of interactions between plants and generalist herbivores.

ACKNOWLEDGMENT

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CLASSIFYING AFRICAN SAVANNA TREES AND SHRUBS IN TERMS OF THEIR PALATABILITY FOR BROWSING UNGULATES

Norman Owen-Smith and Susan M. Cooper

ABSTRACT: We studied food selection by hand-reared kudus, impalas, and domestic goats in savanna vegetation in South Africa. Woody plant species were assigned to four palatability classes: (1) palatable deciduous species favored throughout the year while in leaf; (2) relatively palatable evergreen species favored during the dry season; (3) unpalatable evergreen species, eaten only toward the end of the dry season; (4) unpalatable deciduous species, favored only when in new leaf if at all. Thorns or spines modified the acceptability of class 1 species. The primary factor discriminating palatable from unpalatable species was the condensed tannin content; crude protein levels were of secondary importance. Other nutrients, total polyphenols, fiber, alkaloids, cyanogenic compounds, and ether-soluble resins had little influence on acceptability.

INTRODUCTION

Some 65 percent of the African continent supports savanna vegetation, characterized by an association of trees or shrubs with a grass layer sufficiently well developed to sustain frequent fires. Rainfall is strongly seasonal, with a more or less regular alternation between wet and dry seasons. Two basic forms of savanna have been distinguished: arid/eutrophic savanna, typified by Acacia and other genera of the Mimosoideae; and mesic/dystrophic savanna, typified by genera such as Brachystegia and Burkea of the legume subfamily Caesalpinioideae (Huntley 1982). Acacia-dominated savanna is associated not only with low precipitation, but also with areas of 600-850 mm annual rainfall having clayey soils derived from volcanic or fine-grained sedimentary deposits. Brachystegia-dominated savanna (also referred to as miombo woodland) is typically associated with sandy leached soils of the central African plateau, underlaid by basement igneous rocks. Somewhat intermediate in their characteristics are combretaceous savannas, dominated by the genera Combretum and Terminalia, occurring on sandy soils under moderate rainfall with less leaching.

Bell (1982) pointed out that regions with soils derived from basement igneous rocks carry a lower biomass of large herbivores for the same rainfall than regions underlaid by volcanic deposits or fine-grained sedimentary rocks. He suggested that low soil nutrient status promotes a high ratio of structural carbohydrates to metabolic constituents in grasses, and that woody plants in such areas are likely to contain high levels of secondary chemicals deterring herbivory.

Our observations were carried out at the study site of the South African Savanna Ecosystem Project (SASEP), located in the Nylsvley Nature Reserve in northern Transvaal. Prevailing soils are derived from Waterberg sandstone. Soils are sandy and low in available phosphorus (2 to 3 p/m) and cations, though not in nitrogen. Rainfall is moderate, averaging 630 mm annually, with some 85 percent falling during the summer months of October-March. The predominant vegetation is a savanna dominated by the tree species Burkea africana, with the multistemmed shrubs Ochna pulchra and Grewia flavescens dominating the understory. Also present are small 1 to 4 ha patches of Acacia-dominated vegetation, located on the sites of former human settlements. Here soils are locally enriched in phosphorus (10 to 30 p/m) and cations. Beyond the limits of the SASEP study area are more extensive areas of Acacia savanna on clayey soils along the flood plain margin of the Nyl River.

Our study was aimed at explaining the factors controlling the utilization of woody plant and forb species by browsing ungulates. Our specific objectives were to answer these questions:

1. What are the plant factors underlying variations in the utilization of different plant species?
2. How do different species of ungulate vary in their responses to these factors?
3. How do ungulates control their dietary intake from different vegetation components through the seasonal cycle?

A first step was to classify plant species in terms of the relative palatability of their foliage to browsing ungulates. Relationships between palatability and various chemical and physical factors could then be analyzed. In this report we summarize our findings on these

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questions; full details of results are published elsewhere (Owen-Smith and Cooper 1985, in press; Cooper and Owen-Smith 1985, 1986, University of the Witwatersrand in preparation).

METHODS

The animal species investigated included (a) greater kudu (*Tragelaphus strepsiceros*), a large, primarily browsing antelope; (b) impala (*Aepyceros melampus*), a medium-sized antelope known to be a mixed grazer-browser; (c) domestic "Boer" goats, also known for their mixed feeding habits. Wild populations of both kudu and impala occurred in the Nylsvley Nature Reserve and adjoining cattle ranches.

To enable close-range observations, young impalas and kudus were captured and bottle-reared. While in the rearing pen these animals were provided with cut branches from various woody species. They were also allowed into an adjoining 2-ha enclosure containing natural vegetation. Goats aged about 6 months were acquired from a nearby farm.

When aged 6 months the young impalas and kudus were released into a 213-ha enclosure in the study area, where they were allowed to range freely. The goats were observed in the same enclosure, but had to be locked overnight in a shed because of the presence of predators in the area.

Individuals of the three animal species were watched feeding at close range (1 to 5 m). To assess the relative acceptability of different plant species, we devised two measures for different observation conditions. During 1-hour observation sessions, the "Plant-based Acceptance" (PA) was defined as the proportion of available plants encountered during a foraging spell that the animal fed on. A plant was regarded as available if it was within neck reach of the animal's path of movement. The foraging pathway was marked with string and checked subsequently. For all-day observation sessions, the "Site-based Acceptance" (SA) was defined as the proportion of sites where a species was eaten in relation to the proportion of sites where that species was available. A woody species was regarded as available at a site if it was within readily visible range of the animal (within a radius of about 10 m of the foraging pathway). For practical convenience, each 30-minute foraging period was regarded as representing a separate site.

Supporting measurements of biting rates and bite sizes were made for particular plant species. Bite sizes were recorded by noting the number of leaves and length of stem ingested by the animal with each bite; samples of leaves of similar size were subsequently collected, dried, and weighed. Eating rates were calculated as the product of bite size and biting rate. Feeding times during daylight hours were determined from all-day observations.

Table 1.-- Plant species analyzed

Species and abbreviation	Family or subfamily	Growth form
Acacia nilotica (Acni)	Mimosoideae	tree
Acacia tortilis (Acto)	Mimosoideae	tree
Burkea africana (Buaf)	Caesalpinioideae	tree
Combretum molle (Como)	Combretaceae	tree
Dichrostachys cinerea (Dici)	Mimosoideae	shrub
Dombeya rotundifolia (Doro)	Sterculiaceae	tree
Euclea natalensis (Euna)	Ebeneaceae	shrub
Grewia flavescens (Grfl)	Tiliaceae	shrub
Ochna pulchra (Ocpu)	Ochnaceae	shrub
Peltophorum africanum (Peaf)	Caesalpinioideae	tree
Rhus leptodictya (Rhle)	Anacardiaceae	shrub
Strychnos pungens (Stpu)	Logoniaceae	tree
Terminalia sericea (Tese)	Combretaceae	tree
Vitex rehmannii (Vire)	Verbenaceae	tree

Fourteen common woody species, including both well-utilized and little-utilized plants, were chosen for chemical analysis (table 1). Composite samples of leaves were collected from 5 to 10 plants of each species in an adjacent unbrowsed enclosure. Samples were ovendried at 60°C, and stored for subsequent analysis. The following quantitative chemical analyses were carried out: (1) crude protein, multiplying Kjeldahl nitrogen content by a factor of 6.25; (2) phosphorus, by reduction of phospho-molybdates to give a blue color; (3) potassium, calcium, magnesium, and sodium, by atomic-absorption spectroscopy; (4) fiber components, by the detergent method of Van Soest and Wine (1967); (5) total polyphenols, by the ferric ammonium citrate method (Jerumanis 1972; Daiber 1975); (6) condensed tannins, by the butanol-HCl method (Bate-Smith 1977; Swain 1979), using sorghum tannin as a standard; (7) ether-extract. Qualitative tests were carried out for alkaloids, cyanogenic glycosides, saponins, and terpenoids.

RESULTS

Palatability Classes

The woody species in the study area could be grouped into four fairly discrete palatability classes, considering seasonal variations in acceptability (fig. 1): (1) *Grewia flavescens*, *Vitex rehmannii*, *Combretum molle*, *Dichrostachys cinerea*, and *Acacia nilotica* were highly acceptable to the animals year-round, as long as they retained leaves; (2) *Acacia tortilis*, *Rhus leptodictya*, *Strychnos pungens*, and *Dombeya rotundifolia* became highly acceptable during the dry season, after class 1 species had started to shed their leaves; (3) *Euclea natalensis* was of low acceptability, except toward the end of the dry season when green foliage was generally in short supply; (4) *Burkea africana*, *Ochna pulchra*, *Terminalia sericea* and *Peltophorum africanum* were of low acceptability, except in the case of the first two species during the new leaf flush period.

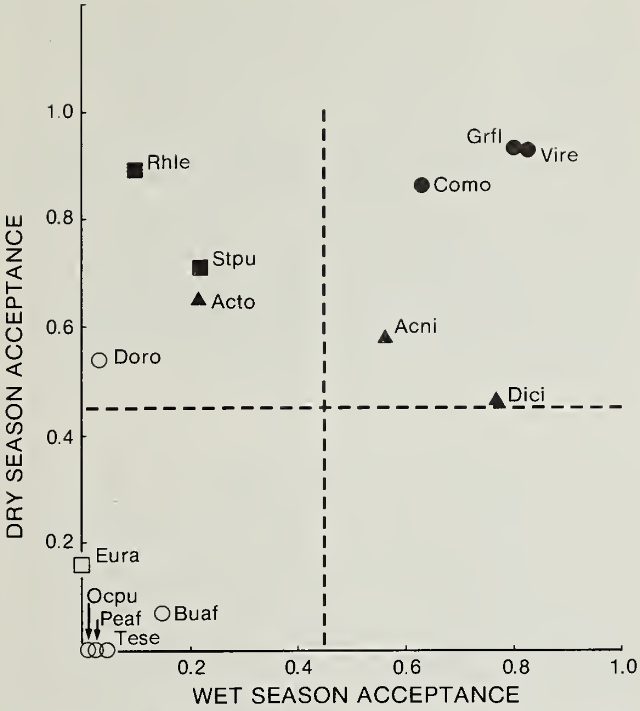

Figure 1.--Woody plant species ordinated in terms of their acceptabilities to kudus over the late wet season (December-April) and dry season (June-September) periods. For key to species abbreviations, see table 1.

For kudus category 1 included only deciduous species, including all except Acacia tortilis among spinescent species. Evergreen species were subdivided between categories 2 and 3. Category 4 species were all deciduous. The impalas differed by favoring both A. tortilis and T. sericea year-round. However, since the major portion of impala diet consisted of grass, T. sericea made up less than 1 percent of the food intake of the impalas. The goats showed a higher acceptance of E. natalensis and other evergreen species than did the two wild ungulate species, eating these species even during the wet season. This pattern was probably due largely to the fact that the goats foraged over a very limited area covering only about 10 ha around the shed where they were housed overnight. In consequence the foliage of more palatable species became depleted.

The impalas showed a relatively higher acceptance of spinescent species than did either the kudus or the goats. With their small mouths, impalas were adept at nibbling leaves from between thorns. The kudus at times ate shoot ends despite their thorns. The goats suffered a disadvantage from their floppy ears, which tended to become hooked on thorns. The reduced acceptability of certain spinescent species can be related to the restricting effects of thorns or spines, when coupled with small leaf size, on bite sizes. The effects of this restriction on eating rates were relatively greater for the larger kudus than for the smaller impalas and goats. Notably Acacia tortilis had the smallest leaves of any of the plants in the sample.

The impalas and goats included a considerable amount of leaf litter from deciduous species in their diets during the dry season. The kudus ate less leaf litter than the impalas and goats, due to the restricted eating rates obtained from the scattered leaves. Species with unpalatable foliage when intact were also rejected as leaf litter.

Nutrient Contents

There was no clear distinction between palatable and unpalatable species in terms of nutrient levels in leaves. However, all palatable species exhibited crude protein concentrations above 10 percent even in mature foliage. Some of the unpalatable species showed protein levels below this threshold. Correlations between acceptance and crude protein concentrations in leaves achieved statistical significance for kudus during the early growing season period, but not at other times of the year.

There was no distinction between phosphorus concentrations in the mature leaves of palatable and unpalatable species. However, certain of the unpalatable deciduous species showed markedly reduced phosphorus concentrations in their leaves ($<$ 0.5 mg/g dry mass) shortly before leaf abscission.

Fiber Components

There were no clear distinctions between palatable and unpalatable species in terms of fiber components. Nevertheless, the most fibrous species (ADF$>$ 40 percent, ADL$>$ 25 percent) was Ochna pulchra, one of the least unpalatable deciduous species. However, condensed tannins may be incorporated in the fiber fractions determined by detergent methods (Mould and Robbins 1981).

Polyphenols

There was no relation between total polyphenol contents and palatability. Acacia nilotica, which yielded polyphenol concentrations exceeding 25 percent (relative to a tannic acid standard) was a favored species. However, all five species showing condensed tannin (proanthocyanidin) contents exceeding 5 percent in mature leaves (relative to our sorghum tannin standard) fell into the unpalatable category. These included Burkea africana, Dombeya rotundifolia, Ochna pulchra, Euclea natalensis, and Terminalia sericea; but new leaves of the first three of these species were eaten despite their high condensed tannin levels.

Other Secondary Compounds

Alcoholic extracts of the leaves of Burkea africana, Peltophorum africanum, and Terminalia sericea foamed vigorously when shaken with water, suggesting the presence of saponins. Only Strychnos pungens and Vitex rehmannii gave a consistent reaction with Mayer's reagent, indicating the presence of alkaloids. Certain highly favored forbs gave even stronger reactions to tests for alkaloids.

Leaves of *Vitex rehmannii* had a strong odor suggesting a high content of monoterpenes, but this species was highly favored. None of the species in the sample responded positively to tests for cyanogenesis, and none had high contents of ether-soluble resins.

DISCUSSION AND CONCLUSIONS

Our findings suggest that unpalatability is associated mainly with high contents of condensed tannins. However, *Peltophorum africanum* was rejected by the animals despite a low condensed tannin content, indicating that other factors may be involved. Furthermore, new leaves of certain species were favored despite high condensed tannin concentrations. Notably, protein contents were also high in these young leaves. Discriminant function analysis separated palatable from unpalatable species on the basis of a canonical axis influenced positively by nitrogen and negatively by condensed tannin, with fiber having little further effect (fig. 2).

Zucker (1983) suggested that condensed tannins could benefit plants growing on nutrient-poor soils, by restricting rates of leaf decomposition and hence nutrient losses through leaching. In our study area those plant species prevalent on dystrophic soils all showed high leaf contents of condensed tannins. In contrast the species typical of the nutrient-enriched soils associated with former human dwelling sites were generally low in condensed tannins: although certain of these species showed high levels of total polyphenols (most notably *Acacia nilotica*).

Bryant and others (1983) suggested that deficiencies in soil nutrients promote the production of carbon-based secondary metabolites. Their hypothesis is that the carbohydrate excess is shunted into the shikimic acid pathway leading to polyphenol synthesis. In our sample of African savanna trees and shrubs, condensed tannin contents in leaves are in accordance with this hypothesis. However total polyphenols show a conflicting pattern, and furthermore seem unrelated to palatability, at least to large herbivores. Zucker (1983) suggested that hydrolyzable tannins may function mainly as deterrents against insect herbivores. We noted outbreaks of defoliating caterpillars on *Burkea africana* and *Ochna pulchra*, indicating that high condensed tannin levels are not effective in preventing heavy foliage losses to insects. Possibly condensed tannins function mainly to restrict leaf degradation by microbes and fungi, with secondary effects on mammalian herbivores dependent on microbial fermentation.

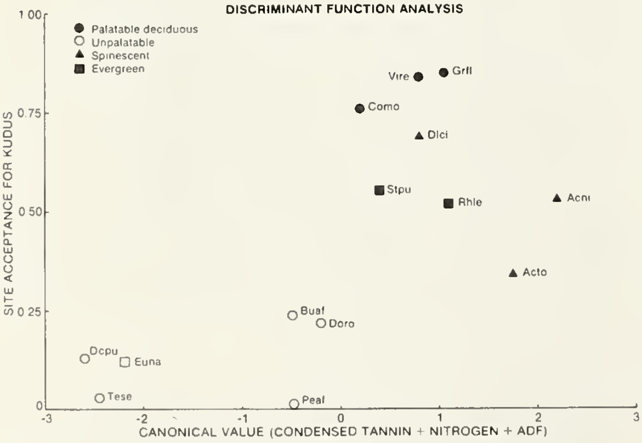

Figure 2.--Acceptance values of woody plant species for kudus, averaged over the complete year, plotted in relation to the first canonical axis discriminating the a priori classes of palatable and unpalatable species. For key to species abbreviations, see table 1.

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STUDIES ON INTERACTIONS BETWEEN MOOSE AND TWO SPECIES OF BIRCH IN SWEDEN

A REVIEW

Kjell Danell and Roger Bergström

ABSTRACT: Two treelike birch species (*Betula pendula* and *B. pubescens*) constitute an important winter food for moose (*Alces alces*) in Sweden. Reviewed are here recent studies on: (1) moose browsing on these two species, (2) moose browsing on individual birches, (3) responses of birches to moose browsing, and (4) responses of moose to birches browsed previously.

INTRODUCTION

In Sweden there are three species of birch: *Betula nana* L., *B. pendula* Roth (= *verrucosa* Ehrh.), and *B. pubescens* Ehrh. (including *tortuosa* Ledeb.). (For a discussion of hybridization between the birches, see Danell and Ericson 1986). The first-mentioned species is a low-growing shrub, while the other two can form large trees. The two species *B. pendula* and *B. pubescens* are similar-looking and widely distributed throughout Sweden, but *B. pendula* becomes sparser in the mountain range and in the northernmost inland region close to the mountains (Hultén 1971). *Betula pendula* also generally has a higher growth rate (Fries 1964; Raulo 1977) and occurs in somewhat drier habitats (Arnborg 1946).

The birches are of medium preference as winter browse for moose, but due to their wide distribution and abundance in many habitats they form an important component of the moose diet (see review by Bergström and Hjeljord, in press). During winter twigs are browsed, but leaves as well as young shoots are taken during summer.

High moose densities in Sweden in recent years (Cederlund and Markgren, in press) focused interest on the interactions between moose and their browse plants, especially during winter. Here we review Swedish studies, as well as present unpublished research, on: (1) moose browsing on the two birch species, (2) moose browsing on individual birches, (3) responses of birches to moose browsing, and (4) responses of moose to birches previously browsed:

MOOSE BROWSING ON THE TWO BIRCH SPECIES

Betula pendula and *B. pubescens*, closely related and similar in appearance, offer a good opportunity to study the underlying mechanisms governing food selection by moose.

Results of four browse surveys in central Sweden (59-62°N) show that the relative usage of *B. pendula* was 1.4-5.0 times higher than its relative availability (Danell and others 1985) (table 1). Higher usage of *B. pendula* than of *B. pubescens* was also found in another, but less quantitative, browse survey in central Sweden (59-60°N) by Stålfelt (1970).

Betula pendula and *B. pubescens* often grow in mixed stands, but the former is often more abundant in somewhat elevated and drier habitats. One possible explanation of the higher utilization of *B. pendula* is that moose for some reason, such as snow conditions, prefer these elevated habitats. To test whether the preference for *B. pendula* may be due to the habitat rather than to characteristics of the birch itself, we cut 2.5-3.0 m high birches of the two species in early winter and placed them side by side at test stations (Danell and others 1985). Fifty such stations were dispersed through a forest area of 140 km^2 in northern Sweden (64°N), where the two birch species were about equally abundant. After one winter's exposure, we estimated consumption of twigs from the test trees and found that 74-84 percent of the consumed twigs were from *B. pendula*

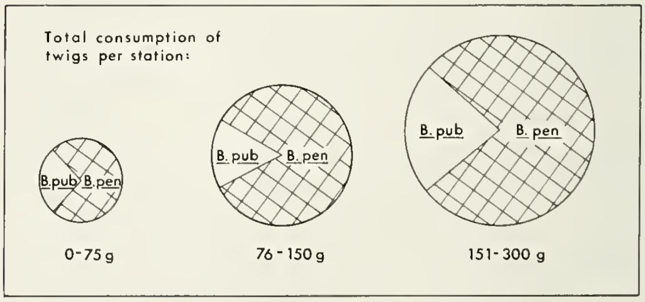

Figure 1.--Moose consumption of twig dry mass from *Betula pendula* (B. pen) and *B. pubescens* (B. pub) exposed at test stations within a 140-km^2 forest area in northern Sweden. Data from the 23 test stations visited by moose are divided into three groups according to the total consumption per station (after Danell and others 1985).

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Table 1.--Availability and usage of Betula pendula shoots by moose reported for four browse surveys in central Sweden. The availability of B. pendula is expressed as the production of B. pendula over the total production of B. pendula and B. pubescens; the usage of B. pendula is expressed as the consumption of B. pendula over the total consumption of B. pendula and B. pubescens (after Danell and others 1985)

Locality	Geographic position	Size of area	Availability of B. pendula	Usage of B. pendula
		Km^2	Percent	
Furudal	61-62°N; 14-15°E	1 350	2	10
Sunnäs	61°06'N; 17°05'E	6	66	94
Grimsö[1]	59-60°N;15-16'E	30	13	47
Brommö	58°50'N; 13°40'E	15	34	87

[1] Unpublished information by A. Nyström.

(fig. 1). Approximately the same proportion of B. pendula was taken whether browsing pressure was low or high.

It is likely that the relative abundance of a birch species affects usage by moose. If moose have an instinct to mix various browse species in their diet, the rarest species will always be overutilized. Betula pendula was the rarest one in three of the four browse surveys (table 1). Therefore, we investigated 21 mixed birch stands in northern Sweden (63-65°N), where B. pendula cover ranged from 2 to 97 percent (Danell and Ericson 1986). In stands of 60 percent or less B. pendula, there was a preference for this species with regard to 1.5 to 3.0-m high trees (fig. 2).

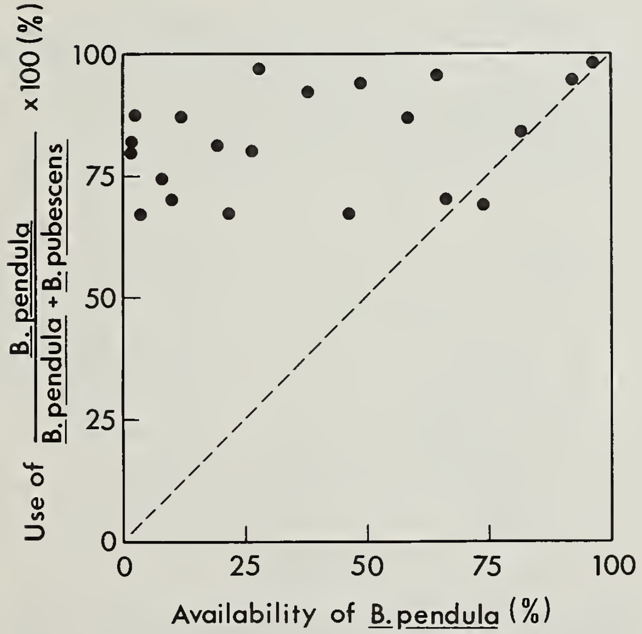

Figure 2.--Use (number of trees with more than 10 moose bites) by moose of Betula pendula in relation to the total use of B. pendula and B. pubescens in 21 mixed birch stands in northern Sweden with different availabilities (frequencies) of B. pendula (after Danell and Ericson 1986).

Birches of this height carry the largest amount of available browse for moose per tree. When comprising over 60 percent of a stand, B. pendula was still preferred but then its usage was close to availability. However, in all stands there were significantly more moose bites per tree on B. pendula than on B. pubescens. Thus, the preference for B. pendula seem to be more or less independent of its proportion in the stand.

The investigations reported here, which cover many localities in central and northern Sweden from around 59-65°N, indicate a common preference for B. pendula. From more northern areas the information is limited (table 2), but the same pattern prevails. Data from field surveys in southeastern Norway (59-61°N) also show that B. pendula is preferred to B. pubescens as a winter browse species (Rostad 1983).

However, some published data indicate differences in preference for B. pendula. Nyström (1980) found a reverse order of preference when studying selection and consumption of winter browse by four hand-reared moose calves that were introduced into a previously unbrowsed enclosure (5.42 ha) at Grimsö Research Station. On the other hand, unpublished data by A. Nyström from the forest area outside the fence show a preference for B. pendula (table 1). In inventories of moose damage in southern and central Sweden (56-60°N) (Westman 1958) and southern Finland (60-62°N) (Löyttyniemi and Piisilä 1983), no clear differences were found in damage to the two birches. The information reviewed here thus suggests that preference for B. pendula is strongest in northern Sweden and decreases with decreasing latitude. To test this hypothesis we analyzed data from a recent nationwide survey on damage in young forest stands (B.-Å. Näslund, unpublished observations). In the two birch height classes, 0 to 1.5 m and 1.6 to 3.0 m, there was a highly significant greater proportion of damaged B. pendula than of B. pubescens from the latitudes 64-67°N and 60-63°N (fig. 3). For 56-59°N there were only small differences in the frequency of damage. We do not yet know if this north-south pattern is consistent in critical field experiments.

Table 2.--Numbers of moose bites on 1.5- to 3.0-m high Betula pendula and B. pubescens at four locations in northern Sweden. The proportion of B. pendula in the birch stand (at least 700 birches determined to species) is given for each locality as well as the number of moose bites per tree on a random sample of 30 birch pairs (one specimen of each species; equal height; within <1.5 m from each other) (K. Danell, unpublished observations)

Locality	Geographic position	Proportion of B. pendula	Number of moose bites per tree		
			B. pendula	B. pubescens	Statistical test[1]
		Percent			
Kihlangi	67°41'N; 23°27'E	19	14.7±1.7	2.3±0.6	$P < 0.001$
Överkalix	66°14'N; 22°28'E	8	21.6±2.9	1.3±0.3	$P < 0.001$
Matojärvi	66°05'N; 23°44'E	57	48.3±3.3	5.9±1.0	$P < 0.001$
Gagsmark	65°07'N; 21°15'E	40	32.4±4.0	4.7±1.1	$P < 0.001$

[1] Wilcoxon matched-pairs signed ranks test.

Besides this geographical effect on the relative preference between the birches, there is also an effect of tree height/age. Browsing on 1.0- to 1.5-m as well as on 1.5- to 3.0-m high birches was studied at four localities in northern Sweden (Danell and Ericson 1986). For both height classes we found a preference for B. pendula, but the difference was less pronounced for the 1.0- to 1.5-m height class. When comparing smaller birches the preference order may be totally reversed, as indicated by data presented by Löyttyniemi and Rousi (1979) for a deciduous plantation in Finland. Further, we exposed 3-m high birches of the two species together with 3-m high tops of 6- to 9-m high trees to penned moose (Danell and others, in press). More twig biomass was taken from the tops of older trees (13 to 18 years) than from the younger (5 to 8 years) 3-m trees (fig. 4). There was a tendency for greater relative consumption of older B. pendula tops than younger trees.

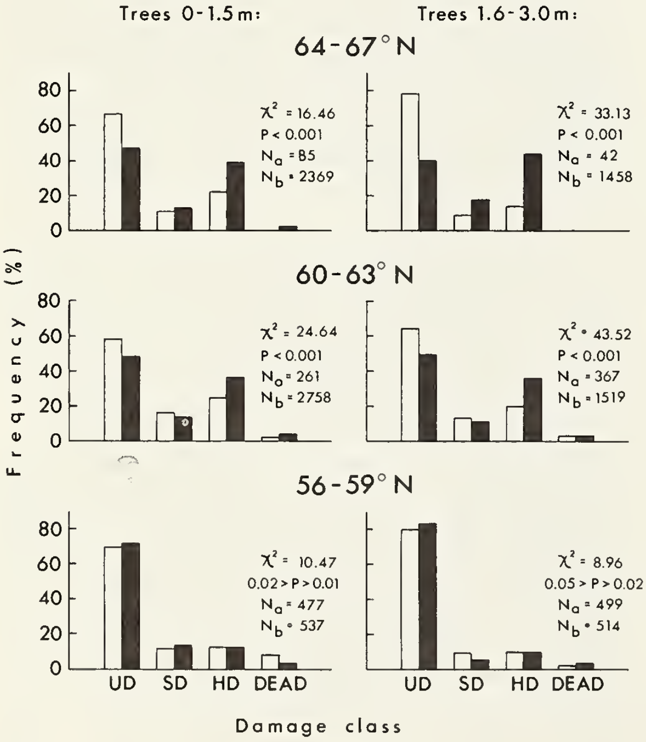

Figure 3.--Frequency distributions of Betula pendula (solid bars) and B. pubescens (open bars) stems classified according to the degree of moose damage during a survey of young forest stands in Sweden (B.-Å. Näslund, unpublished observations). UD = undamaged, SD = slightly damaged, and HD = heavily damaged. The sample size of B. pendula (N_a) and B. pubescens (N_b) is given for each case.

To summarize, based on existing knowledge we find that 1.5- to 3.0-m high B. pendula are preferred to B. pubescens in large areas of northern and central Sweden. With decreasing latitude as well as decreasing tree height the difference in preference decreases or may even disappear. The

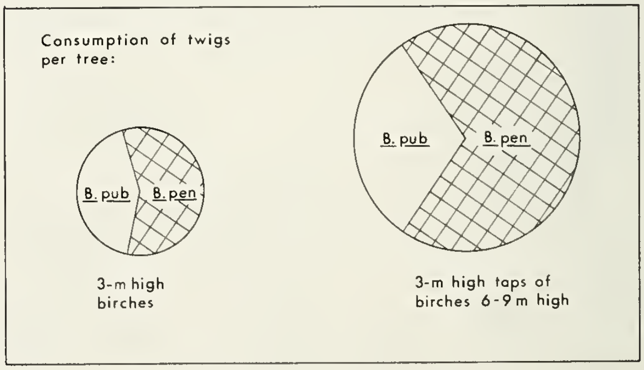

Figure 4.--Consumption of Betula pendula (B. pen) and B. pubescens (B. pub) by penned moose at Grimsö Research Station in Sweden. Cut 3-m high birches as well as 3-m high tops of birches 6 to 9 m high were "planted" in mixed stands inside the moose pen on February 10 1983 (after Danell and others, in press).

underlying mechanism that explains this food choice by moose is not yet known. For a discussion of inter- and intraspecific differences in morphology and chemistry of the two birch species refer to Danell and others (1985).

MOOSE BROWSING ON INDIVIDUAL BIRCHES

The spatial density of birches in a stand also affects moose browsing behavior. Vivås (in press) "planted" 2.5- to 3.5-m high B. pubescens at 10 different densities (0.04-0.4 birches per m^2) on a mountain flank in central Norway. At the lowest birch densities, the mean number of moose bites per birch and mean bite diameter were larger than at higher birch densities. Consequently, the consumption of twig mass per birch was highest at low birch densities. However, the food intake per square meter of plot increased almost linearly with increasing birch density.

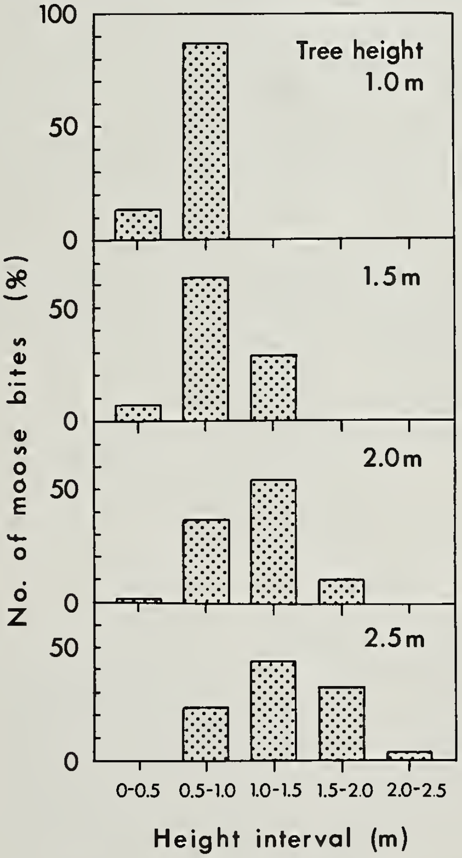

Figure 5.--The frequency distribution of moose bites at different height intervals of B. pendula (from 1.0 to 2.5 m high) exposed at 75 test stations inside the Sunnäs moose pen in central Sweden (R. Bergström, unpublished observations). The birches were available for moose from December 1, 1984, to January 25, 1985.

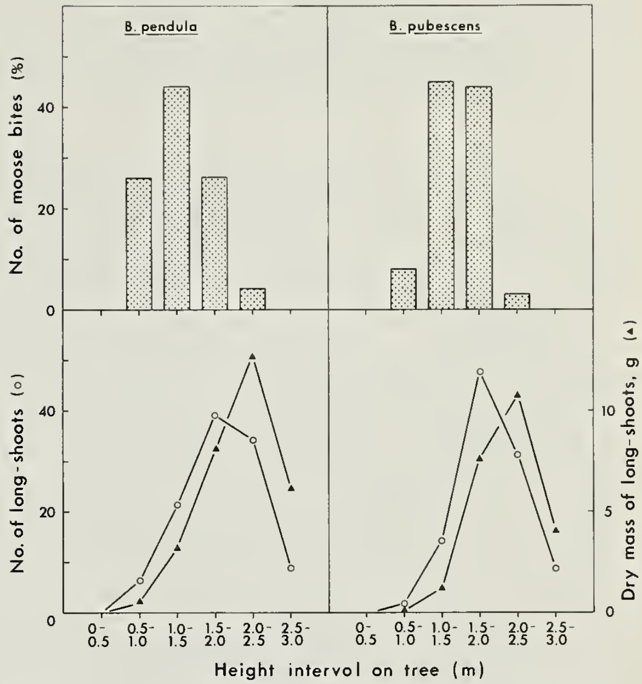

Figure 6.--The frequency distribution of moose bites on 2.5- to 3.0-m high birches as well as the distribution of long-shoots and their dry mass. The birches were exposed at test stations and visited by free-roaming moose in a forest area in northern Sweden from late October 1981 to late May 1982. For details see Danell and others 1985. (K. Danell, unpublished observations).

When moose browsed on 1.0 m high B. pendula during winter, 87 percent of the moose bites were taken at the height interval 0.5 to 1.0 m (fig. 5). With increased tree height (at least up to 2.5 m) a greater proportion of the bites were found in successively higher intervals. On 2.5-m birches, 72 percent of the bites were within the 1.0 to 2.0 m interval. Another field experiment with 2.5- to 3.0-m high B. pendula and B. pubescens showed that 70 and 89 percent of the moose bites, respectively, were taken from positions 1.0 to 2.0 m high on the birches (fig. 6). Distributions of moose bites on birches recorded during a field survey yielded a similar picture (Danell 1983). The frequency distributions of moose bites at various height levels are not directly related to the number or dry mass of long-shoots available at different height intervals (fig. 6). A more simple explanation is that browsing mainly at the 1.0- to 2.0-m level is the least energy-demanding behavior for moose. However, sometimes stems of birches are broken by the moose in order to reach twigs situated at higher positions. In the Sunnäs moose pen there was a general increase in the frequency of broken birch stems with increasing moose density (table 3). The preferred B. pendula generally had a higher frequency of stem breakage than B. pubescens. In small, individual birch stands it is, however, difficult to demonstrate that high browsing pressure always leads to a high frequency of stem breakage.

The mean diameter at the point of browsing on birches is commonly around 2 or 3 mm (Danell 1983; Rostad 1983; Vivås in press) (fig. 7). When the

Table 3.--Frequency of stembreakage by moose on *Betula pendula* and *B. pubescens* in the Sunnäs moose pen (6.2 km^2) during an increase in the moose population. The frequencies recorded for the winters 1979-80 to 1983-84 are from forest stands with a mean age around 10 or 25 years in 1979 (R. Bergström, unpublished observations)

Stand	Frequency of stem breakage during the winters				
	1979-80	1980-81	1981-82	1982-83	1983-84
	Percent				
10-year-old stands:					
B. pendula	0.7	2.0	7.1	11.0	13.1
B. pubescens	.0	.6	1.0	1.7	2.5
25-year-old stands:					
B. pendula	3.9	3.8	7.2	7.7	21.6
B. pubescens	.0	.0	.0	3.1	2.9
No. of moose per km^2	1.3	2.3	3.4	4.6	5.2

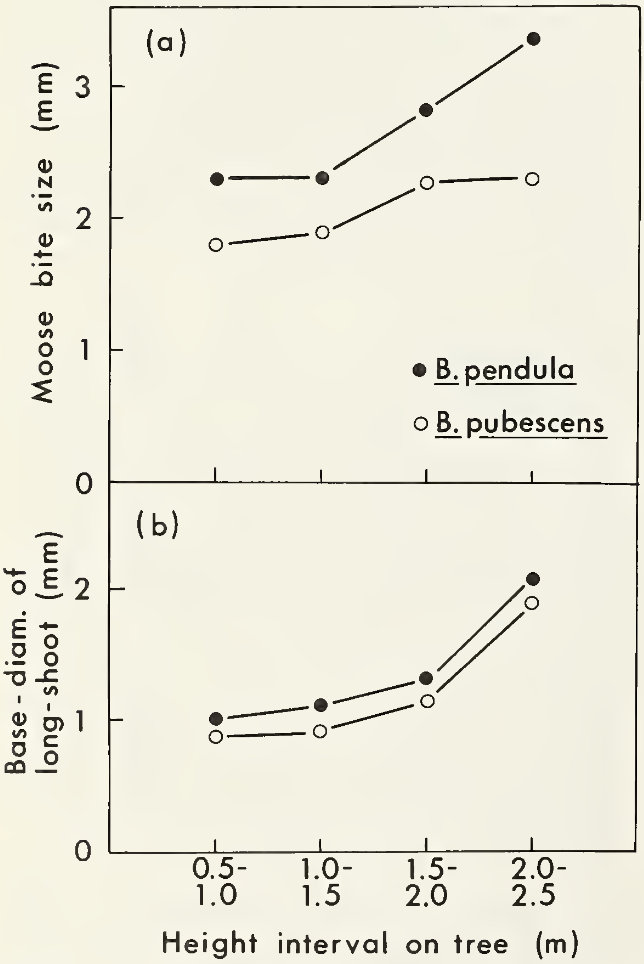

Figure 7.--Mean diameter of moose bites (a) and mean base diameter of long-shoots (b) on 2.5- to 3.0-m high birches exposed to moose browsing during one winter.

bite diameter increases more twig biomass is harvested, but at the same time the bite composition changes (Palo and others 1984). With increasing twig diameter the proportion of wood increases, while the proportion of buds decreases (fig. 8). However, the proportion of bark is more or less the same. Occurrence of phenols and other secondary metabolites in birch may deter the intake of fine twigs while fiber content may deter the intake of coarse twigs. Presumably, moose select food in a way that minimizes intake of harmful metabolites and fiber (Palo and others 1984). Phenols may constitute a major chemical defense against browsing vertebrates by reducing digestibility and increasing toxicity (Palo and others 1985). For a review of secondary metabolites in birch see Palo (1984).

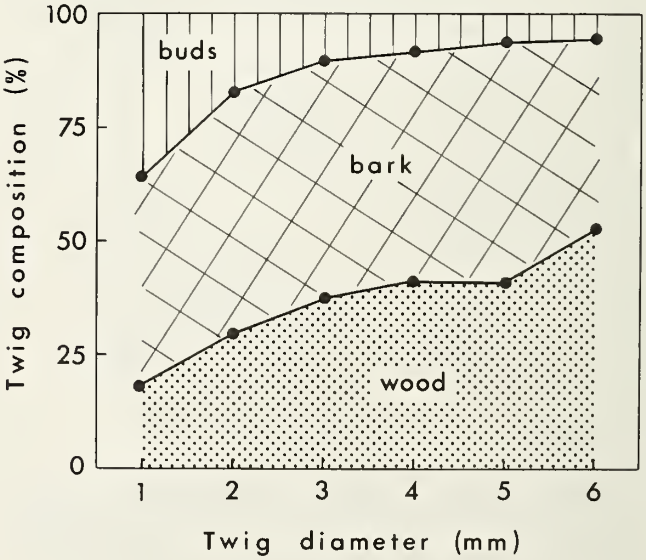

Figure 8.--The relative composition of 1- to 6-mm *Betula pendula* winter twigs (after Palo and others 1984).

Measurement of moose bite diameters revealed that larger bites were taken from higher levels on the tree than from lower levels (Danell 1983). When moose browsed B. pendula, the mean bite diameter was generally somewhat larger than on B. pubescens (Danell 1983; Rostad 1983). As the browsing itself can change shoot size, we conducted a field experiment in which unbrowsed birches, as similar as possible, of the two species were exposed to free-roaming moose at test stations during one winter (fig. 7). Here we again found that the bite diameter increased with increased height on the tree; there were also larger bite diameters on B. pendula. Interestingly, there is a close relation between these patterns and the mean shoot size (figs. 7a, b). It is not yet known whether this relation is due to chemical or mechanical properties.

RESPONSES OF BIRCHES TO MOOSE BROWSING

The vegetative and generative responses of birches to browsing have been studied on naturally browsed birches (Danell 1983; Danell and Huss-Danell 1985; Danell and others 1985). In more detailed studies of the responses due to winter browsing by moose, birches were clipped (Gröning 1980; Bergström and Danell 1985; Danell and Huss-Danell 1985; Danell and others 1985). The birch responses (tables 4 and 5) were, among other things, dependent on the intensity (proportion of biomass removed) and the frequency (number of winters browsed) of moose browsing. For simplicity, we here consider "moose browsing" as the removal of approximately 50 per cent of the long-shoots produced during the last summer.

Moose browsing leads to a prolonged growing season; bud abortion occurs later on trees affected by natural or simulated browsing. A somewhat higher mortality has been noted for terminal shoots on browsed birches than unbrowsed ones in northernmost Sweden after an extremely hard winter (K. Danell, unpublished observation). It is likely that these shoots on browsed birches were not fully prepared for the winter.

Height as well as stem diameter are negatively affected by moose browsing.

The number of long-shoots produced by a tree during the growing season following the winter when it was browsed was lower on browsed trees than on unbrowsed ones of the same age (fig. 9a). With increased browsing the proportion of branched long-shoots increased (fig. 9b). Short-shoots can be converted into long- shoots after browsing; this response was more frequent in open habitats than in shaded ones. However, this change in shoot type seldom compensates for high losses of long-shoots following moose browsing.

Shoot biomass will only occasionally be higher on birches affected by browsing than on unbrowsed ones (fig. 10). In most cases we measured either no change or decreased shoot production. Apart from the intensity and frequency of browsing, the production of long-shoots is also affected by competition from other birches. We found a negative correlation between the shoot biomass produced by B. pubescens after heavy simulated browsing during three winters and the number of stems in the neighborhood (stand density) (fig. 11).

Since browsing reduces height growth, the long-shoots on browsed birches will be produced at lower levels than on intact ones. On unbrowsed birches the shoots will grow farther out of reach for moose each year. For example, on a 4-m high birch the majority of the shoots within the 1- to 2-m height interval are small sized and unfavorable for moose browsing. So, even if browsing does not change the biomass of shoots produced per tree, more shoots can be available for moose on birches previously browsed (Danell 1983). The fewer but larger shoots available on such trees also make harvesting easier.

Table 4.--Vegetative and generative responses of birches following natural or simulated moose browsing during winter. Data on Betula pendula and B. pubescens from different studies are summarized (Gröning 1980; Danell 1983; Bergström and Danell 1985; Danell and Huss-Danell 1985; Danell and others 1985). Increases are marked with (+) and decreases with (-). No change is indicated by (=)

Vegetative responses

On the tree level:
- Length of growing season (+)
- Height and stem diameter growth (-)
- Number of long-shoots (-)
- Frequency of branched long-shoots (+)
- Conversion of short-shoots into long-shoots (+)
- Shoot biomass produced (+) (=) (-)[1]
- Shoot biomass available for moose (+)
- Total number of winter buds on long-shoots (-)

On the shoot level:
- Shoot size (+)
- Number of leaves (+)
- Number of winter buds (+)
- Shoot chemistry (See table 5)

On the leaf level:
- Leaf size (+)
- Green leaf color (+)
- Leaf chemistry: chlorophyll concentration (+)
  - nitrogen concentration (+)
  - carbon:nitrogen ratio (-)

Generative responses

Number of catkins per tree (-)
Individual seed weight (+)

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[1] The responses in shoot biomass produced are strongly dependent on browsing intensity and frequency as well as habitat conditions.

Table 5.--Changes in birch winter shoot quality as a response to natural or simulated moose browsing. Data from B. pendula and B. pubescens collected in different studies (Bergström and Danell 1985; Danell and Huss- Danell 1985; Danell and others 1985). Increases are marked with (+) and decreases with (-). No change is indicated by (=)

Item[1]	Natural browsing whole shoots		Simulated browsing whole shoots				Simulated browsing 2 mm shoots	
			B. pe		B. pu		B. pe	B. pu
	B. pe[2]	B. pu	I	III	I	III	III	III
Na		=	=	=	=	-	=	=
K		=	=	=	=	=	-	=
Ca		-	-	=	=	-	=	=
Mg		-	=	-	=	=	-	=
P		=	=	-	=	=	=	-
N	=	=	=	-	=	=	=	=
Crude fat	-	- =	-	=	-	-	=	=
Crude fiber			+	+	+	+	+	+
Phenols			=		=			
Water solubles			-		-			
Digestibility (IVOMD)			-	=	-	=	=	=

[1] All items are compared in terms of per cent of dry mass.

[2] B. pe = Betula pendula; B. pu = B. pubescens; shoots collected after 1 year (I) or 3 years (III) treatment.

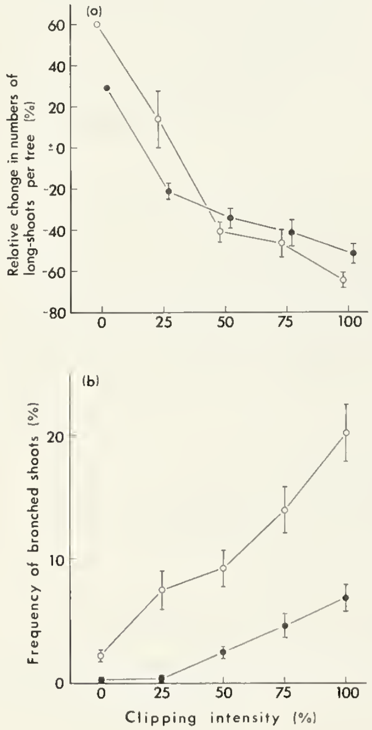

Figure 9.--Effects of different intensities of simulated browsing on the total number of current long-shoots per tree (a) and the frequency of branched long-shoots (b) on Betula pendula (●) and B. pubescens (o). The responses are from birches 1.6 and 2.6 m high, respectively, clipped during one winter only. Mean + S.E. given for N = 19-20. (The sampling procedure for estimation of control values (0) in figure 9a does not allow calculation of precision estimates.) For details see Bergström and Danell (1985).

With increasing browsing intensity during winter, the individual shoots produced the following summer increased in size (fig. 12). There were also more leaves per shoot and winter buds. Even if the number of buds per shoot increases as a response to browsing, it cannot compensate for the loss of buds through the decreased number of long-shoots at medium and high browsing intensities. At these browsing pressures the total reserve of buds on long-shoots is reduced from year to year.

The changes in shoot quality due to browsing are more complex. In addition to the effect of

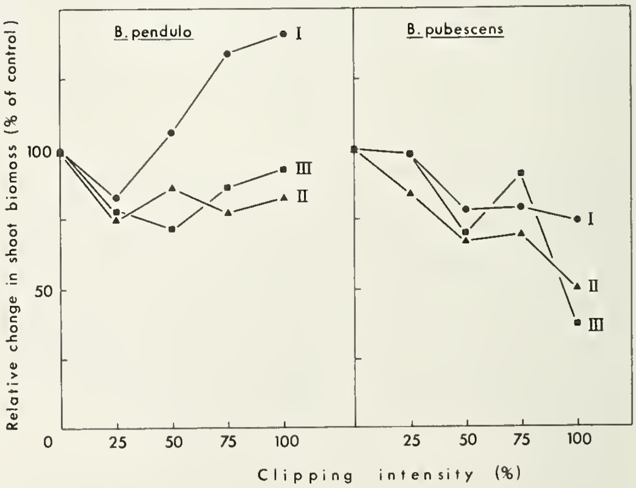

Figure 10.--Effects of different intensities of simulated browsing on the total dry mass of long-shoots produced per tree after treatments during one (I), two (II) and three (III) winters. For details see Bergström and Danell (1985).

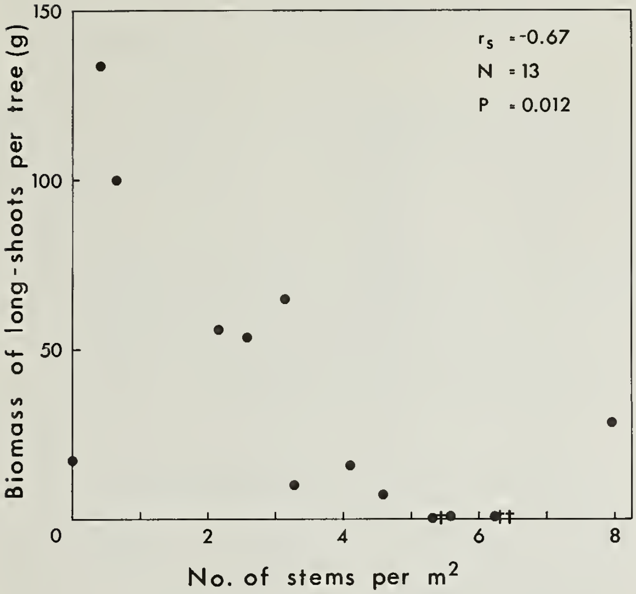

Figure 11.--Dry mass of long-shoots produced by Betula pubescens exposed to 100 per cent clipping (removal of all long-shoots produced during the previous summer) during three winters. The individual biomass for 13 birches still alive (●) is correlated with the number of other stems in the neighbourhood. When the three dead (+) individuals are included the corresponding statistics are r_s = -0.71, N = 16, P = 0.002. For details see Bergström and Danell (1985).

browsing intensity and frequency, shoots enlarge with increased browsing.

Therefore, discussion of quality changes must include whole shoots as well as fixed diameters (here we have chosen the 2-mm limit).

Data on whole shoots from birches affected by natural or simulated browsing (table 5) show decreased concentrations of Ca, Mg, crude fat, and water solubles in two or more of the samples or experiment groups. Likewise, increased fiber content and decreased digestibility occur. On the other hand, when we consider the 2-mm shoots, only Mg and the fiber content are similar to the whole shoot fraction. We therefore suggest that most of the changes found when we compare whole shoots from browsed and unbrowsed birches are due to the difference in shoot size between the groups. Data presented in figure 8 show an increase in the wood component and a decrease in the bud component when the shoot diameter increased from 1 to 4 mm.

Individual leaf area increased with increased browsing intensity and the leaves were greener. The leaves on previously browsed birches were richer in chlorophyll and nitrogen and had a lower C:N ratio than leaves from unbrowsed birches. Moderately browsed birches often carried a higher load of invertebrate herbivores (ants, psyllids, leaf-miners, and other leaf-eating insects) than intact birches. Leaves from such affected birches were more palatabile to a generalized herbivore (Arianta arbustorum (L.)) (K. Danell, unpublished observations).

With increased browsing intensity, the number of catkins per tree decreased but the individual seed weight increased in B. pubescens.

The responses of birches to moose browsing during winter are to a large extent growth responses (such as prolonged growing season and shoot enlargement). The pattern of responses indicates that the birches allocate more effort to growth than reproduction by reducing seed production. At the moment, it is difficult to argue that some of the responses are specific to moose browsing. What we have documented are most likely an array of general responses to mechanical damages of abiotic (such as stem breakage by snow) and biotic (such as herbivory) nature. Inter- and intraspecific competition are important features in many plant populations. Height growth is therefore extremely important for young trees; it helps to grow above the competitors and out of the reach of mammalian herbivores.

RESPONSES OF MOOSE TO BIRCHES PREVIOUSLY BROWSED

Studies of individually tagged B. pendula and B. pubescens demonstrated that browsed birches have a greater probability of being browsed the next winter than previously unbrowsed birches (Bergström 1983; Danell and others 1985). One possible explanation of this is that it reflects the availability of individual birches in the moose habitat. The browsed birches may be closer to pathways used by moose. We therefore set up a field experiment in northern Sweden (within a forest area of 140 km^2) where we placed cut 2.5- to 3.0-m high birches, unbrowsed or slightly browsed and moderately browsed, of the two species side by side (Danell and others 1985). Fifty stations were set up in late October and revised in late May the following year. At stations where the consumption of twig biomass from the trees had been low, about 80 and 90 percent of B. pendula and B. pubescens, respectively, were taken by moose from the birches earlier browsed. At stations with medium or high biomass removal, approximately equal amounts were taken from the unbrowsed/slightly browsed and moderately browsed birches.

The higher palatability to moose of previously browsed birches may be due to strong individual differences in palatability between birches. It is possible that moose select some birches and then browse on them for several winters irrespective of changes due to the browsing itself. Therefore we conducted another field experiment where we selected pairs of unbrowsed B. pubescens that were as similar as possible (Danell and others 1985). We randomly chose one individual in each pair and simulated moose winter browsing on this birch, while the other was left as a control. During the following summer the treated birches responded by producing larger shoots etc. After the next winter we compared utilization by moose of the two types of birches. There were a higher frequency of moose bites, a larger moose bite diameter, and

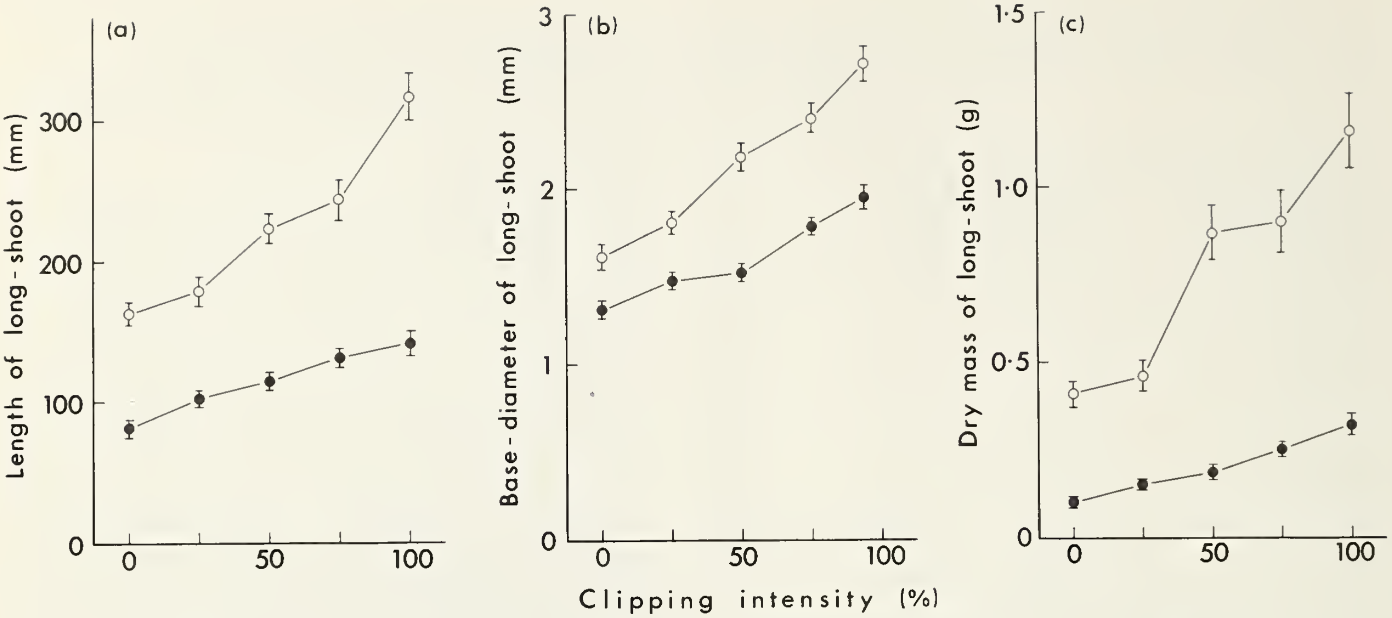

Figure 12.--Effects of different intensities of simulated browsing on the length (a), base diameter (b) and dry mass (c) of the individual current long shoots of Betula pendula (●) and B. pubescens (o). Mean ± S.E. given for N = 18-20. For details see legend to figure 9 and Bergström and Danell (1985).

about five times more twig biomass removed from the treated trees compared to the control trees.

CONCLUSIONS

For some reason, the birches previously browsed are more attractive to moose than unbrowsed ones. One explanation is that they are easier to harvest due to the relatively few but large shoots and their distribution. Other explanations are that shoots on trees responding to browsing are more palatable due to decreased concentrations of deterrent compounds, or due to increased concentrations of compounds acting as attractants. When moose browse on birches that have larger shoots, mean bite diameter generally increases and we can expect that the animals get less Ca, Mg, crude fat (resins), and water solubles, but more fiber per kilogram dry mass consumed (table 5). The overall effect on food quality is difficult to evaluate, but it is likely that digestibility decreases slightly. It is questionable if the advantage of affected birches being easier to harvest compensates for their decreased digestibility. On the other hand, if moose only slightly increase the bite diameter, the qualitative differences between browsing on previously browsed and unbrowsed birches are of a lower magnitude.

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INTRASPECIFIC VARIATION IN MOOSE PREFERENCE FOR WILLOWS

Kenneth L. Risenhoover

ABSTRACT: Moose (Alces alces) preferences for Alaskan feltleaf willow (Salix alaxensis) and grayleaf willow (Salix glauca) were compared among different habitats in Denali National Park and Preserve, AK, during the winter-spring period. Observations during the searching phase of diet selection indicate that moose are selective browsers, and feed on only a fraction of the plant stems available. Moose preferences for individual willow species varied considerably among habitat types, and did not appear to be related to the availability of biomass. Observed variations in willow preference could not be attributed to plant nutritional quality, or to the amounts of phenols and condensed tannins they contained. Further descriptive studies of Salix chemistry using more specific assays will be necessary to adequately test hypotheses explaining intraspecific variation in willow preference by herbivores.

INTRODUCTION

Willows (Salix spp.) are a primary food source for moose throughout much of their range, and are therefore considered an important component of moose habitat. In some areas, willows may comprise up to 95 percent of moose winter diets (Peek 1974; Penner 1978; Risenhoover unpublished data). However, despite the obvious importance of willows to moose and other herbivores, and the recognition that moose preferences for individual willow species may vary regionally (Milke 1969; Peek 1974; Penner 1978), there have been surprisingly few studies investigating the underlying reasons for variations in willow preference.

Preliminary results from studies of moose winter foraging strategies and resource use in Denali National Park and Preserve (DNPP), AK, (Risenhoover, in preparation) indicate that moose preferences for individual willow species are not consistent among habitat types. Possible explanations for the observed variations in willow preference include: (1) Individual plants within and between habitats vary in their chemical composition and therefore palatability to moose. (2) Species preferences are determined by the availability of alternative diet species, and their relative value to moose. (3) Species preference is a function of its abundance and the economics of feeding on it relative to other available forage.

In this paper, I attempt to evaluate moose preferences for two widely distributed willows in DNPP, feltleaf willow and grayleaf willow, and examine possible reasons for the observed variations in moose preferences for individual plant species among habitats.

STUDY AREA AND METHODS

DNPP is located in central Alaska (60°40'N., 149°20'W.) bordering the Alaska Range, about 240 km south of Fairbanks (fig. 1). The study area consisted of the eastern portion of the park between the Teklanika and Nenana Rivers. Habitats in the study area are mountainous; U-shaped glacial valleys are drained by the Savage and Sanctuary Rivers, and by Riley Creek. Elevations range from 540 to 1,825 m; the majority of the study area occurs near treeline (about 760 m).

Vegetation types occurring in the study area are typical of the region and have been described by Viereck and Dyrness (1980) and by Van Cleve and others (1983). Open forest stands of primarily white spruce (Picea glauca) occur in the eastern portions of the study area, and in scattered patches or in strips along major creeks and rivers. Occasional stems of grayleaf willow, feltleaf willow, diamondleaf willow (S. planifolia) and

Figure 1.--Location of Denali National Park and and Preserve in interior Alaska.

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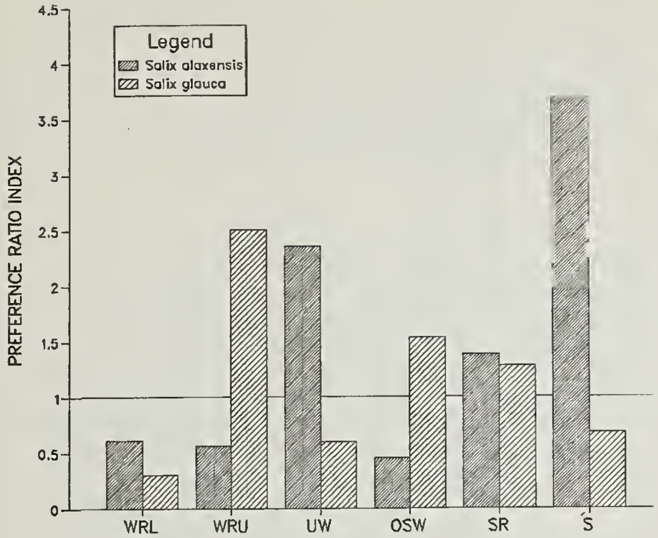

Figure 2.--Comparison of moose preferences for Salix alaxensis and Salix glauca in habitats in Denali National Park and Preserve, AK. (WRL=willow riparian lowland; WRU=willow riparian upland; UW=upland willow; OSW=open spruce willow; SR=spruce riparian; S=spruce).

resin birch (Betula glandulosa) may be present in the forest understory. Below treeline, willows and green alder (Alnus crispa) are most abundant along riparian zones. Above treeline, willows form dense thickets along riparian areas. For this study, vegetation in DNPP was subdivided into six habitat types based primarily on species composition and productivity (Risenhoover, unpublished data).

Moose diet selection and species preferences were determined in the different habitats in DNPP during January-April, 1983 and 1984. Sixteen moose were radio-collared and available for study. During foraging bouts (the periods of activity between bedding periods), free-ranging moose were followed at close range (<20 m) by two observers and all plant stems visited and the number of bites taken at each stem were recorded. In addition, moose search paths during foraging bouts were flagged, and the habitat volume within 1.5 m (the lateral reach of a moose) of the search path was sampled systematically using 3- by 3-m rectangular plots to determine the production biomass (grams/meter^2) of potential food items available. Forage production and consumption by moose were calculated using twig diameter-length-weight regression equations developed for each species (Risenhoover, unpublished data). An average weight for both browsed and current annual growth twigs was calculated by measuring a minimum of 50 browsed and unbrowsed twigs on stems of all species available within the search volume.

Preference is demonstrated when certain resources are utilized more often than would be predicted from the frequency with which they are encountered in the environment. For this study, preference was estimated using the preference ratio index (P_i) given by the equation:

$$P_i = \frac{N_i/\Sigma N_j}{E_i/\Sigma E_j}$$

where N_i=the number of resource items i used; N_j= the total number of resource items used; E_i=the number of resource items i in the environment; and E_j=the total number of resource items in the environment. To control the large influence of rare species on this index, P_i values were not calculated for species that constituted less than 5 percent of the available biomass unless they made up more than 10 percent of the biomass consumed during the foraging bout.

Composite samples of current annual growth twigs from a minimum of 20 plant stems were collected from representative sites in each habitat type and analyzed to determine their apparent nutritional quality. Samples were dried at 60° C in a forced-draft drying oven and then ground twice in a Wiley mill (2-mm screen). Ground samples were stored in vapor-proof bags at -20° C until analyzed. The nutritional quality of forage samples was determined at the Animal Nutrition Laboratory, Michigan State University (East Lansing) according to AOAC procedures (Horwitz 1980). Gross energy (Kcals/g) was determined using an adiabatic bomb calorimeter. Crude protein (N x 6.25) was determined by semi-microkjeldahl techniques. Percent ash was determined by burning in a muffle furnace at 650° C. In addition, the relative fiber components (cell walls, cell solubles, cellulose, hemicellulose, and lignin) of forage samples were determined according to procedures described by Goering and Van Soest (1970).

The apparent digestibility of forage samples was estimated using in vitro techniques described by Pearson (1970). Rumen innoculum was obtained from a yearling moose collected at the Moose Research Center (Kenai National Wildlife Refuge, AK) that had been feeding on native forages. Forage samples were tested in triplicate. The apparent digestible energy of samples was calculated by multiplying the in vitro digestibility of forage samples by the gross energy x 0.85 according to Hobbs and others (1981).

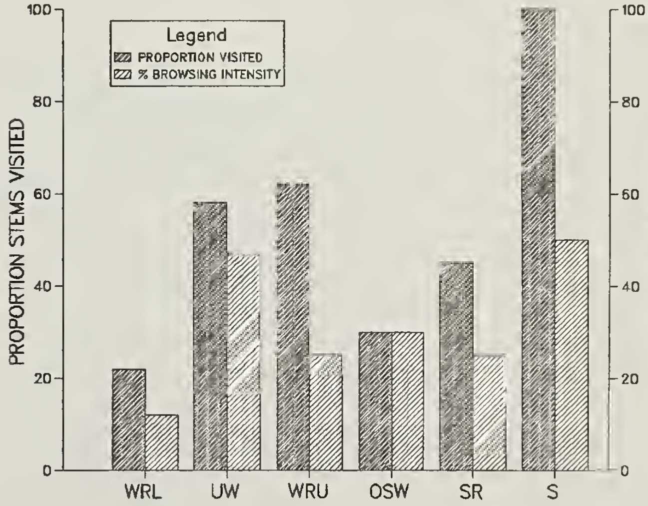

Figure 3.--Comparison of moose visitation patterns and utilization of Salix alaxensis stems in various habitat types in Denali National Park and Preserve, AK. (Abbreviations follow fig. 2).

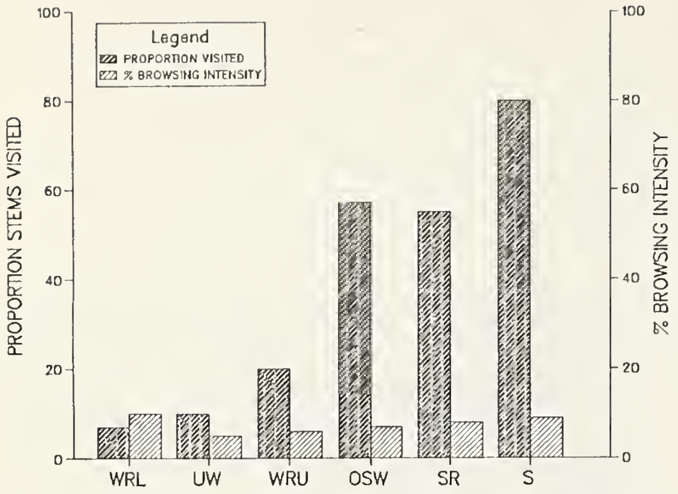

Figure 4.--Comparison of moose visitation patterns and utilization of Salix glauca stems in various habitat types in Denali National Park and Preserve, AK. (Abbreviations follow fig. 2).

Additional forage samples were collected, freeze-dried and analyzed to determine the total phenolic and condensed tannin fractions, and the ether-soluble component. Procedures for aqueous methanol extraction, and analyses for Folin-Dennis reactives and proanthocyanidins followed Martin and Martin (1982). Vanillan reactives were analyzed as described by Burns (1971) as modified by Price and others (1978), and astringent substances were analyzed by the hemoglobin precipitation method of Schultz and others (1981) using freshly collected sheep's blood as a source of hemoglobin. Concentrations of Folin-Dennis reactives and astringent substances were expressed as tannic acid equivalents; concentrations of vanillan reactives were expressed as catechin equivalents, and concentrations of proanthocyanidins were expressed as quebracho tannin equivalents.

RESULTS

Salix alaxensis was the major browse species in the winter diet of moose in DNPP and accounted for 44 percent of all biomass consumed during observed foraging bouts (Risenhoover, in preparation). Salix glauca was also an important species in moose winter diets and comprised 11 percent of the total biomass consumed. However, moose preferences for willows were not consistent among habitat types (fig. 2). Despite its importance in the diet, moose demonstrated a strong preference for S. alaxensis in only three of the six habitat types available. Salix glauca was also preferred in three of the six available habitat types.

Observations during the searching phase of diet selection indicate that moose were very selective browsers and fed on only a fraction of the S. alaxensis and S. glauca stems they encountered along their search path (figs. 3 and 4). Moose generally visited a higher proportion of available stems in habitats where species were preferred. In addition, there was a significant ($r=0.85$, $P<0.05$) positive correlation between moose preference for S. alaxensis and the degree of browsing intensity (proportion of available twigs browsed by moose) observed on stems within habitats. In contrast, the average browsing intensity observed on S. glauca stems was similiar among habitat types.

Preference and Production Biomass

Relationships between moose preferences for S. alaxensis and S. glauca and plant production biomass were compared to determine if the observed variations in moose preferences were density related (a functional response). Current ecological theory suggests that the degree of preference exhibited by a predator (in this case an herbivore) for a specific prey type may be dependent on the relative abundance of that prey and/or the other acceptable prey available (Emlen 1985). However, when moose preferences for S. alaxensis and S. glauca were compared to the total production biomass (grams/meter^2) available, and to the abundance of S. alaxensis or S. glauca biomass, respectively, no significant relationships were detected (figs. 5-8).

Preference and Plant Chemistry

Analyses of forage samples collected from the various habitats indicated that the chemical composition of individual plants may vary greatly between areas (Risenhoover, in preparation). Correlations between moose preference values and the digestible energy, crude protein, and minerals in plant tissues were generally weak and not significant (table 1). Although there was a strong negative correlation between moose preference values and lignin content ($r= -0.624$), no significant ($P >0.05$) correlations were detected between moose preferences and plant fiber content.

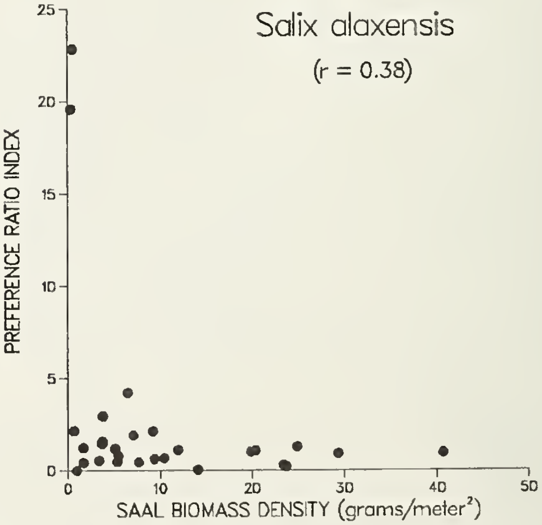

Figure 5.--Relationships between moose preference for Salix alaxensis and the density of Salix alaxensis production biomass.

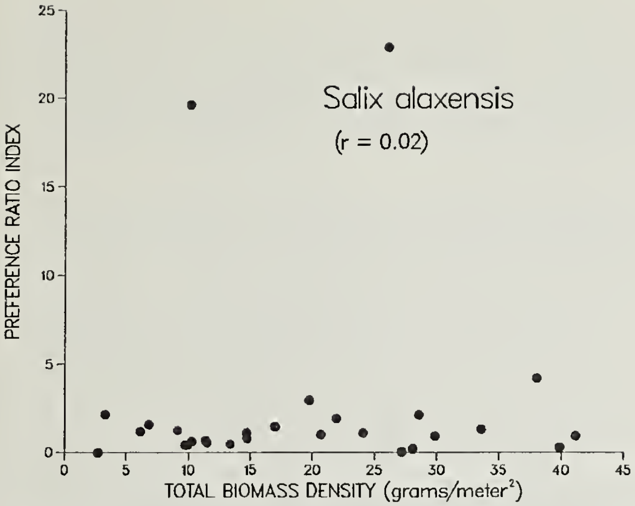

Figure 6.--Relationships between moose preference Salix alaxensis and total biomass density.

Overall, there was a negative relationship between moose preference and plant phenolic content. However, only the correlation between preference and astringent substances was significant (r= -0.733, P <0.05). The correlation coefficient for proanthocyanidins was also strongly negative (r= -0.601), but was not significant. However, despite the significant negative relationship, variation in the astringency of willow samples from different habitats was small, and could explain only 54 percent of the variation in moose willow preference. Thus, it would seem unlikely that astringency alone is responsible for the observed variability in moose willow preference.

Within habitat types, it was not uncommon to find unbrowsed willow stems growing alongside plants that had been heavily utilized by moose (Risenhoover, in preparation). We compared pooled twig samples from 20 browsed and unbrowsed stems in an attempt to evaluate any possible chemical differences between plants used and avoided by moose. No significant differences were detected in the chemical characteristics of browsed and unbrowsed plant tissues (table 2).

DISCUSSION

The forage selection patterns of moose in DNPP strongly suggest that there are important differences in the relative value of willows growing within different habitats. Direct observations of moose selectivity and browse utilization patterns within habitats also support this hypothesis. However, our preliminary analysis clearly favors rejection of all three possible explanations for the observed intraspecific variation in moose preferences for willows.

It is possible that the variations in willow preference observed between habitats were due to errors in our assessment of diet and forage availability. Indeed, diet preference and selectivity are particularly difficult to assess under field conditions. However, in this study, differences in willow preference between habitat types were pronounced and mostly consistent. The methods employed in this study allowed observers to quantify diet selection with a high degree of precision. Further, since our assessment of forage availability was limited to the actual search volume traversed by the moose, we are confident that our estimates of relative forage availability provide an accurate portrayal of what was actually available to the foraging moose.

Therefore, despite the lack of strong supportive evidence, the most likely explanation for the observed differences in preference remains that moose were selecting stems on the basis of plant

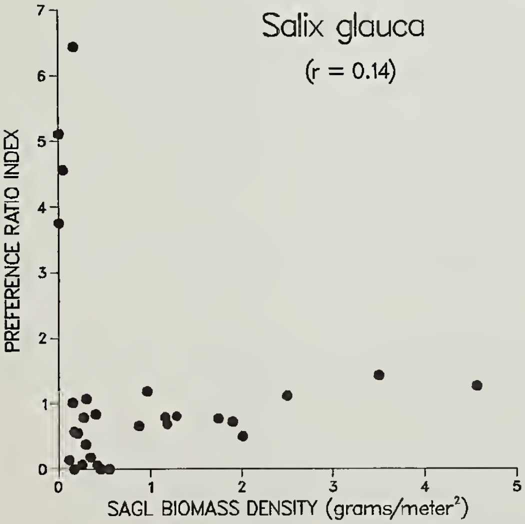

Figure 7.--Relationships between moose preference for Salix glauca and the density of Salix glauca production biomass.

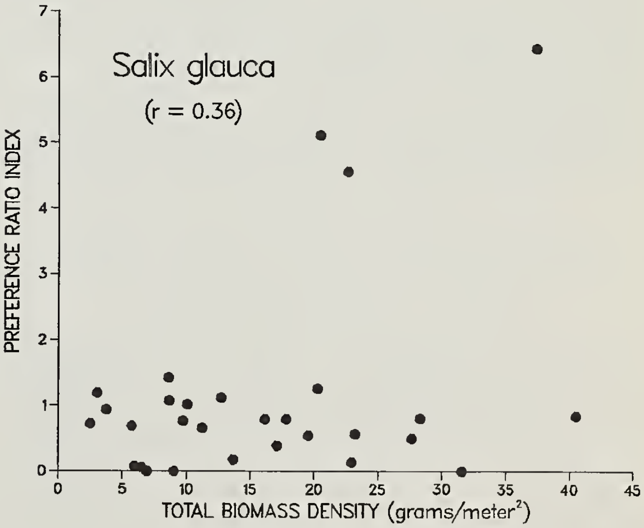

Figure 8.--Relationships between moose preference for Salix glauca and total biomass density.

Table 1.--Correlation coefficients (r) between moose preference ratio values and the concentrations of nutrients, fiber and phenols present in *Salix alaxensis* and *Salix glauca* plant tissues in Denali National Park and Preserve, AK

Chemical characteristic	Correlation coefficient[1]
Digestible energy	-0.351
Crude protein	-0.387
Ash	-0.500
Ether extract	-0.027
Fiber components:	
Neutral detergent fiber	0.441
Acid detergent fiber	0.000
Lignin	-0.624
Cellulose	0.570
Hemicellulose	0.376
Phenolics:	
Astringent substances	-0.733**
Proanthocyanidins	-0.601
Vanillan reactive	0.168
Folin-Dennis reactive	-0.510

**Significant at $P < 0.05$.

[1] Correlation coefficients were calculated from combined results for *S. alaxensis* and *S. glauca*.

characteristics that vary within, and possibly among willow species. Despite much recent interest (Palo 1984; Rowell-Rahier 1984; Bryant and others 1985; Palo and others 1985; Tahvanainen and others 1985; Waring and others 1985), our understanding of the antiherbivore chemistry of willows is still in its infancy, and it is possible that an important component in the chemical defense of these species has been overlooked in our analyses.

To date, phenolics are the only chemical class of secondary substances reported to occur within the family Salicaceae (Audette and others 1966; Palo 1984). Bryant (unpublished report) found a negative correlation between levels of plant phenols in *S. alaxensis* leaves during summer and their palatability and digestibility by snowshoe hare (*Lepus americanus*). However, in agreement with this study, Bryant found no relationship between winter plant phenols in woody twigs and hare palatability. Although phenolic glycosides are commonly found in willows (Palo 1984; Rowell-Rahier 1984; Tahvanainen and others 1985), and are known to be antibacterial, Bryant (unpublished report) found no differences in concentrations of phenolic glycosides in palatable and unpalatable forms of *S. alaxensis*.

To date, there has been very little descriptive work completed on the ether-soluble fraction of Alaskan willows. Although the ether-soluble fraction of Alaskan willows is largely composed of lipids (Bryant and others 1985), it is possible that an, as yet, unidentified deterrent compound present in this fraction could be responsible for the observed variations in moose willow preference. For example, Reichardt and others (1984) showed that although snowshoe hare preferences for Alaskan paper birch (*Betula resinifera*) could not be explained by gross chemical fractions (ether extracts or phenols), they clearly demonstrated that hare preferences were related to the distribution of specific resinous phytochemicals present in birch stems. Further descriptive studies of *Salix* chemistry using more specific assays will be necessary to adequately test the plant chemistry hypothesis.

The intraspecific variations in moose preference for willows observed during this study indicate that moose-forage relations in DNPP are complex and poorly understood. While considering each plant species as a biological unit may simplify the description of moose-plant relationships, it may obscure important aspects of moose food-seeking behavior and diet preference (Risenhoover, in preparation). Accurate descriptions of herbivore diet preferences and herbivore-plant relations will require the consideration of intraspecific variation in herbivory across geographic ranges.

ACKNOWLEDGMENTS

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Table 2.--Comparison of the chemical composition of browsed and unbrowsed *Salix alaxensis* from the willow riparian lowland habitat type

	Digestible energy	Crude protein	Acid detergent fiber	Neutral detergent fiber	Percent lignin	Percent ash
Browsed	2.14	8.22	41.3	53.3	17.1	2.11
Unbrowsed	2.33	8.20	40.7	54.5	17.3	2.34

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SAGEBRUSH (ARTEMISIA TRIDENTATA) MONOTERPENOID CONCENTRATIONS AS FACTORS IN DIET SELECTION BY FREE-GRAZING SHEEP

Wilson K. Yabann, Elizabeth A. Burritt and John C. Malechek

ABSTRACT: Summer and fall grazing trials were conducted to study the effect of monoterpenoid concentrations on the diet selection of sheep grazing big sagebrush (Artemisia tridentata ssp. tridentata) range. Total monoterpenoid concentrations were significantly lower in browsed sagebrush plants than in rejected plants. Sheep selected older plants and plant parts, not current season's growth. As annual grasses in the community declined, sheep consumed more sagebrush, resulting in an increase in dietary crude protein but a decline in *in vitro* organic matter digestibility. This study indicates that monoterpenoid levels, not nutritional constituents, may influence sheep diet selection of sagebrush.

INTRODUCTION

Diet selection is a feature that has enabled grazing animals to survive on ranges with varying levels of food resources. Optimal foraging theory predicts that an animal will maximize its net energy intake while foraging. However, research has failed to demonstrate a consistent relationship between animal dietary preferences and the proximate composition of plants. Arnold and Dudzinksi (1978) stated that animals are not capable of recognizing such entities as crude protein, crude fiber, energy, silica, or ash because these fractions do not exist in those forms at the molecular level in plant tissue. Researchers have correlated animal preferences with certain secondary compounds found in plant tissue (Bryant and Kuropat 1980; Provenza and Malechek 1984; Cooper and Owen-Smith 1985). In addition, bioassay techniques have been used to isolate compounds deterrent to herbivores (Bryant 1981; Bryant and others 1983; Reichardt and others 1984).

The poor palatability of both sagebrush and juniper (Juniperus spp.) species has been attributed to their monoterpenoid content (Dietz and Nagy 1976; Schwartz and others 1980). However, other researchers (Scholl and others 1977; Welch and others 1983; Behan and Welch 1985) have reported that such a relationship does not exist. The objectives of this study were to determine if monoterpenoid concentrations and nutritional constituents relate to dietary selection of big sagebrush (Artemisia tridentata ssp. tridentata) by sheep, and to examine the effects of seasonal variations in monoterpenoid concentrations and nutritive value of big sagebrush on dietary selection by sheep.

MATERIALS AND METHODS

The study was conducted at the Utah State University Tintic Valley Research Facility, located in Juab County, west-central Utah. Vegetation on the study site is dominated by big sagebrush (Artemisia tridentata ssp. tridentata) with a sparse understory consisting mainly of cheatgrass (Bromus tectorum) with lesser amounts of western wheatgrass (Agropyron smithii) and crested wheatgrass (Agropyron desertorum). Two 14-day grazing trials were conducted, one in mid-August and the other in mid-November. During each trial, a 0.06-ha paddock containing approximately 650 shrubs was grazed by 30 mature ewes. A new paddock was used for each trial. The resulting stocking rate of 1,344 animal unit days/ha was extremely heavy and was designed to achieve complete use of the understory and heavy utilization of sagebrush. Five of the ewes used in the trials were esophageally fistulated for the collection of dietary samples. All sheep used in the study had prior experience grazing big sagebrush.

Biomass of sagebrush was inferred from previous studies done in the same area (Narjisse 1981). Density of sagebrush plants was determined by counting all individuals in each pasture. Percent utilization of sagebrush was defined as either light ($\leq$ 50 percent) or heavy ($\geq$ 50 percent) and was determined by ocular estimates.

Five days prior to each trial, sheep were placed in a holding paddock adjacent to the study area to familiarize them with the conditions of the experiment. During each trial, sheep were observed at distances of 2 m or less, and the following information was recorded: which individual sagebrush plants sheep browsed, the type of plant parts sheep consumed, how sheep consumed these parts, and which sagebrush whole plants and plant parts were avoided. From these

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observations, selected plants were lateled either browsed or rejected. A browsed plant was defined as a plant that sheep were observed to sniff and select one or more bites from. Samples of browsed plants were taken in such a way as to simulate sheep browsing. Each browsed plant was paired with its closest totally rejected neighbor. A rejected plant was one that sheep were observed to sniff but did not browse. Hand-harvested parts from the rejected plants were as similar as possible to those parts collected from browsed individuals.

An analysis of the specific plant parts consumed or rejected from a browsed plant was also conducted. A browsed plant part was one representative of the portions of sagebrush sheep were observed to consume. Rejected plant parts were those portions of sagebrush that appeared to be consumable and sheep sniffed but did not consume. Also, any parts sheep removed from the plant but did not ingest (such as those dropped to the ground) were also classified as rejected.

Samples were collected at the same time of day to avoid possible diurnal variation in plant monoterpenoid concentrations. Upon collection, samples were sealed in plastic bags, placed on ice, and later frozen. Sample preparation and analysis for monoterpenoid concentrations followed the gas chromatography procedure of Welch and McArthur (1981). Subsamples of the hand-harvested material were freeze-dried, ground to pass a 40-mesh screen, and analyzed for Kjeldahl-N and *in vitro* organic matter digestiblity (IVOMD) (Tilley and Terry 1963). In addition to hand-harvested samples, diet samples were collected on days 1,3,5 and 7 of each trial using esophageally fistulated sheep. These samples were freeze-dried, ground, and evaluated for Kjeldahl-N and IVOMD as described above.

Analysis of variance (Neter and Wasserman 1974) was used to compare treatments (browsed versus rejected plants and plant parts), seasons, and their interactions.

RESULTS AND DISCUSSION

Monoterpenoid concentrations were about 2.6 times higher in rejected plants than in browsed plants during summer (fig. 1). In fall, rejected plants contained 3.3 times the monoterpenoid concentrations of browsed plants. Monoterpenoid concentrations in plant parts followed similar trends, with rejected plant parts containing 5.9 and 3.3 times the monterpenoid concentrations of browsed plant parts for summer and fall, respectively (fig. 2). In addition to higher monoterpenoid levels in rejected versus browsed forage, rejected forage generally contained twice as many individual monoterpenoid compounds as browsed forage. In general, sheep refused to consume plant parts that contained more than 0.33 percent monterpenoids.

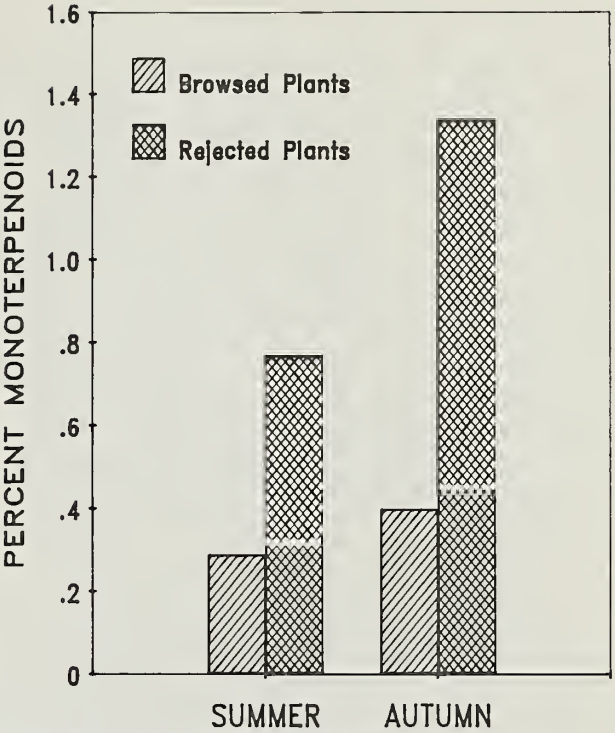

Figure 1.--Percent total monterpenoid concentrations of browsed and rejected whole plants for summer and autumn, 1983 ($LSD_{.05}$ = 0.31).

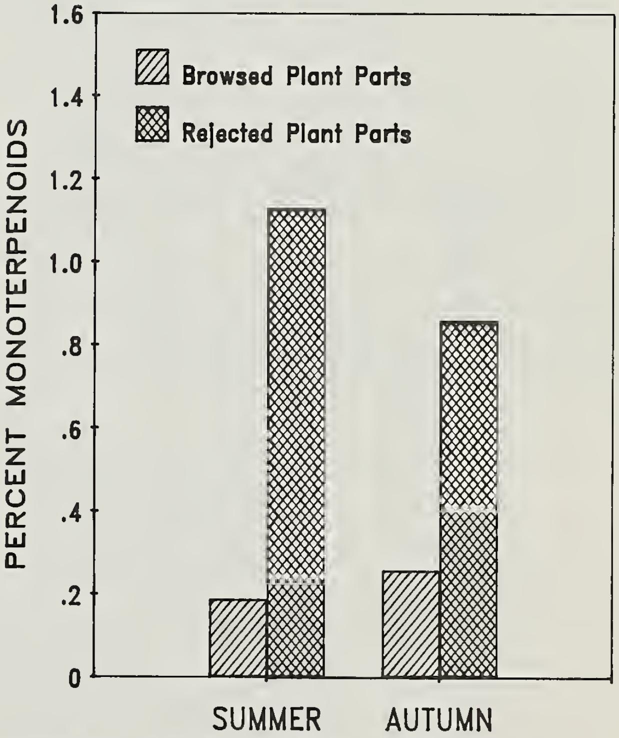

Figure 2.--Percent total monoterpenoid concentrations of browsed and rejected plant parts for summer and autumn, 1983 ($LSD_{.05}$ = 0.17).

Correlative studies relating monoterpenoid concentrations to dietary habits are conflicting. Several researchers (Scholl and others 1977; Welch and others 1983; Behan and Welch 1985) reported that plant preferences exhibited by mule deer (Odocoileus hemionus) for different accessions of sagebrush were not related to total or individual monoterpenoid concentrations. Schwartz and others (1980) reported that in feeding trials comparing several species of juniper browse, deer preferred species lowest in oxygenated monoterpenoids. Results of studies using deer or other herbivores may not be directly applicable to sheep, because sheep and deer apparently prefer different taxa of sagebrush (Sheehy and Windward 1981). Narjisse (1981) reported that sheep discriminated against monoterpenoid odor while goats discriminated against monoterpenoid taste, implying genetic-based differences in sensory modalities and perceptions.

No seasonal differences in monoterpenoid concentrations were noted for browsed whole plants, but monterpenoid concentrations were higher in rejected whole plants in fall than in summer. This is inconsistent with results reported by Narjisse (1981) and Cedarleaf and others (1983). They found higher sagebrush monoterpenoid concentrations in August than in November. However, their studies surveyed current season's growth and our study primarily involved older growth. The reported increase in whole plant monoterpenoid levels during fall in our study may have been due to heavier use of sagebrush in fall than summer, leaving fewer rejected sagebrush plants and therefore artificially elevating monoterpenoid levels. We found no differences in total monterpenoid concentrations for summer- and fall-browsed plant parts, but concentrations were higher in summer than fall for rejected plant parts.

Despite uniform soil type and a homogeneous plant community on our study site, a high degree of variability existed in monoterpenoid concentrations among and within individual sagebrush plants (table 1). Narjisse (1981) also observed a high degree of plant to plant variability in monoterpenoid concentrations of sagebrush. This variability probably accounted for complete consumption of some shrubs while others were completely rejected. Similarily, Wright (1970) reported that the palatibility of three-tip sagebrush (A. tripartita) was so variable that some plants died due to overuse while others remained untouched.

Whether sheep were selecting against monoterpenoid concentrations or on the basis of some other constituent in sagebrush, they were selecting their diet at the expense of crude protein and digestibility. Crude protein content of big sagebrush on a whole plant basis was significantly higher in rejected (8.5 percent summer and 10.8 percent fall) than in browsed (7.2 percent summer and 8.2 percent fall) individuals (fig. 3). Similar trends were observed for rejected versus browsed plant parts (fig. 4). In fall, both rejected and browsed whole plants were statistically higher in crude protein than summer.

Digestibility followed trends similar to crude protein, although no differences existed between IVOMD of browsed and rejected whole plants in the summer (fig. 5). IVOMD was higher for rejected (58 percent) versus browsed (41 percent) whole plants in the fall trial. Rejected plant parts were significantly higher in IVOMD than browsed plant parts in summer and fall (fig. 6).

In general, sheep browsed older plants that were larger and had exfoliating bark, rejecting smaller, greener plants (fig. 7) In addition, sheep were observed to break twigs, ingest the older portion of the twig, and drop the younger growth. Sheep preferred older growth (previous years' twigs or exfoliating bark) to current season's growth, resulting in lower levels of dietary crude protein and digestibility (figs. 3-6) than they could have obtained had they consumed current season's growth. Provenza and Malechek (1984) reported that goats browsing blackbrush (Coleogyne ramosissima) preferred older growth to current season's growth despite

Table 1.--Percent range of monoterpenoids in individual sagebrush whole plants and plant parts[1]

Season	Whole plants Browsed	Whole plants Rejected	Plant parts Browsed	Plant parts Rejected
		Percent		
Summer	0.06 - 0.63	0.30 - 1.80	0.16 - 0.27	0.86 - 1.27
Fall	0.21 - 0.70	0.75 - 2.15	0.21 - 0.32	0.59 - 1.27

[1] percent monoterpenoids on a dry matter basis.

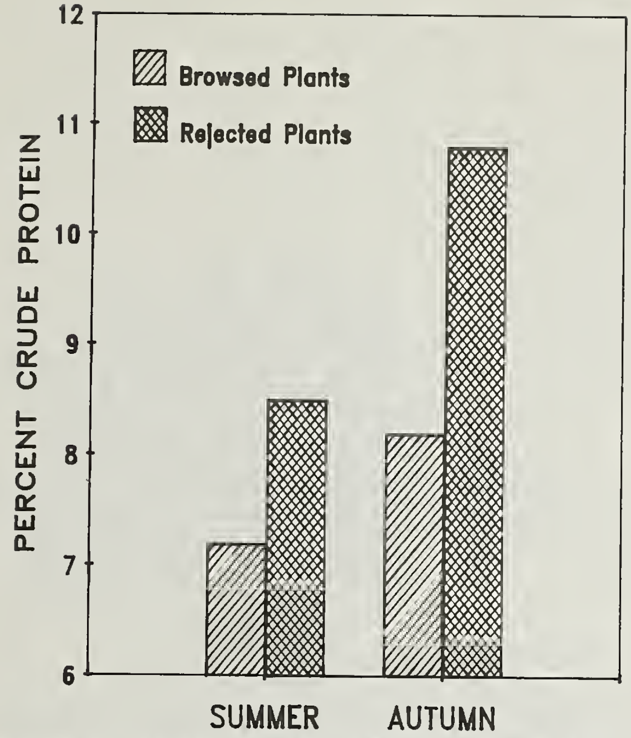

Figure 3.--Percent crude protein of browsed and rejected whole plants during summer and autumn, 1983 ($LSD_{.05} = 0.62$).

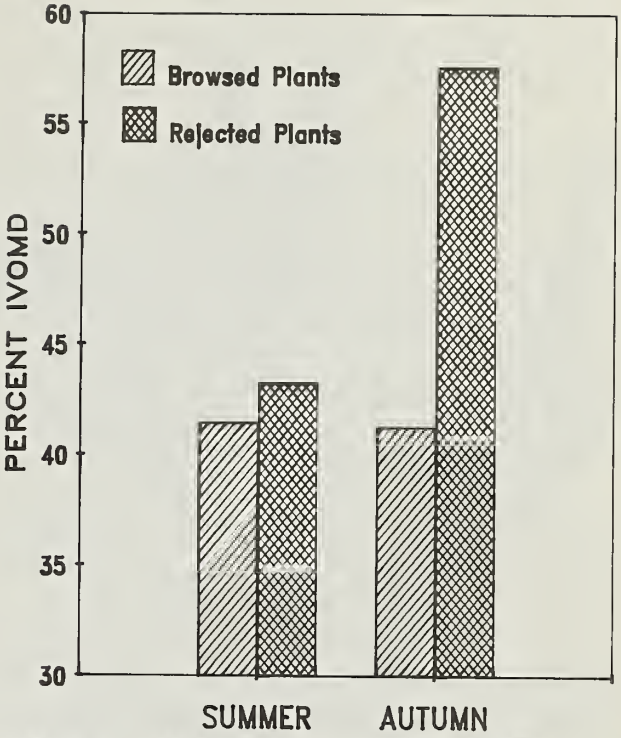

Figure 5.--Percent *in vitro* organic matter digestibility (IVOMD) of browsed and rejected whole plants during summer and autumn, 1983 ($LSD_{.05} = 5.0$).

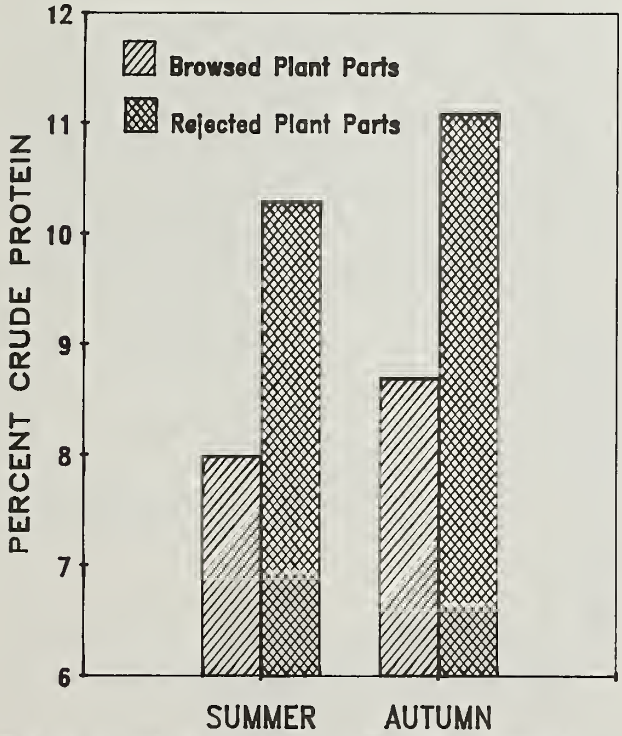

Figure 4.--Percent crude protein of browsed and rejected plant parts during summer and autumn, 1983 ($LSD_{.05} = 0.66$).

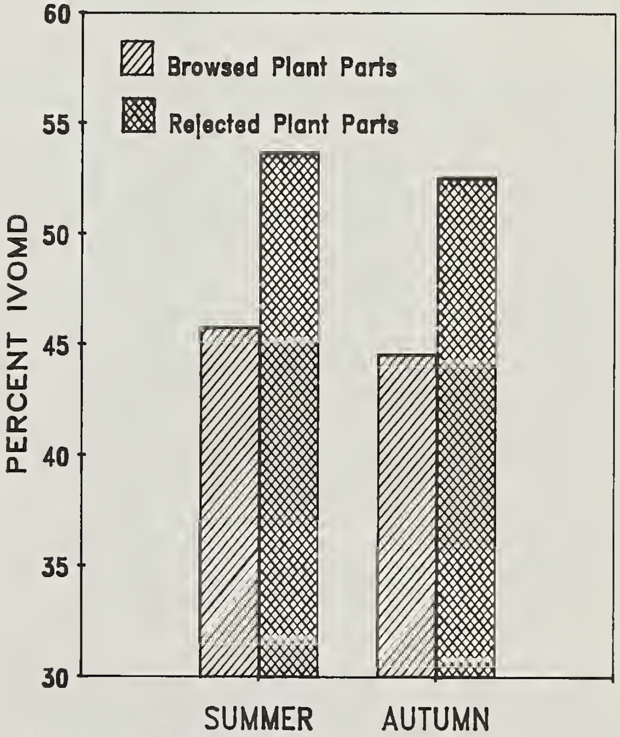

Figure 6.--Percent *in vitro* organic matter digestibility (IVOMD) of browsed and rejected plant parts during summer and autumn, 1983 ($LSD_{.05} = 5.0$).

Figure 7.--An example of a preferred older sagebrush plant (left) and a rejected sagebrush plant (right).

lower digestibility and crude protein content of older growth. They concluded that a higher concentration of tannins or some other secondary metabolite found in current season's growth was the chief factor governing diet selection.

As stated earlier, mean monoterpenoid concentrations were higher for fall whole plants (0.87 percent) than for summer (0.53 percent) (fig. 1). Despite this fall increase, sheep utilized sagebrush more heavily in fall than summer. About half of the individual sagebrush plants received a 50 percent or heavier utilization in summer, while 78 percent of the plants in fall were browsed to this level. In addition, sheep were observed to shift from grasses to sagebrush earlier in fall (day 3) than in summer (day 5). During both trials, sheep consumed all the available herbaceous material, including club mosses (Selaginella spp.), before browsing sagebrush. Sheep consumed the grasses more quickly in fall than summer, leaving no alternative forage source except sagebrush. Sheehy and Windward (1981) reported that during a palatability trial comparing seven taxa of sagebrush, including Artemisia tridentata ssp. tridentata, sheep had to be induced to browse sagebrush by removal of other food sources.

The crude protein content of the diet generally increased during the course of both trials (fig. 8). As sheep switched from grasses to shrubs, dietary crude protein content would be expected to increase because shrubs contain higher crude protein levels than mature grasses (Narjisse 1981). Dietary crude protein levels were also higher in fall than in summer. This increase can be attributed to: (a) the earlier switching from grasses to shrubs, and (b) higher levels of crude protein in sagebrush during fall than summer (fig. 3).

The IVOMD of diets were comparable on day 1 in both summer and fall (fig. 9). However, in summer, digestibility of sheep diets fell sharply by day 3 and remained low through day 5. Sheep ate everything possible prior to eating sagebrush and in the process of consuming leaf litter from the ground they consumed substantial amounts of soil. Large quantities of soil in the diet samples may have depressed in vitro digestibility values. Digestibility increased

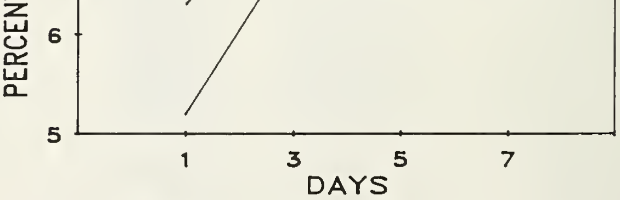

Figure 8.--Comparison of percent crude protein of esophageal fistula extrusa collected from sheep every second day during two seasons ($LSD_{.05} = 0.65$).

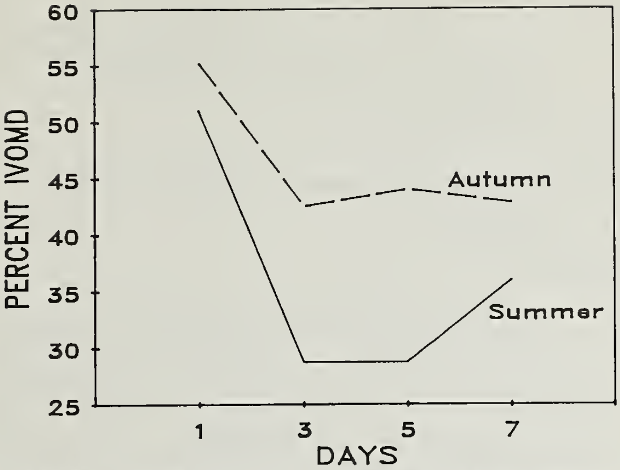

Figure 9.--Comparison of in vitro organic matter digestibility of esophageal fistula extrusa collected from sheep every second day during two seasons ($LSD_{.05} = 4.7$).

after sheep began browsing sagebrush (day 7). In fall, digestibility declined on day 3 and remained at that level through day 7. Sheep made the transition from grass to sagebrush earlier, preventing the drastic decline in IVOMD noted in summer. The overall decline in IVOMD can be attributed to the incorporation of woody stem and bark material from sagebrush into sheep diets (Otsyna 1983).

In conclusion, the often-observed positive relationship between dietary selection and proximate chemical constituents (Heady 1964; Fontenot and Blaser 1965; Lindlof and others 1974) did not hold for animals in a big sagebrush community. Sheep generally preferred to browse older growth to current season's growth. Therefore, the strong negative influence of monoterpenoids (or related phytochemicals) appeared to overshadow any positive nutritive considerations. However, Reichardt and others (1984) cautioned that significant correlative data do not necessarily dictate a cause-effect relationship. One or more other phytochemicals that vary in concert with monoterpenoids may have been the causitive factor(s). In view of the conflicting reports in the literature relating palatability of sagebrush to monoterpenoid content, more definitive work in this area is needed.

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PREFERENCE AND DIGESTIBILITY OF THREE BIG SAGEBRUSH SUBSPECIES AND BLACK SAGEBRUSH AS RELATED TO CRUDE TERPENOID CHEMISTRY

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Karl D. Striby, Allen F. McNeal, and Kris M. Havstad

ABSTRACT: Mule deer (Odocoileus hemionus hemionus) demonstrated an order of preference for time spent in five habitat types dominated by four sagebrush (Artemisia L.) taxa: basin big sagebrush (A. tridentata Nutt. tridentata), Wyoming big sagebrush (A. t. wyomingensis Beetle and Young), mountain big sagebrush (A. t. vaseyana [Rydb.] Beetle), and black sagebrush (A. nova Nels.). The taxa were also assigned forage preference ranks based on their winter utilization by mule deer. The in vitro organic matter digestibility of these taxa was determined from samples of intact and extracted (crude terpenoids removed) brush, using rumen fluid inocula from wild mule deer, sheep, and steer. The importance of crude terpenoid chemistry to preference was investigated by identifying and quantifying compounds in the taxa for comparison with preference ranks among taxa.

INTRODUCTION

Sagebrush habitat types are extensive on western rangelands (Beetle 1977); and sagebrush is an important component in the diets of many herbivores (Welch and McArthur 1979). However, when reviewing the literature, it is apparent that there is considerable confusion regarding forage relationships and forage values of the various sagebrush taxa. This is a problem for scientists and rangeland resource managers. Thus, the overall objective of the projects collectively reported in this paper was to relate the forage utility of four sagebrush taxa to their digestibility and unique chemistry.

STUDY AREA

The area studied and from which sagebrush samples were obtained for laboratory tests is located within the Gallatin National Forest and adjacent to Yellowstone National Park near the town of Gardiner in southwestern Montana. Elevation ranges from 5,300 ft (1 615 m) in the Yellowstone River Valley to 11,000 ft (3 353 m) on the surrounding peaks. The mountains to the south and west create a rain shadow on the study area, making benches and adjacent slopes of the Yellowstone Valley a preferred winter range for large herbivores forced from higher elevations by deep snow. Wintering populations include Rocky Mountain mule deer (Odocoileus hemionus hemionus), which spend a large part of their foraging time during the winter on the relatively exposed range dominated by sagebrush.

Annual precipitation at the lower elevations along the Yellowstone River averages 12 inches (300 mm). Most of the winter range receives about 16 inches (400 mm), while the surrounding mountains, snowbound in the winter, receive up to 30 inches (760 mm) (Farnes 1975). About half of the moisture is in the form of snow. The dominant shrub taxa on the area are four sagebrushes (Artemisia L. spp.): basin big sagebrush (A. tridentata Nutt. ssp. tridentata), Wyoming big sagebrush (A. t. Nutt. ssp. wyomingensis Beetle & Young), mountain big sagebrush (A. t. Nutt. ssp. vaseyana [Rydb.] B. Boi.), and black sagebrush (A. nova A. Nels.). The important grasses, codominant with the shrubs, are bluebunch wheatgrass (Agropyron spicatum [Pursh] Scribn. & Sm.) and Idaho fescue (Festuca idahoensis Elmer) (McNeal 1984).

PREFERRED SAGEBRUSH HABITAT TYPES

Investigations began when McNeal (1984) studied the way mule deer use the Gardiner winter range. He learned that the five shrub habitat types dominated by the four sagebrush taxa were not used by mule deer at an equal rate. This was based on mean pellet-group counts that were believed to represent animal preference for different areas within the winter range.

The high number of deer pellet-groups found within the Wyoming big sagebrush/bluebunch wheatgrass habitat type appeared to show their preference for that type. Sagebrush utilization was heavy in that type, but the area also provided some of the best thermal and security

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cover on the winter range in the form of rolling topography and nearby breaks. In addition, nearly all of this habitat type was on south and west exposures, generally without snow accumulation. Intermediate in use were the mountain big sagebrush and black sagebrush habitat types; they had a greater variation in pellet count numbers from one location to another than did the Wyoming big sagebrush type. This variation apparently reflected selective use by deer within these two types with most use found on south or west exposures and on areas near cover. Deer use of the basin big sagebrush habitat type was lowest. Although deer did feed in the basin big sagebrush communities, feeding appeared to be incidental while traveling through the type.

SAGEBRUSH DIGESTIBILITY

A great variety of factors might cause differential use of sagebrush habitat types as observed by McNeal (1984). Examination of forage values of the dominant taxa appeared to be a logical means of relating mule deer preferences to different sagebrush taxa within the winter range. Pursuing this reasoning, we studied the digestibilities of these four sagebrush taxa at three different dates (January 1, February 15, and April 1) with rumen inocula from a domestic sheep and steer as well as a wild mule deer killed on the study area. Concurrently, we measured the change in crude terpenoid content (Kelsey and others 1982) through the winter. In addition, crude terpenoids were extracted from certain sagebrush samples to test the digestibility of sagebrush material not containing these compounds. Investigation of crude terpenoid effects was encouraged by the conjecture of Nagy and others (1964) that monoterpenoids can inhibit deer rumen microbial functions, and the conclusions of research in Utah that rumen microorganisms do not have to adjust to monoterpenoids (Welch and Pederson 1981) and that no relationship could be found between total monoterpenoids and digestibility (Pederson and Welch 1982).

In our investigation (Striby 1985), in vitro organic matter digestibility (IVOMD) was nearly the same for the three inocula sources (mule deer, sheep, and steer). This was true for the different sagebrush taxa, collection dates, and between intact and extracted (crude terpenoids removed) sagebrush materials. The IVOMD of intact sagebrush ranged from a low of 38 percent for the January 1 collection of black sage in mule deer inocula to a high of 63 percent for the February 15 collection of basin big sagebrush, also in mule deer inocula. The IVOMD of extracted sagebrush varied from a low of 44 percent for the February 15 collection of mountain big sagebrush in steer inocula to a high of 76 percent in the April 1 collection of basin big sagebrush in mule deer inocula. Combining all dates, taxa, and inocula sources, the IVOMD of sagebrush averaged 51 percent and 63 percent for intact and extracted sagebrush, respectively. Digestibility of the intact sagebrush taxa increased in the following order: black sagebrush < mountain big sagebrush < Wyoming big sagebrush < basin big sagebrush. This trend was true regardless of collection date. The order of IVOMD for extracted material differed somewhat from the intact sample; as a rule, the differences among taxa became less significant. Mountain big sagebrush was the taxon with the lowest IVOMD, while black sagebrush, Wyoming big sagebrush, and basin big sagebrush increased in digestibility in that order.

Intact sagebrush taxa had increasing IVOMD through the collection period. This was an inverse relationship to the crude terpenoid level found in the taxa, which decreased over the same time period. For extracted materials, taxa showed few significant changes in digestibility over time, further emphasizing the relationship of crude terpenoids to sagebrush digestion.

Despite our findings regarding sagebrush digestibility and the influence of crude terpenoids on digestion, it was revealing to learn that the order of intact taxon digestibility was not governed strictly by crude terpenoid levels. Basin big sagebrush contained the highest levels of crude terpenoids, yet was the most easily digested. Mountain big sagebrush only exceeded black sagebrush in digestibility yet contained the lowest levels of crude terpenoids followed by black sagebrush and Wyoming big sagebrush. Thus, it became of interest to investigate the preference displayed by browsing mule deer for the four taxa on this range and to subsequently investigate the influence of crude terpenoids on preference.

SAGEBRUSH PREFERENCE

We were able to isolate 32 compounds from the crude terpenoid extract (Personius 1985). Eighteen were identified. The relationship of these compounds to mule deer forage preference on the winter range for the four sagebrush taxa was our main consideration. The order of increasing preference was black sagebrush (least preferred), basin big sagebrush, Wyoming big sagebrush, and mountain big sagebrush (Wambolt, unpublished).

Many of the compounds identified have been tested for biological activity (Tatken and Lewis 1983). Although mule deer were not the subject of these tests, they serve to interpret the possible effects of certain crude terpenoid fractions on mule deer preference. All of the compounds tested were either toxic or irritating, or both, when encountered in sufficient quantities, although the threshold level for mule deer is uncertain. The biological activities of the unknown compounds still remain a question. Some of these are probably toxic or irritating, but there is no way at this time to discern their effects on mule deer preference.

Certain identified biologically active compounds occurred in quantities that seemed both sensible and in sufficiently different concentrations among the sagebrush taxa that correlations to observed preference appeared meaningful. In addition to being preference indicators, they may be active preference determinants. For example, the amount of methacrolein+ethanol in the three subspecies of big sagebrush had a consistent negative correlation with their preference. Although black sagebrush was the least preferred taxon, and did not contain significant concentrations of methacrolein+ethanol, it did have significantly greater quantities of ρ-cymene. The aforementioned compounds are known to be irritants. The role of certain other compounds in determining preference is less clear. Some were positively correlated to preference; others were less consistent. Compounds that remained unidentified and had a significant correlation to preference provide stimuli for conjecture, but no inference about their possible effect on displayed preference can be made without some knowledge of their biological activity.

SUMMARY AND CONCLUSIONS

Mule deer on the Gardiner winter range displayed a preference among five sagebrush-dominated habitat types. They also displayed a distinct preference for specific sagebrush taxa in their diet. Although many reasons may be responsible for the preference of specific sagebrush habitat types, it is likely that the forage values of the dominant sagebrush taxa play a role. In general, sagebrush taxa were highly digestible throughout the winter browsing period, although high digestibility did not correlate positively to high preference by mule deer. The crude terpenoid chemistry of sagebrush negatively influences digestibility despite the relatively high digestibility of sagebrush with crude terpenoids intact. However, the digestibility of an individual taxon is not directly related to total crude terpenoid content. A distinct preference was displayed for each of the four taxa by mule deer on the winter range and served as a basis for investigating the role of sagebrush compounds on preference. The quantities and biological activities of certain compounds are correlated with the preference demonstrated by mule deer for the four taxa studied.

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SAPONIN EFFECT ON SMALL MAMMAL FORAGE PREFERENCE IN A PLANTING OF ATRIPLEX CANESCENS

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ABSTRACT: Accessions of *Atriplex canescens* transplanted into a newly established common garden were damaged to different degrees by rodents living on the site. The more severely affected plants originated from a small endemic hexaploid race near Grantsville, UT. The remaining collections were two tetraploids and a diploid from other Utah locations. The Grantsville plants were the only ones not bitter to the taste and testing negative in a red blood cell assay for the presence of saponins.

INTRODUCTION

Atriplex canescens has been reported to contain triterpene saponins derived from the aglycone oleanolic acid (Nord and Van Atta 1960). Saponins of this type are not cardiotoxic, but do exert an irritant effect through lysis of cell membranes (Windholz and others 1976; Birk and Peri 1980). Once the glycoside portion of the molecule has been removed in the digestive system it is no longer active, so effects are mostly limited to the throat, or perhaps the lungs in the case of plant dust inhalation. Mammals restricted to saponin-containing diets tend to lose weight, but this may be due to reduced intake (Cheeke 1976).

During the establishment of a garden of *Atriplex canescens* clones in the spring of 1982, rodents, which are abundant on the site, damaged plants from some sources more than others. Small rodents that are to be expected in this vegetation type include kangaroo rats (*Dipodomys*), deer mice (*Peromyscus*), kangaroo mice (*Microdipodops*), and grasshopper mice (*Onychomys*) (Fautin 1946; Shelford 1963; Institute for Land Rehabilitation Staff 1978). *A. canescens* plants from the Grantsville, UT, hexaploid population (Stutz and others 1979), which are nonbitter tasting were especially heavily damaged.

In preparing the site for planting, native vegetation (*Atriplex falcata* and *Ceratoides lanata*) was left undisturbed except in the planted rows. Although the garden had been fenced and the fence lined with partially buried chicken wire to exclude sheep and rabbits, heavy damage was observed on susceptible plants during the spring of planting, and again the following spring in spite of intensive trapping and poisoning. Damage decreased thereafter as plants gained in size. This report documents visible differences in grazing preference by the rodent population.

METHODS

Leaves were dried at 40 °C, ground, and saponin content analyzed by red blood cell assay (Jones and Elliott 1969) using human blood obtained from the American Red Cross. (It was found, however, that drying is better omitted; see Results section). To give a wider range of sensitivity, a single dilution series was used rather than two overlapping series as described by Jones and Elliott (1969). The saponin (1 g or 2 g of dried plant material leached with 23 mL of saline solution) was diluted 1/2, 1/4,... $1/2^9$ (10 tubes) using the following procedure. One milliter of red blood cell suspension in saline solution (2 percent, v/v) was placed in each of the 10 tubes and 1 mL of the original saponin solution was then added to the first tube. Then half of that mixture from the first tube was transferred to the second tube and half of that mixture to the third, and so on. The solution in tubes where saponin concentration was sufficient to hemolyze the blood cells became a transparent red color, while the solution in unhemolyzed tubes remained translucent red and eventually became clear and colorless as the cells sedimented to the bottom (fig. 1). Titer is referred to as the number of tubes showing hemolysis (tables 1 and 2).

Saponins were also quantified by weight after partial purification. Ten mL aliquots of saponin solution were extracted with three portions (5, 2.5, 2.5 mL) of n-butanol; then n-butanol was evaporated in a tared aluminum foil weighing boat at 50 °C.

A rapid qualitative test for saponins is the foam test (Harborne 1973). The method used in the present study was as follows: 1 g dry weight of ground leaves was mixed with 200 mL water and shaken vigorously. An abundant foam, standing

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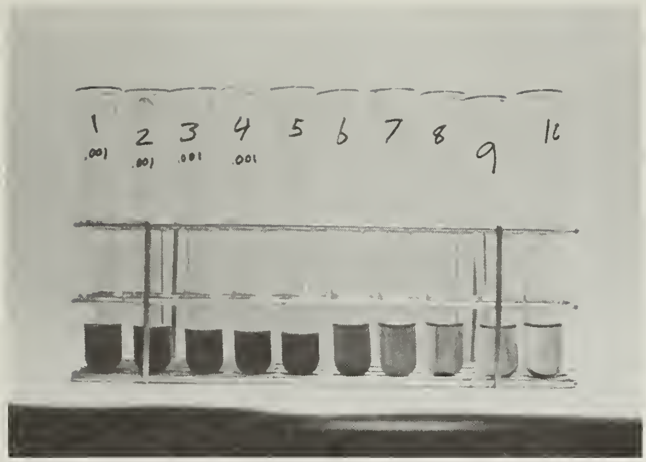

Figure 1.--Hemolysis of blood cells by saponins extracted from *Atriplex canescens*--hemolyzed (left test tubes), partially hemolyzed (tube 6) and unhemolyzed (right test tubes). After standing overnight, cells in the unhemolyzed tubes have sedimented out, leaving a clear solution. Hydrolyzed tubes are colored because of dissolved hemoglobin remaining from disrupted cells.

overnight, was considered a positive test (fig. 2). Human gustatory capabilities are also able to detect *Atriplex* saponins, although the result was usually a rawness of the throat that persisted all day. It was somewhat helpful to wash the mouth copiously with water after performing a test and avoid contact of plant juices with the throat. A small handful of leaves was chewed for 1-2 min, and if the sample contained saponin, a strong bitter taste gradually became apparent.

Table 1.--Saponin content of native *A. falcata* and garden grown *A. canescens* plants of three origins, by erythrocyte assay, from 1 g leaf samples. Plant of origins belonging to separate SNK groupings were statistically different

Origin or species	n	Mean saponin titer	SNK grouping
A. falcata	9	5.89	A
Kingston Canyon	10	4.05	B
Spanish Fork	15	3.80	B
Grantsville	8	0	C

Samples for laboratory analysis were collected from the Rush Valley garden and also from natural populations at Grantsville and Spanish Fork. Rodent damage was recorded the second spring. Plants (10 clones of each) were scored for the presence of chewing damage and the number of plants damaged was converted to a percentage. Percents were arc-sine transformed and treated by one-way analysis of variance followed by the Student Neuman-Keuls multiple mean comparison test (GLM procedure, SAS program for personal computers, Joyner 1985).

Figure 2.--Positive persistence foam test (two left flasks) in contrast to negative tests (two right flasks). The left flasks contain ground leaves from Spanish Fork *Atriplex canescens*; the right flasks contain leaves from the Grantsville *A. canescens* accession.

Controlled feeding trials were run using a kangaroo rat (*Dipodomys ordi*, male) captured at the Rush Valley site. After capture the animal was fed Hartz Mountain guinea pig pellets (containing primarily alfalfa and soybean meal).

Table 2.--Saponin content of native *A. canescens* from Grantsville and Spanish Fork, by extract weight, foam test, and erythrocyte assay from 2 g leaf samples

Location	n	Mean extract weight, mg	Foam test mode	Mean saponin titer
Spanish Fork	15	81	positive	8.2
Grantsville	15	56	negative	.6

Saponins for feeding trials were obtained from plants of the Spanish Fork *A. canescens* population. Branches were harvested in the month of December and oven dried at 35 °C, and a total of 684 g dry weight of leaves was obtained. These were ground and extracted with 5 gal of 5 percent acetic acid; the acetic acid solution was in turn extracted with n-butanol. The butanol extract was reduced by azeotropic vacuum evaporation and saponin was precipitated from the concentrated solution by removal of dissolved water by azeotropic evaporation. Phenolic impurities were removed by repeated precipitation using this method or the addition of acetone. Twenty-five grams of relatively pure saponins were obtained (as an off-white, chalky solid) and smaller additional amounts appeared to be present in impure fractions, representing a yield of about 3.6 percent or more of the leaf dry weight.

One gram of the final saponin preparation was applied to 49 g of guinea pig food pellets, either as an alcohol slurry or in water, and the treated pellets were dried under a vacuum. Saponin was incorporated better into the pellet using water, but the pellets were more susceptible to disaggregation if left in water for too long a time. Controls consisted of pellets wetted with water or alcohol and vacuum dried.

RESULTS

Strong statistical documentation was obtained of differences in grazing preference among accessions of *A. canescens* in the garden (table 3).

Table 3.--Rodent grazing data from the Rush Valley garden of four accessions of *A. canescens*. "Damage score" is the percentage of plants grazed, arcsine transformed

Origin	n	Mean damage score	SNK grouping
Jericho	11	1.7	A
Spanish Fork	11	4.7	A
Kingston Canyon	11	16.8	B
Grantsville	11	68.0	C

Evidence that this preference was related to saponin content was obtained by measurement of saponins for these accessions. Plants of the Grantsville accession for the most part evidenced no detectable saponins (tables 1 and 2). However, out of 15 plants collected in the field at the Grantsville location (table 2), one plant, perhaps an alien from another *A. canescens* race, did have a high saponin concentration and a second plant showed a trace. Extract weights shown in table 2 likely consisted of a large amount of phenolic material in addition to saponins.

The accessions in the Rush Valley garden had differing saponin levels but *Atriplex falcata* growing between the rows tested higher for saponins than any of the *A. canescens* populations, except inferrentially that from the Jericho sand dunes. Although it might be utilized by livestock (Stutz and others 1975), the Jericho accession was grazed least of any *A. canescens* populations by rodents. However, it was not directly tested for saponins because of early mortality and disappearance from the garden, apparently due to drought sensitivity.

A marked difference is evident between the results of table 1 and 2 with respect to the Spanish Fork accession. In table 1 a mean saponin titer of 3.8 was measured; in table 2 the comparable value was 8.2. This result was partly due to the use of only 1 g of leaf tissue for the measurements in table 1 while in table 2, 2 g were used. Nevertheless each additional titer unit represents a doubling of the initial saponin concentration [conc. = $2^{(n-1)}$], neglecting erythrocyte concentration, so that an eightfold increase in hemolytic power remains unexplained. The collections for the two tables were both made during the winter and plants seemed in a comparable state of health. However, in the processing, the samples of table 2 were inadvertently overheated in the drying oven to the point that their color was changed somewhat. Myer and Cheeke (1975) found that alfalfa, which contains a type of saponin, became much less palatable to rats when heated during drying. These variations probably result from incomplete cleavage of the inactive saponin precursor by milder treatments (Domon and Hostettmann 1984; Marston and Hostettmann 1985). Drying at mild temperatures might have destroyed the capacity for enzymatic activation of saponins but stronger heating apparently was sufficient to bring about non-enzymatic cleavage of the weak bond of the saponin precursor. In spite of the resulting problem of analysis, which might have been avoided by using fresh rather than dried plant material, the two tables remain internally consistent.

Feeding trials with the kangaroo rat easily demonstrated an animal preference for non-saponin treated pellets when the food was presented in excess above amounts consumed (table 4). However, it was found difficult to demonstrate preference using small amounts because all was commonly taken irrespective of saponin content.

Table 4.--Feeding preference of a kangaroo rat from the Rush Valley site for control versus saponin treated alfalfa pellets

Treatment	n	Mean pct. taken	Std. dev.
Control	4	.9979	.0024
Saponin	4	.1450	.1330

T for unequal variances = 12.8253
df = 3, p = 0.001

DISCUSSION

Although native vegetation, chiefly *Ceratoides lanata* and *Atriplex falcata*, of the Rush Valley garden had been mechanically disturbed only in the planting rows, it was adversely affected the first two springs, perhaps by weather or pathogens, to the extent that *A. falcata* seemed unhealthy and *Certoides* appeared nearly dead. The same was true of areas outside of the garden. As a result a partial food scarcity may have occurred, tending to focus herbivore activities on the newly placed transplants. Fautin (1946) and Shelford (1963) reported that kangaroo rats eat *Atriplex confertifolia* and *A. tridentata* (*A. nuttallii*) leaves, and in spite of the poor conditions of *A. falcata*, this species was probably abundant enough to be a good food source if it had been sufficiently palatable. The observed differences between *A. canescens* and *A. falcata* saponin concentrations (table 1) were probably responsible for the *A. canescens* transplants being grazed preferentially.

Measurements of saponin content of A. canescens plants showed that a sharp difference existed among the accessions, which is suggested to have influenced herbivore preference. This hypothesis is supported by the response of a captive kangaroo rat to the addition of saponin to commercial food pellets. It may be noted that alfalfa, which formed a major part of the pellets, may contain as much saponin as the Atriplex species examined. However, because of the low reported hemolytic activity of alfalfa (Jones and Elliott 1969) compared with that observed for Atriplex, alfalfa saponin could be expected to produce little aversion in this species of animal. Hence it is not surprising that a clear discrimination was possible on the basis of added Atriplex saponins (table 4).

An attempt was made to demonstrate a feeding preference of the captive kangaroo rat for fresh A. canescens vegetation on the basis of saponin content. However, this was unsuccessful because stems were often gnawed and consumed in preference to leaves. Stems of A. canescens were found to be nonbitter, but splintery. While gnawed off branches of Ceratoides were frequently observed at the site in Rush Valley, Atriplex falcata and A. canescens stems were apparently not gnawed. Perhaps an appetite for stems can be readily satisfied in nature without resorting to those of Atriplex.

Knowledge of variation in saponin levels among A. canescens populations documents an additional character of that species' interpopulational variation to add to those reviewed by McArthur and others (1983) (soil chemistry, ash content, crude protein, stem rooting, palatability, winter hardiness, seed and flower characteristics, growth rate, and chromosome number).

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ALKALOIDS AND PALATABILITY OF POISONOUS PLANTS

M. H. Ralphs and J. D. Olsen

ABSTRACT: The alkaloid content of some species (*Phalaris arundinaceae*, *Lupinus* spp., *Crotalaria* spp., and *Senecio* spp.) is inversely related to palatability or has been shown to deter grazing. However, some species (*Delphinium* spp. and *Oxytropis* spp.) high in total alkaloids are apparently palatable to livestock. Other palatability factors appear to override the high alkaloid levels.

INTRODUCTION

C. D. Marsh, principal investigator of the Bureau of Plant Industry for more than 20 years, was an astute observer of poisonous plant/livestock interactions. He made the statement in 1913 that "it is generally recognized that the heaviest losses of livestock from poisonous plants occur in seasons when feed is short. . . . Stock seldom eat poisonous plants by choice, but only when induced or compelled by the scarcity of other food" (Marsh 1913). This concept has been perpetuated in range management literature to the present (Stoddart and Smith 1955; Heady 1975), largely because no one has seen anything drastically contrary to it. Dwyer (1978) addressed a global workshop on poisonous plants 61 years after Marsh's observation and essentially concluded the same thing: "We assume animals do not prefer to graze poisonous plant when given choices." Two exceptions will be mentioned later in this paper. But generally, livestock do not consume poisonous plants in sufficient quantities to cause problems when they have a choice. Most large losses of livestock from poisonous plants result from management mistakes, such as confining hungry livestock on dense concentrations of poisonous plants. Hunger lowers the smell and taste rejection thresholds, thus causing animals to eat plants they normally would avoid (Arnold and Hill 1972).

We can assume then, that there is something in many poisonous plants that livestock find objectionable and deters them from consuming the plants in sufficient quantities to cause harm.

Alkaloids are the principal toxin in some of the important poisonous plants on rangelands, pastures, and even in cultivated forages. There is some evidence that alkaloids are negatively correlated to palatability for some of these species. Alkaloids are considered to be bitter due to their basic nature. Bate-Smith (1972) made the generalization that bitterness is universally repellent to all animals. However, bitterness is a relative term and may be dependent on the concentration of the alkaloid. Garcia and Hankins (1975) also concluded that natural aversions to bitter substances have been acquired by a wide variety of animal species through natural selection.

There is disagreement, however, on the evolutionary role of alkaloids as defense mechanisms in plants. Waller and Nowacki (1978) suggested that insect herbivory played a large role in the evolution of alkaloids as protective mechanisms in some plant families. However, Robinson (1979) disagreed and stated "sweeping generalities about the protective influence of alkaloids are groundless." He conceded that there are specific cases in which the presence of an alkaloid could influence plant selection by a particular enemy at a particular time. Laycock (1978) reviewed the literature on coevolution of poisonous plants and large herbivores and concluded that there are many examples of the effectiveness of these compounds in deterring grazing. However, he stated that "proof" that they evolved for that purpose is impossible. There is general agreement, though, that if alkaloids in plants are responsible for deterring grazing by large vertebrate herbivores, it is the bitterness or some other factor that renders the plant unpleasant rather than the animal consciously avoiding the toxin (Bate-Smith 1972; Waller and Nowacki 1978; Robinson 1979).

Yet, some poisonous plants with high levels of alkaloids are palatable to livestock. The purpose of this paper is to examine the relationship between palatability and alkaloid content of forage species and poisonous plants consumed by livestock. Specific cases from the literature, published observations, and data from our research will be presented to show cases in which alkaloids deter livestock grazing, as well as instances where livestock select plants that are high in alkaloids.

ALKALOIDS DETER GRAZING

Some forage crops that contain alkaloids present strong evidence of a negative correlation between alkaloid content and palatability.

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Reed Canarygrass

Reed canarygrass (Phalaris arundinaceae) is a hardy, high-yielding forage species adapted to upland and poorly drained soils in temperate regions throughout the world. There have been sporadic reports of poor performance by cattle and sheep grazing reed canarygrass pastures, and Phalaris staggers is common in Australia and New Zealand. Several dimethylated tryptamine alkaloids have been isolated from reed canarygrass. They have been shown experimentally to cause "sudden death" syndrome, acute nervous disorders, and the more common symptoms of incoordination of gait and nodding head associated with Phalaris staggers (Marten 1973).

The major criticism of reed canarygrass is its poor palatability. Simons and Marten (1971) conclusively demonstrated a strong negative correlation between total alkaloid concentration (TAC) and palatability. Concentration of individual alkaloids and TAC was determined for 18 clones of reed canarygrass transplanted in a common garden. Palatability ratings were obtained by estimating the proportion of individual plants consumed by sheep given the choice of all the plants in the garden. There had been some discussion that palatability was related to the presence or absence of certain alkaloids, but this research showed that TAC was the major determinant of palatability. TAC ranged from 0.03 percent in the palatable strains to 0.4 percent in unpalatable strains (Hagman and others 1975). This research showed that alkaloids hindered the acceptability of reed canarygrass when a choice was given. Further research revealed that livestock significantly reduced voluntary intake of high alkaloid varieties of reed canarygrass when there was no choice (Marten and others 1976).

Lupine

The Lupinus genus is another example where considerable effort has been made through selective breeding to reduce alkaloid content and thus improve palatability. Quinolizidine alkaloids are the major toxins and teratogens in lupine. Two species of lupine, Lupinus albus in the Mediterranean region and L. matabilis in South America, have been cultivated as grain for over 3,000 years (Gladstones 1970). The seeds traditionally have been debittered by boiling and steeping in running water and then ground as meal or fed to livestock. Gladstones (1970) speculated that the bitterness resulting from alkaloids in seed and foliage has played a large role in protecting the seed source. On the other hand, bitterness in seeds and foliage has probably protected grazing animals by preventing consumption of lethal quantities (Gladstones 1977).

Following World War II, considerable effort was made to breed alkaloid-free or reduced alkaloid "sweet" varieties of lupine for both human and livestock use. Keeler and Gross (1980) analyzed seed from bitter and sweet varieties of lupine used for human consumption from around the world. They found sweet varieties contained less than 0.10 percent TAC, semisweet varieties contained 0.20 - 0.35 percent TAC, and bitter varieties contained greater than 0.44 percent TAC.

Livestock and other herbivores also discriminate between the high alkaloid bitter varieties and low alkaloid sweet varieties. Blue lupine (L. angustifolius) is a winter annual used as a cover crop in the Southeastern United States. Livestock totally refuse the bitter varieties, but readily graze the sweet varieties (Forbes and others 1961). Lupanine is the principal alkaloid. Bitter varieties contain 0.21 percent lupanine in the leaf and stem as opposed to less than 0.007 percent in the sweet varieties, "Borre" and "Blanco" (Forbes and Burton 1960).

It is difficult to visually distinguish between seeds and growing plants of the sweet variety "Borre" and the original bitter variety. However, cattle rejected pasture of "Borre" sweet lupine when as little as 5-10 percent of the plants were of the bitter variety. Forbes and Beck (1954) developed a biological assay to distinguish bitter from sweet varieties. Thrips fed on pollen of both varieties. When the pollen was exhausted, they went on to attack the foliage of the sweet varieties, but didn't damage the bitter variety. Evidence of thrips damage on foliage was just as accurate as quantification of alkaloids in the plants. Waller and Nowacki (1978) stated that hares grazing L. angustifolius in Poland relished sweet varieties, but left the bitter varieties alone, or if they made a "mistake" and cut the plant off, they left it lying in the field.

Marsh and Clawson (1916) were early investigators of Lupine poisoning of sheep on western ranges. They reported that they had problems getting sheep to eat enough of the plant to cause symptoms of toxicity in pen feeding trials. Seeds were particularly bitter and had to be ground and mixed with bran before sheep would consume them. They concluded that poisoning on the range occurs only when hungry sheep graze the plant and that the alkaloid content is a natural inhibitor.

Davis (1982) reported TAC of several native and improved varieties of lupine ranging from 0.3 to 2.4 percent. The changes in TAC of Lupinus caudatus through its phenological development (fig. 1) is typical of Western United States lupines (Keeler and others 1976). TAC is fairly low at the beginning of growth, rises to a peak prior to flowering, then drops to a low level during the pod stage. Seed TAC range from 2.3 to 9.5 percent. The early vegetative foliage and immature seed pods are palatable to sheep, and correspond to relatively low TAC (fig. 1).

Crotolaria

Crotolaria spp. are used as forage legumes on sandy soils on the coastal plain in the Southeastern United States. Becker and others (1935) evaluated 11 species in palatability trials and found C. spectabilis to be toxic. Cattle did not

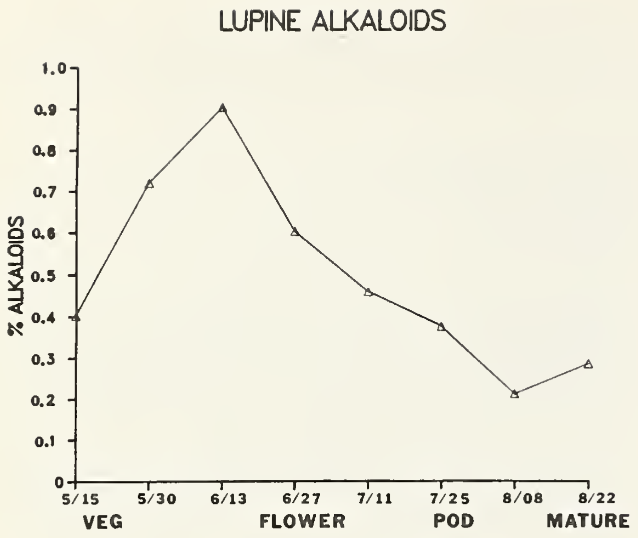

Figure 1.--Percentage of total alkaloids in the total aboveground plant parts of *Lupinus caudatus* through its natural phenological growth stages (Keeler and others 1976).

select *C. spectabilis* in common garden selection trials, and little was eaten as hay or silage when a choice was given. It ranked lowest in palatability. Furthermore, three steers died several weeks following trials in which they were force-fed *C. spectabilis*. Later investigators identified the toxin to be the pyrrolizidine alkaloid, monocrotaline, a hepatotoxin causing cronic liver damage. Animals die weeks to months following the initial insult to the liver (Kingsbury 1964).

Senecio

Senecio spp. also contain pyrrolizidine alkaloids that cause severe problems from hepatotoxicosis throughout the world. Tansy ragwort (*S. jacobaea*) causes severe problems in maritime regions of Australia, New Zealand, Great Britain, the Northwestern United States, and Canada. Threadleaf groundsel (*S. douglasii* ssp. *longilobus*) and Riddell's groundsel (*S. riddellii*) are common on ranges throughout the Southwest United States. The USDA Forest Service Range Plant Handbook (1937) states that *Senecio* species are seldom grazed except on depleted or over-stocked range. Tansy ragwort is considered quite unpalatable, and cases of poisoning in cattle and horses occur from accidental ingestion while the plant is in the rosette stage and intermixed in low-growing pasture (Muth 1968; Hepworth and Guelette 1979). Threadleaf groundsel is eaten by cattle only when snow covers desirable vegetation or during dry periods (Jones and others 1982). Total pyrrolizidine alkaloid contents for the three species are quite high: Riddell's groundsel 6.4 percent, threadleaf groundsel 2.19 percent, and tansy ragwort 0.2 percent (Johnson and others 1985).

ALKALOIDS THAT DO NOT DETER GRAZING

We have presented some experimental data and several observations of the adverse influence toxic alkaloids have on acceptability of forage species. We now turn to two poisonous plants high in alkaloids, but also palatable to livestock.

Larkspur

The tall larkspurs, duncecap larkspur (*Delphinium occidentale*) and Barbey larkspur (*D. barbeyi*) are responsible for more cattle deaths on mountain ranges in the Western United States than any other plant (Cronin and Nielsen 1981). On the Manti cattle allotment in central Utah, where accurate records were kept from 1956-1970, average annual cow loss was 4.3 percent; a total of 540 cows lost in a 15-year period (Cronin and Nielson 1979). Tall larkspur is palatable to both cattle and sheep. However, sheep tolerate four times more larkspur than cattle (Olsen 1978), and the larkspurs in the tall forb vegetative communities on high mountain ranges are considered good sheep forage.

The larkspurs contain several monobasic diterpenoid alkaloids. They present a paradox in that they are really quite high in total alkaloids, yet are readily selected. Figure 2 illustrates the TAC in the plant parts of *D. occidentale* as the plant matures. Observations of cattle grazing the two species indicate that the flowering raceme and immature seed pods are the preferred parts of the plant. Cattle appear to relish the developing seed pods (Knowles 1974; Cronin and Nielsen 1979). These selection patterns correspond to relatively high levels of TAC in the flowering racemes and seed pods.

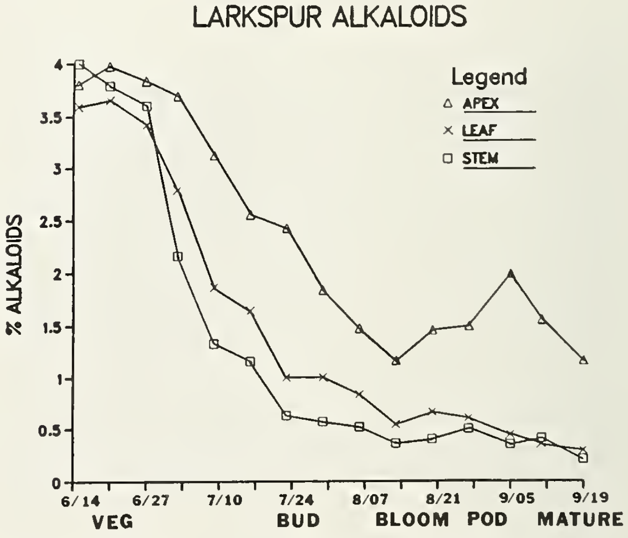

Figure 2.--Percentage of total alkaloids in separate plant parts of *Delphinium occidentale* through its natural phenological growth stages (Kreps 1969).

Williams and Cronin (1963) reported that total alkaloid content in Barbey larkspur increased by 50 and 100 percent following application of 2,4,5-T and Silvex, respectively. In spite of this large increase in TAC, utilization of sprayed plants by cattle increased (Cronin and Nielsen 1972). The plants became more toxic and more palatable, resulting in additional losses. It appears that other palatability factors override the high alkaloid content in tall larkspur.

Locoweed

There are many species of locoweed from the Astragalus and Oxytropis genera throughout the Western United States. The indolizidine alkaloid, swainsonine, has been identified and implicated as the cause of chronic neurological damage associated with loco poisoning (Molyneux and James 1982). In early studies on loco poisoning, Marsh (1909) observed palatability differences between white locoweed (silky crazyweed; O. sericea Nutt.) and wooly locoweed (A. mollissimus Torr.). White locoweed was fairly palatable and selected even when grass was abundant, while wooly locoweed was totally rejected when a choice was offered. However, both species appeared equally toxic.

Because of the apparent palatability of white locoweed, grazing trials were conducted to determine how much of the plant cattle consume under natural grazing conditions, which plant parts are selected, and under what environmental and management conditions cattle consume the plant. We found that the reproductive heads were highly preferred (Ralphs and others 1986) and readily consumed even when grass was abundant. Intensive grazing trials, designed to separate the effects of increasing grazing pressure from phenological growth stage of the plant, revealed that steers selected only the immature succulent pods. When other forage was depleted, they began to consume some of the flowers, but no leaves were consumed during the trials even though other forage was depleted (Ralphs, in review). We concluded that the immature succulent pods were the only palatable part of the loco plant.

Technology to quantify swainsonine has not been developed, but the relative concentration, as determined by the intensity of color in the dots on thin-layer chromatography, shows that leaves contain low amounts throughout the season (table 1). Swainsonine content is high in the flower, drops slightly in the immature seed pod, and rises as seeds ripen in the mature pod. It is interesting to note the relationship between swainsonine concentration and nutrient content of loco leaves and heads. Loco leaves are consistently low in swainsonine, but very little leaf is consumed. Loco heads are higher in swainsonine, but also higher in crude protein. Perhaps the higher protein content of the immature pods, other associated nutrients, or palatability factors override the high alkaloid content in cattle preference of pods over leaves.

Table 1.--Relative magnitude of alkaloid concentration and nutrients (percent of dry weight) in white locoweed (Ralphs and others 1986)

		Bloom	Immature pod		Mature pod
	Loco	Week of grazing season			
Nutrient	part	0	2	4	7
Alkaloid	Head	high[1]	moderate	moderate	high
	Leaf	low	low	low	low
Crude Protein	Head	17.3	17.3	17.4	16.4
	Leaf	12.9	12.1	11.8	11.1
Fiber (NDF)	Head	26	38	41	40
	Leaf	32	36	36	36
Water (succulence)	Head	65	60	57	43
	Leaf	69	65	65	51

[1] Relative concentration of the alkaloid swainsonine as determined by intensity of color in dots on thin layer chromatography.

CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

We agree with Robinson (1979) that alkaloids in plants are not universal repellents to herbivory. In some poisonous plants, the presence or high concentration of alkaloids has been shown to deter livestock grazing. For these particular species, poisoning problems result mainly from management mistakes. Hungry animals are confined to areas with high concentrations of the poisonous plant, or other palatable forage is scarce. By knowing the poisonous plants on the range and knowing under what conditions livestock are likely to consume them, a manager can generally avoid serious loss.

Other poisonous plants high in alkaloids are also palatable. Other palatability factors appear to override high alkaloid levels. Further research is necessary to identify these factors and determine their influence on palatability. Further information is also needed on grazing behavior to identify the stages of growth when species are palatable, the amount of the plant an animal must consume to become intoxicated, and the environmental and management conditions under which poisoning is likely to occur. Managing livestock to avoid these conditions may significantly reduce losses. Perhaps aversive conditioning of livestock to avoid these palatable poisonous plants, as described by Provenza and Balph in this proceedings, may be effective in reducing losses. Selective herbicide control may be required to reduce the concentration of specific poisonous plants if livestock loss is sufficiently high to justify the cost.

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PHYTOCHEMICAL CONSTITUENTS IN A SONORAN DESERT PLANT COMMUNITY

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and Philip W. Rundel

ABSTRACT: A Sonoran Desert wash woodland plant community at the Philip Boyd Desert Research Center was examined for the distribution of six phytochemical classes. No survey chemical class was represented in more than 7 of the 23 species analyzed. No plant contained more than 3 classes.

INTRODUCTION

The growth and reproduction of plants in an arid desert environment is constrained by a number of environmental factors, primarily the lack of water and nitrogen (Fisher and Turner 1978). Loss of biomass to herbivores represents an additional environmental constraint on these plants. Leaf tissue loss has been proposed as a major barrier to be overcome in such resource limited environments (Janzen 1974) due to the difficulty in replacing lost resources, specifically nitrogen. Phytochemicals have been proposed as one mechanism used by plants to reduce or prevent such losses (Rosenthal and Janzen 1979).

As part of our continuing study of the environmental and biotic parameters of plant growth for a Sonoran Desert wash woodland community, we initiated a survey of six phytochemical classes. Twenty-three species in this community were selected for the survey (table 1). Leaf tissue and stem tissue for the stem photosynthetic plants were analyzed for the presence or absence of the six classes. The survey classes were grouped into nitrogen- and carbon-based defenses. The two nitrogen-based classes were alkaloids and cyanogenic glycosides. The four carbon-based classes were phenolic acids, tannins, saponins, and cardiac glycosides.

METHODS

Phytochemical Analysis

All plant material was collected in a 2-day period at the University of California's Philip L. Boyd Deep Canyon Desert Research Center, Palm Desert, CA. Chemical class analyses were performed on fully mature leaves of all species except Phorodendron (stems, as an aphyllous parasite) and the two stem-photosynthetic plants, Dalea (stems only) and Cercidium (leaves and stems).

Cyanogenic glycosides were measured by macerating fresh plant material in the presence of a Feiger-Angle detection strip. Alkaloid presence was determined by testing acidic hot water extracts of fresh plant material with four reagents (Marne's, Mayer's, Wagner's, and Dragendorf's) (Farnsworth 1966; Wisdom and Smiley 1985). Saponins were assayed by shaking fresh leaf material in deionized water for more than 30 minutes to check for significant foam formation (>2.0 cm). For the remaining three chemical classes, about 1 g of fresh plant material was placed in 30 mL of 80 percent aqueous methanol within 4 hours of collection. After overnight extraction, each sample was filtered for further testing. Ten mL of this extract was evaporated to dryness and resuspended in 20 mL of hot deionized water. Half of this suspension was tested with ferric chloride solution for phenol presence and the other half tested for protein precipitating ability (Wisdom and Smiley 1985). Cardiac glycosides were measured by the application of 80 percent aqueous methanol to filter paper, drying, and spraying the filter paper with 2 percent 2,4-dinitrobenzoic acid solution (Farnsworth 1966).

Phenolic acid presence was determined by a High Performance Liquid Chromatograph (HPLC) system capable of detecting 13 separate acids. Separation of the phenolic acids was performed using a Beckman HPLC (a 421 gradient controller, two 110A pumps, a 504 autosampler, and a Hewlett-Packard 3390A integrator). Solvent A was 100 percent water and solvent B was 100 percent methanol. The flow rate was 2 mL/min for the entire program. The gradient system started with 5 percent solvent B at 0 minutes, ramping linearly to 7 percent, starting at 2 minutes and finishing at 6 minutes. At 12 minutes, the gradient ramped linearly to 25 percent solvent B, ending at 25 minutes. At 30 minutes, the gradient ramped to 100 percent ending at 32 minutes. The gradient stayed isocratic at 100 percent until 36 minutes, the end of the program.

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Table 1.--Plant species and growth forms surveyed for the six natural product classes

Plant species	Family	Growth form	Common name
Acacia greggii	Fabaceae	Tree	Gregg Catclaw
Cercidium floridum	Fabaceae	Tree	Blue Paloverde
Chilopsis linearis	Bignoniaceae	Tree	Desert-willow
Dalea schottii	Fabaceae	Tree	Indigo bush
Dalea spinosa	Fabaceae	Tree	Smoke tree
Fouquieria splendens	Fouqueriaceae	Tree	Ocotillo
Hyptis emoryi	Lamiaceae	Tree	Desert lavender
Larrea tridentata	Zygophyllaceae	Tree	Creosote bush
Tamarix aphylla	Tamaricaceae	Tree	Tamarisk
Agave deserti	Agavaceae	Shrub	Century plant
Ambrosia psilostachya	Ateraceae	Shrub	Rag weed
Bebbia juncea	Asteraceae	Shrub	Sweet bush
Beloperone californica	Acanthaceae	Shrub	Chuparosa
Datura discolor	Solanaceae	Shrub	Jimson weed
Hymenoclea salsola	Asteraceae	Shrub	Cheese weed
Krameria grayi	Krameriaceae	Shrub	Krameria
Petalonyx thurberi	Loasaceae	Shrub	Sandpaper plant
Prunus fremontii	Rosaceae	Shrub	Desert apricot
Simmondsia chinensis	Buxaceae	Shrub	Jojoba
Phoradendron californicum	Loranthaceae	Parasite	Mistletoe
Brandegia bigelovii	Cucurbitaceae	Vine	Brandegia
Cucurbita palmata	Cucurbitaceae	Vine	Gourd
Euphorbia micromera	Euphorbiaceae	Herb	Sandmat

RESULTS

Table 2 shows the results of the screening of the 23 plant species for the first 5 chemical classes. A presence/absence (+/-) scoring for cyanogenic glycosides indicated a very weak reaction that developed over a 24 hour period. The +/- reaction for the tannin score resulted from a positive phenol test, but a negative score for protein precipitating ability. No plants yielded a positive score for cardiac glycosides.

Seven of the 13 phenolic acids assayed were detected (table 3). Not present in any of the assayed plants were coumaric, dimethoxybenzoic, gentisic, ferulic, proto-catechuic, syringic, or vanillic acids. Cinnamic acid was the most common phenolic acid found in the surveyed species.

DISCUSSION

Previous chemical class surveys have been confined primarily to a single class among several different communities (Web 1949; Smolenski and others 1972). Other surveys have broadened the number of chemical classes and have included other attributes, such as fiber, but have restricted the surveyed plant species to host choice of a particular herbivore (Janzen and Waterman 1984). Our chemical class study, in contrast, focused on a group of chemical classes from a particular community of plants as part of our efforts to understand the biological and environmental impacts on the community.

Of the plant species assessed in our survey, none contained cardiac glycosides (table 2). Additionally, no one class of compounds in table 2 was represented in more than 30 percent of the surveyed species. After the phenolic acids, tannins and cyanogenic glycosides had the widest representation, while alkaloids were represented in only a few species (table 2). No species contained more than 3 classes; when present, were always tannins, cyanogenic glycosides, and phenolic acids (tables 2 and 3). Finally, of the 6 classes assayed, only phenolic acids were detected in *Tamarix aphylla*, *Ambrosia psilostachya*, *Petalonyx thurberi*, *Cucurbita palmata* and *Brandegia bigelovii*.

Phenolic acids were much more widely represented than any of the other classes (table 3). Cinnamic acid was the dominant phenolic acid present, occurring in over 60 percent of the species surveyed. Salicyclic and benzoic acids were the next most common acids (30 and 22 percent), followed by gallic, caffeic, proto-catechinic and p-hydroxybenzoic acids (all less than 15 percent). *Dalea spinosa*, *Belaperone californica*, and *Agave deserti* had no detectable simple phenolic acids present in leaf tissue (table 3).

Table 2.--Results of the presence/absence (+/-) tests for five chemical classes. Species are in the same order as in table 1

Plant species	Cyanogenic glycosides	Alkaloids	Tannins	Saponins	Cardiac Glycosides
Acacia greggii	+	-	+	-	-
Cercidium floridum	+/-	+	-	-	-
Chilopsis linearis	++	-	-	-	-
Dalea schottii	+/-	-	-	-	-
Dalea spinosa	+/-	-	-	-	-
Fouquieria splendens	+/-	-	+	-	-
Hyptis emoryi	+	-	+/-	-	-
Larrea tridentata	-	-	+	-	-
Tamarix aphylla	-	-	-	-	-
Agave deserti	-	-	-	+	-
Ambrosia psilostachya	-	-	-	-	-
Bebbia juncea	+/-	-	-	-	-
Beloperone californica	+/-	-	-	-	-
Datura discolor	+/-	+	-	-	-
Hymenoclea salsola	+	-	-	-	-
Krameria grayi	+	-	+	-	-
Petalonyx thurberi	-	-	-	-	-
Prunus fremontii	+	-	+	-	-
Simmondsia chinensis	+	-	-	-	-
Phoradendron californicum	+/-	-	+	-	-
Brandegia bigelovii	-	-	-	-	-
Cucurbita palmata	-	-	-	-	-
Euphorbia micromera	+/-	-	+	-	-

Table 3.--Distribution of the individual phenolic acids among the species surveyed. Species are in the same order as in table 1

Plant species	p-Hydroxy benzoic	Cinnamic	Gallic	Salicyclic	Caffeic	Benzoic	p-Catechuic
A. greggii		+		+	+		
C. florida		+					
C. Linearis		+				+	+
D. schottii		+					
D. spinosa							
F. splendens				+			
H. emoryi		+					+
L. tridentata	+	+		+	+		
T. aphylla				+			
A. deserti							
A. psilostachya		+					
B. juncea		+				+	
B. californica							
D. discolor			+			+	
H. salsola						+	
K. grayi		+		+			
P. thurberi		+		+		+	
S. chinensis			+				
P. fremontii				+			
P. californicum		+					
B. bigelovii		+	+				
C. palmata		+					
E. micromera		+					

Table 4.--Phytochemical classes not included in the survey, known or suspected in examined plants

Plant species	Additional known or potential classes
Ambrosia psilostachya	Sesquiterpene lactones
Bebbia juncea	Terpenes[1]
Cucurbita palmata	Cucurbitacins[1]
Euphorbia micromera	Latex
Hymenoclea salsola	External flavonoid resins
Hyptis emoryi	Mono- and di-terpenes
Larrea tridentata	External leaf phenolic and lignin resins
Tamarix aphylla	Salt secreting glands

[1] Suspected.

While some plants in our survey contained none of the assayed classes, other defense compounds are known or suspected to be present in some of the survey species include lignin, terpene and flavonoid resins, sesquiterpene lactones, cucurbitacins, and latex (table 4). Additional defenses against herbivory appear to be ephemerality of resources (deciduous, permitting only seasonal use) and structural defenses (spines, leaf toughness, and fiber).

This desert washland community appears to be dominated by carbon-based defenses, particularly phenols and terpenes. Such a chemical profile has been described for other nitrogen-limited communities (Janzen 1974; McKey and others 1978). In light of this, a surprising number of species appear to have a limited ability to produce cyanide. This part of our investigation clearly should be reconfirmed. In future studies we plan to study the influence of nitrogen and water on phytochemical class distributions and amounts and how herbivores respond to these plant changes.

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JACKRABBIT-SHRUB INTERACTIONS IN THE MOJAVE DESERT

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ABSTRACT: Jackrabbits in the Mojave Desert have been shown to be severely water stressed during dry weather. I postulate that, rather than being absolutely dependent on drinking water, they utilize vegetation growing on the more mesophytic microhabitats. Season, local soil moisture reserves, and local soil fertility were significant variables determining jackrabbit utilization of desert shrubs. With few exceptions, plant species appeared to be of less significance to browsing preference than moisture and nutrient levels.

INTRODUCTION

Jackrabbits (Lepus californicus) are the largest herbivorous mammals in the Mojave Desert. Larger herbivores, such as burros, horses, deer, and mountain sheep are restricted to higher altitudes and wetter habitats. Smaller rodents are abundant and diverse (O'Farrell and Emery 1976), and they are adapted to survive on seeds and metabolic water, though some aestivate during summer. Jackrabbits alone are conspicuously dependent on plants for sustenance during the summer-fall-winter dry seasons.

Zoologists and ecologists working on jackrabbits in the Mojave have been concerned with their energy, water, and salt balances (Nagy and others 1976), and their food intake (Hayden 1966b). Botanists have worked primarily on jackrabbit interactions with creosotebush (Larrea tridentata (DC.) Cov.)(Boyd 1983; Steinberg and Whitford 1983).

Data from Nagy and others (1976) suggest that jackrabbits cannot survive more than 1 or 2 weeks without drinking water during dry weather. These data conflict with field observations of rabbits far from water sources weeks after rainfall. However, resolution of this conflict can be based on knowledge of the microhabitats utilized by jackrabbits. The water balance studies of Nagy and others (1976) were done with jackrabbits penned in average Mojave Desert conditions, but I propose free animals escape those conditions by consuming vegetation growing on more mesic and fertile microhabitats.

STUDY AREA AND METHODS

All sites observed were of Mojave Desert vegetation located either on the Nevada Test Site 115 km northwest of Las Vegas, NV or near Daggett, CA. Altitudes ranged from 600 to 1,100 m and rainfall averaged 100-200 mm per year.

Species studied were all native perennials occurring naturally in the areas studied, with the exception of Salsola paulsenii Litv., an introduced summer annual. Transplants of Atriplex Canescens (Pursh) Nutt., A. confertifolia (Torr. & Frem.) Wats., A. hymenelytra (Torr.) Wats., A. polycarpa (Torr.) Wats., Ceratoides lanata (Pursh) Howell, Chrysothamnus viscidiflorus (Hook.) Nutt., Datura innoxia P. Mill., Hymenoclea salsola T. & G., Larrea tridentata, Lepidium fremontii Wats., Menodora spinescens Gray, and Oryzopsis hymenoides (R. & S.) Ricker were grown in a glasshouse from locally collected seed. Specimens of Atriplex canescens, A. confertifolia and Chrysothamnus nauseosus (Pallas) Britt. were obtained from Native Plants Incorporated, Salt Lake City, UT. Many other naturally occurring species have been observed, but in either small numbers, few locations, or with ambiguities in determination of browsing animal species.

Browsing estimates were routinely made by imagining a complete symmetric canopy and subjectively estimating the missing volume as a percentage. Comparison of these estimates to dimensional measurements before and after browsing showed the errors were frequently large, but for estimates of >50 percent loss the averages were accurate. Estimates of loss ≤50 percent averaged 10 percent less than measured losses. Jackrabbit pellet densities were determined by counting pellets in randomly placed 1-m quadrats.

Soil water potentials were determined with thermocouple psychrometers and a dewpoint microvoltmeter. Soil saturation extracts were analyzed with standard techniques (Black and others 1965). Stem water content was determined on sections sealed in scintillation vials immediately after cutting; they were then dried to constant weight over silica gel.

Observations were made in conjunction with research on revegetation of Mojave Desert disturbed areas. Jackrabbits became the major obstacle to restoration of vegetation, and an understanding of their browsing behavior was necessary to efficiently proceed in those efforts.

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OBSERVATIONS AND DISCUSSION

In the Mojave Desert, jackrabbit behavior is very similar to that seen in other regions (Hayden 1966a, 1966b; Nagy and others 1976; Shoemaker and others 1976). Long-term population fluctuations have not been measured, but frequencies of field sightings and road kills are quite variable. Annual plants are the preferred foods (Hayden 1966b); shrubs are significantly browsed only in dry seasons. Even in dry weather, the one major summer annual, *Salsola paulseni*, which is largely restricted to roadsides and disturbed areas, appears to be a major food resource. Thus, on one study site, *S. paulsenii* accounted for 24 of 27 kg/ha of plant material removed (table 1). In spring-time at this same site, pellet densities correlated significantly with annual plant densities (r = +0.60, p<0.01), but not significantly with shrub densities (r = -0.26).

Table 1.-Estimated jackrabbit browsing on desert plants at Daggett, CA, October 1978

Species	Percent of plants browsed	Percent removed	
		Avg	Median
Ambrosia dumosa	8	8±3	5
Atriplex polycarpa	3	6±2	3
Larrea tridentata	9	18±11	3
Salsola paulsenii	91	21±2	20

Spatial Distribution of Jackrabbit Feeding

The term "desert" is a useful but very broad generalization, and it is necessary to keep in mind that desert resources are spatially variable. There are springs, high altitude woodlands, runoff channels, roadsides, and disturbed areas. Beatley (1976) listed 51 plant species largely restricted to arroyos and disturbed sites. Variability in water resources allows both plant species and jackrabbits to escape from "average" conditions to locations of higher water content. I have evidence that demonstrates higher soil water content, higher plant water content, and enhanced vegetation utilization by jackrabbits for individual disturbed areas.

At one borrow pit study site the rapid growth of shrub seedlings (11 times as fast as control area plants) led me to check soil water status. Soil psychrometers placed on the denuded area showed high water potentials throughout the summer of 1979, while those placed in vegetation 20 m away dried to <-30 bars at all depths (table 2). Soil samples taken in the control vegetation February 19, 1981, had 3.4±0.3 percent water by weight (<2.0 mm fraction), while samples from the borrow pit averaged 13.5±1.1 percent.

Stem water content in *Larrea tridentata* was measured in samples taken June 27, 1985. On the borrow pit, stems dried to constant weight over silica gel had 0.46±0.03 g H_2O/gdw±sem, while those from the control area averaged 0.30±0.03 g/gdw. Steinberger and Whitford (1983) noted a 90 percent increase in browsing incidence on *L. tridentata* when stem water content rose from 35.7 to 38.4 percent.

On this borrow pit jackrabbits appeared to be a major source of shrub seedling mortality. On June 23, 1978 only two of 240 (<1 percent) marked seedlings had been browsed, while 8 weeks later 152 (63 percent) had been attacked. My interpretation was that until late June rabbits ate annuals and plants growing on this site, but as natural areas dried out (table 2) they began to selectively browse plants growing on the wetter soils of the borrow pit.

At another site, where I followed survival of *Ambrosia dumosa* (Gray) Payne seedlings, I measured browsing damage to *Oryzopsis hymenoides* along a 100 m transect crossing a 43 m disturbed area. Figure 1 shows the marked discontinuity in grazing intensity coinciding with the edges of the disturbance. The rapid growth of *A. dumosa* seedlings on the disturbed section of the transect is evident in figure 2. Figure 3, a and b is a photographic record of the dramatic growth that occurred between January 1984 and June 1985. These differences in growth and browsing incidence can be explained largely on the basis of soil water content; the disturbance was a mere scraping of the surface, and didn't affect soil structure or fertility.

Figure 1 shows that environment can have a major effect on grazing incidence. Another example occurred in February 1981. We transplanted 134 small plants to a site consisting partly of the slope of a dike constructed of compacted subsoils around a waste disposal site and partly of an adjacent flat area whose surface was scraped to facilitate construction. Nine days after transplanting, jackrabbits had breached the fence surrounding the site and browsed many of the transplants. After repairing the fence the degree of damage to each plant was recorded. To our surprise, plants on the dike were less frequently browsed than those on the adjacent scraped area. Of 39 *A. canescens* plants on the dike, 16 (41 percent) were heavily browsed (>50 percent removed). Of 52 plants on the scraped area, 38 (73 percent) were browsed heavily (table 3). Incidence and degree of damage did not correlate with distance from the hole under the fence, nor with any other obvious spatial factor.

At this time (February) both soils were wet, and growth of annuals and shrubs was limited by temperature. Jackrabbits were obviously selecting plants for some reason other than water availability. In time, another factor became apparent. Growth of plants on the dike was much slower than growth of those on the scraped area (table 3). Psychrometers in the two locations showed higher summer water potentials on the dike (for example, -11 vs. -25 bars on July 29, 1983), contradicting the hypothesis that the dike was drier. Analysis of soil saturation extracts,

Table 2.-Soil water potentials (negative bars) during 1979-80 in a native shrub community and in an adjacent disturbed area without shrubs in Frenchman Flat, NV

		Depth of psychrometer placement									
		15 cm		45 cm		90 cm		110 cm		130 cm	
Date		Bare	Shrubs	Bare	Shrubs	Bare	Shrubs	Bare	Shrubs	Bare	Shrubs
Feb.	8	0	0	1	0	0	0	0	0	0	0
Feb.	16	0	0	0	0	0	0	0	0	0	0
Mar.	29	0	0	0	0	3	0	0	4	0	0
Apr.	12	0	0	0	0	1	0	0	3	0	2
May	7	0	6	1	0	1	2	0	3	0	7
June	1	0	30	2	4	1	0	3	4	1	8
June	7	0	46	0	8	2	4	0	6	2	7
June	14	0	>75	0	10	1	3	0	8	2	17
June	21	0	>69	0	13	3	4	0	9	2	8
July	3	19	>75	1	18	2	5	3	12	0	16
July	9	27	>76	0	25	3	7	0	14	3	14
July	17	>76	>76	0	28	2	12	0	17	3	16
July	25	2	31	0	31	3	20	0	20	0	24
July	31	3	29	1	30	2	24	0	22	1	24
Aug.	7	9	17	0	32	2	28	0	25	3	26
Aug.	14	4	22	0	31	0	28	0	25	1	26
Aug.	21	0	32	0	36	0	31	0	27	2	26
Aug.	28	4	36	0	34	3	31	0	28	2	26
Sept.	4	5	48	0	39	0	33	0	28	2	28
Sept.	11	10	>69	0	38	0	34	0	32	0	--
Sept.	18	30	>73	0	39	2	35	0	32	0	25
Sept.	25	30	>71	0	40	1	35	0	33	0	28
Oct.	9	22	>71	0	40	1	37	0	34	1	30
Oct.	23	14	>64	0	42	2	37	0	33	0	--
Oct.	30	12	--	1	41	0	36	0	34	1	33
Nov.	13	9	--	0	48	2	43	0	35	0	32
Nov.	27	9	>60	0	>59	3	46	0	36	0	32
Dec.	13	7	>59	0	>53	1	42	0	33	0	22
Jan.	8	3	>52	0	>56	0	>52	0	34	0	30
Jan.	22	0	0	0	19	2	>52	0	30	0	16
Feb.	4	0	4	0	0	2	34	0	22	4	15
Feb.	26	0	0	0	--	1	36	0	22	0	15
Mar.	10	0	0	0	0	2	26	0	18	0	13

Table 3.-Size increases (percent) between July 1981 and July 1982, of *Atriplex canescens* transplanted on a dike and adjacent scraped area following jackrabbit browsing in February 1981

	Scraped			Dike		
Percent browsed	N	Survivors	Percent increase	N	Survivors	Percent increase
>90	25	10	4,388	15	2	3,848
50-90	13	10	3,345	1	1	669
<50	2	2	8,563	1	1	332
0	12	11	1,159	22	22	356

however, showed the dike soils to have an EC_{25} of 2.9±1.0 (sem) compared to 1.0±0.4 mMho/cm on the scraped area. Sodium contents were 454±48 and 171±77 mg/L, respectively. Thus, salt content, soil compaction, and undoubtedly several other fertility factors differed in the two soils.

The more fertile soil had higher browsing incidence ($p<0.01$, X^2), lower mortality following severe browsing ($p<0.10$), and more rapid plant growth (table 3). On both soils, plants that survived browsing grew faster than unbrowsed plants. The simplest explanation for all these observations is that jackrabbits preferentially browsed plants in more fertile soil. Thus, by this hypothesis, plants on the scraped area were more palatable, but because of the better fertility they recovered more easily. An alternative idea, that browsing might stimulate "compensatory" growth, can explain the more rapid growth after browsing, but not the differential browsing incidence and mortality, and is thus a less satisfactory hypothesis.

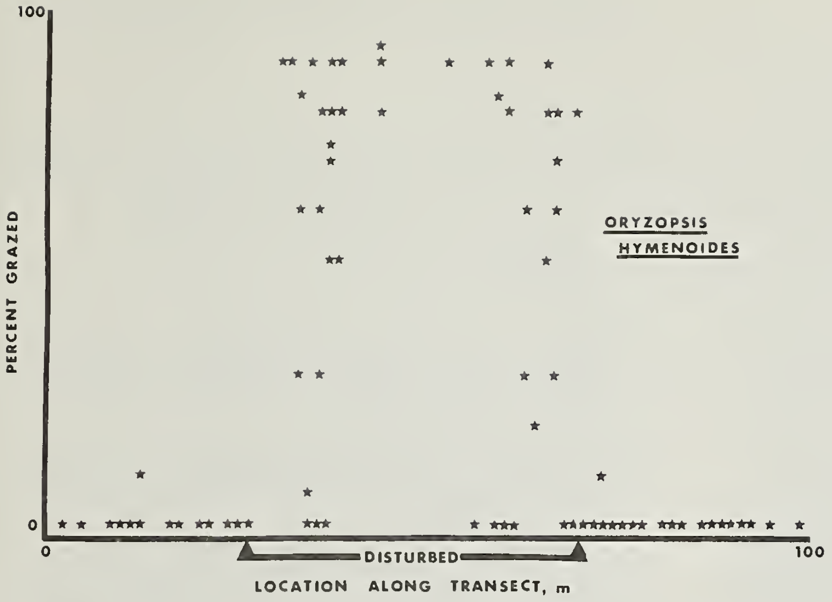

Figure 1.--Grazing incidence and severity along a 100m transect crossing a 42m wide scraped area. January 1984.

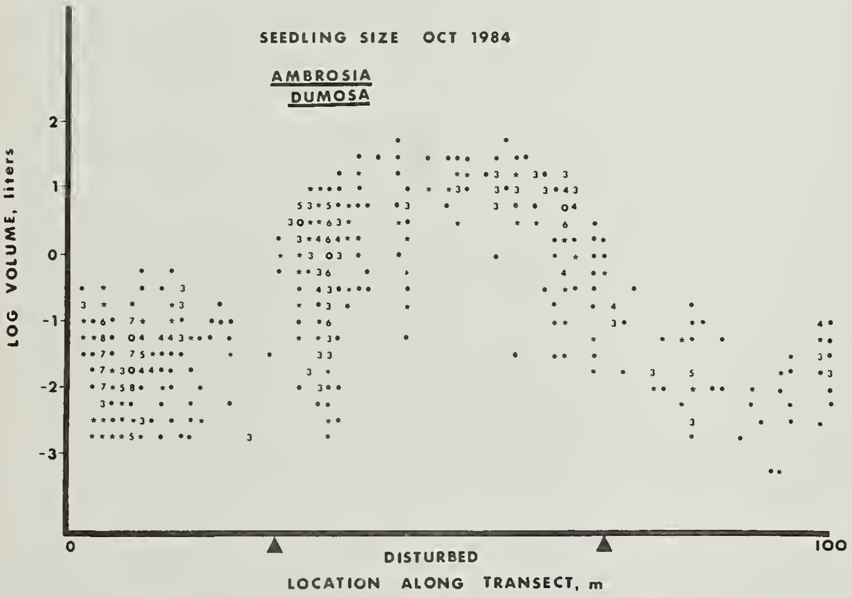

Figure 2.--Sizes of seedlings of Ambrosia dumosa, 14 months after germination, along the transect of figure 1. Growth was much faster on the disturbed and heavily grazed section.

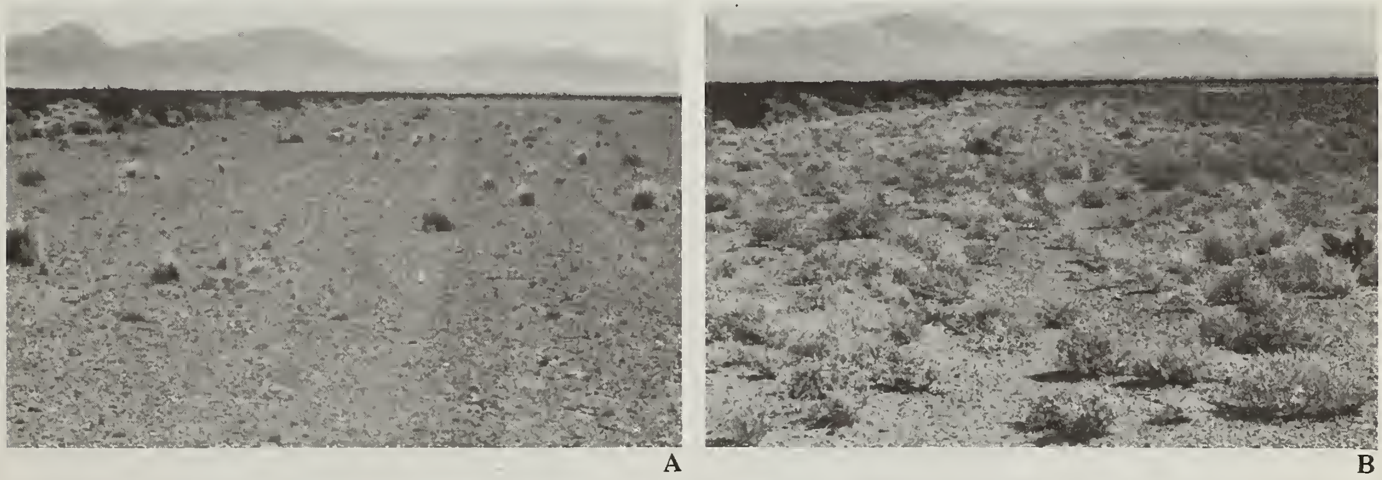

Figure 3.--The scraped area of figures 1 and 2 in A January 1984, and B June 1985, demonstrating the rapid growth of A. dumosa seedlings on the site.

Species Composition of Jackrabbit Diets

One currently favored hypothesis to explain the ubiquity and diversity of "secondary" metabolites" (tannins, alkaloids, nonessential amino aids, etc.) in plants is that they act as feeding deterrents (Harborne 1982). A consequence of that hypothesis is that, where browsing significantly affects a plant community, common species should be unpalatable, and palatable ones rare. Our evidence, however, implied that jackrabbits non-selectively browsed the common species; they avoided only a few rare ones. On the dike, for example, Atriplex canescens (common) was normally reduced to a stub, and Stanleya pinnata (rare) normally suffered only a few bites from a leaf (table 4).

Table 4.-Transplants browsed February 10-19, 1981, by species

Species (N)	Percent not browsed	Percent browsed <50%	Percent browsed <90%	Percent browsed >90%
Atriplex canescens (91)	37	4	15	44
Stanleya pinnata (21)	48	48	4	0
Ambrosia dumosa (7)	57	29	0	14
Others (15)	53	14	6	27

I have transplanted shrubs to quite a number of disturbed sites. The only species I can confidently plant without protection from jackrabbits are Stanleya pinnata, Lepidium fremontii, and Datura innoxia. All three of these species are rare in mature vegetation, though they are more common in washes and disturbed areas. Species that must be fenced to prevent loss include Atriplex confertifolia, A. canescens, A. hymenelytra, A. polycarpa, Ambrosia dumosa, Ceratoides lanata, Chrysothamnus nauseosus, C. viscidiflorus, Hymenoclea salsola, Menodora spinescens, Larrea tridentata, and Oryzopsis hymenoides. These species are all relatively common.

I conclude that species biochemistry evidently holds little importance in jackrabbit-shrub interactions in the Mojave Desert, but soil fertility and moisture content are quite significant. Selection of wetter and more fertile habitats can mitigate, if not obviate, water and calorie stresses in desert jackrabbits in dry seasons. They can then repopulate larger areas in favorable times. Corollaries of these observations are that jackrabbit behavior patterns in mesic areas are also suitable in deserts, and man's disturbance of desert vegetation may significantly increase habitat suitable to jackrabbit survival.

ACKNOWLEDGMENT

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CHEMICAL COMPONENTS OF *CHRYSOTHAMNUS NAUSEOSUS*:

A PRELIMINARY EVALUATION

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ABSTRACT: *Chrysothamnus nauseosus* has a number of subspecies adapted to a wide range of wildland semiarid conditions and can grow from sea level to almost 10,000 ft. They grow on productive as well as saline soils. The species has value in revegetation, as food for wildlife and livestock, for landscaping urban areas, and as a potential source of natural rubber. Gas chromatographic mass spectrometry analysis of the cyclohexane, chloroform, and methanol extracts of *C. nauseosus* indicated a large range of chemical compounds. Using an MS spectra library search, 70 compounds were identified, many of which may be sources of natural insecticides and fungicides. The significance of these compounds in herbivory has not been determined.

INTRODUCTION

Rabbitbrush (*Chrysothamnus*) is a dominant shrub in the western semidesert landscape (McArthur 1984). There are 16 species in the genus *Chrysothamnus* according to Anderson (1986a, 1986b). Three of the *Chrysothamnus* species are very large groups and form species complexes consisting of a number of subspecies. One of these species complexes is *C. nauseosus* (rubber rabbitbrush), which occurs in various subspecfic forms from the Sonoran to the subalpine life zones and grows from Canada to Mexico and from the Great Plains to the Pacific Ocean. *Chrysothamnus nauseosus* is a vigorous pioneer plant on disturbed sites such as road sides. It is a shrub that ranges normally from about 12 to 90 inches in height, although populations of rubber rabbitbrush reaching heights of 10 to 12 ft have been observed. The growth pattern of this plant involves erect stems arising from the base, each stem having moderately flexible leaflet branches (McArthur and others 1979; McMinn 1980). In 1923, Hall and Clements (1923) recognized 20 subspecies of *C. nauseosus*. Some 50 years later, Anderson (1986a, 1986b) recognized 22 subspecies of *C. nauseosus*, many of them different from those first recognized by Hall and Clements. The plant grows in the semidesert regions and produces numerous seeds.

Because of the large amount of reproductive structures that are produced, the plant must be effective in its energy production. *Chrysothamnus nauseosus* exhibits high rates of net photosynthesis (P_n) compared with other woody C_3 photosynthetic pathway species (Davis and others 1985). On both a leaf-area and dry-weight basis, the P_n rate of *C. nauseosus* is similar to those of the C_4 photosynthetic pathway desert shrubs such as *Atriplex canescens*. The RuBP and intracellular CO_2 content of rubber rabbitbrush is similar to those found in C_3 photosynthetic pathway crop species (Davis and others 1985). Another interesting property of its photosynthesizing physiology is that the P_n of *C. nauseosus* is not light saturated at levels equivalent to full sunlight. This may be due to the tomentose vestiture on the leaf's surface that probably shades the chloroplast. In many cases, desert plants possess pubescence as an adaptive means of reducing light absorption. This usually results in a reduced heat load and lower leaf temperature (Ehleringer and Bjorkman 1978). The main effect, however, is that rubber rabbitbrush is capable of maintaining high P_n's and stomatal conductants in nonstress periods. Thus, it is able to produce dry matter at high rates per unit of biomass.

Chrysothamnus nauseosus is cold-hardy and can tolerate temperature to -40 °F. It has also been utilized extensively as a revegetation crop (McArthur and others 1979; Hanks and others 1975) because of its ability to grow on disturbed soil and its browse value to livestock and wildlife.

Chrysothamnus nauseosus also attracts interest because it contains natural rubber (Hall and Goodspeed 1919; Ostler and others 1986). The natural rubber was first of interest during World War I when rubber became an important component of the mechanized world. Hall and Goodspeed (1919) published a rather extensive study indicating that over 3 million pounds of rubber were present in the native population of *C. nauseosus* in the Western United States. Efforts were made during World War I to produce *C. nauseosus* in the arid west for rubber production. The war ended before commercialization occurred, and interest then dropped. Again during World War II, there was interest in obtaining rubber from both guayule (*Parthenium argentatum*) and *C. nauseosus*. After 4 years of work, considerable acreage was near

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commercial rubber production. However, when the war ended, research efforts stopped and plant acquisitions were discarded (Ostler and others 1986). Recently we investigated the rubber and resin content of subspecies of C. nauseosus and found plants with rubber content near 6 percent on a dry-weight basis and resin content up to 16 percent. Ostler and others (1985) obtained similar results in their evaluation of C. nauseosus and found plant populations with 5 percent rubber and 20 percent resin content. Buchannon and others (1978) evaluated desert plant species as potential hydrocarbon crops and found that C. nauseosus contained 11.5 percent hydrocarbons (dry-weight basis). They rated it as having excellent potential as a hydrocarbon crop.

In terms of herbivory and potential significance of the chemicals in the plant, only limited research has been performed. In terms of natural insecticides, Rose and others (1980) found polyacetylenes from C. nauseosus were antifeedants for the Colorado potato beetle. In addition, Maugh and others (1982) found that polyacetylenes from rabbitbrush stimulated plants to produce their own natural insect repellants. Bohlmann and others (1979a, 1979b) found six new labdane acids in C. nauseosus. These may have use as natural insecticides.

METHODS

We investigated more fully the chemical composition of C. nauseosus using gas chromatography and mass spectrometry (MS). The specific epithet, nauseous, refers to chemical odors of the plant; however, these smells are often pleasant rather than offensive. We selected the subspecies turbinatus because previous analyses determined that it was high in rubber (6 percent) and resin content (16 percent). Samples of C. nauseosus ssp. turbinatus were prepared by harvesting the plant, then grinding the pieces of the stem and leaves in a steel mortar and pestle at liquid nitrogen temperatures. This grinding action resulted in a fine powder that was stored at -20 °C until extracted. Next 20 g of the ground material was extracted first with cyclohexane (three times), then with chloroform (three times), and finally with methanol (three times). These three extracts were concentrated and the mixtures separated by capillary gas chromatography. The compounds in the mixtures were characterized by capillary gas chromatography mass spectrometry. Identification was then made by matching the MS spectra of the compounds analyzed with a library of 78,000 mass spectra (Hewlett-Packard 1985). In those cases in which no high correlation was obtained, the spectra were then analyzed further by the STIRS program (Cornell University), which determines chemical groups and the logical molecular weight of the compound. While many compounds were detected, only the major peaks were identified.

RESULTS AND DISCUSSION

The dominant compounds in the cyclohexane fraction were monoterpenes along with some more complex compounds such as napthalenes (table 1). The compounds present in the chloroform fraction are shown in table 2. The methanol fraction compounds are shown in table 3. The methanol fraction contained oxygenated polycyclic hydrocarbons such as methylated phenol. Structures of some of the compounds identified are shown in figure 1.

Rubber rabbitbrush is known to attract many insects (McArthur and others 1979; Haws and Bohart 1982). Haws and Bohart (1982), in looking at 18 taxa of range plants located at three outplanting sites in Utah and Wyoming, found an average 51.5 insects per taxon. Rabbitbrush, with 364 insect species, had more than three times as many associated insects as any other plant taxon. Most of the insects detected were beneficial rather than harmful to plant life (Haws 1982). It may be that the diversity of chemical compounds (tables 1-3) and rich insect fauna of rabbitbrush are related. Further research will be necessary to explore this possibility. While we conducted no assays for toxicity or inhibitory actions against insects, some monoterpenes (myrcene, alpha-pinene, delta-3-carene, alpha phellandrene) have been reported to be inhibitory to bark beetles (Rosenthal and Jansen 1979). In addition, high foliar levels of myrcene in Douglas-fir correlate negatively with female and male spruce budworm dry-weight production (Cates and Redak 1984; Cates and others 1983). The significance of those products we identified is not known at this time, but preliminary testing indicated that nematocidal activity is present in the extract of the hydrocarbon fraction as indicated by biological testing done in cooperation with the Ciba Geigy Company (Dumford, personal communication).

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Table 1.—–Compounds found in the cylcohexane fraction

Peak number	Name of compound	MW	CAS number	Correlation
A01	Cyclohexanol,3-ethenyl-3-methyl-2-(1-methylethenyl)*	222	35727458	
A02	Beta thujene	136	28634891	0.982
A03	Myrcene	136	123353	.971
A04	Beta bisabolol *	222	15352779	
A05	Nonacosane	408		
A06	C-28 branched chain hydrocarbon	394		
A07	Beta pinene	136	127913	.934
A08	Hentriacontane	436		
A09	C-30 branched chain hydrocarbon	422		
A10	Aristolen	204		.790
A11	Alpha pinene	136	80568	.979
A12	C-29 branched hydrocarbon	408		
A13	Bicyclo[2.2.1]hept-2-ene, 1,7,7-trimethyl-	136	464175	.964
A14	Beta elemene	204	515139	.890
A15	Phenanthrene, 9-methyl-	192	883205	.922
A16	Beta cadinene	204	523477	.987
A17	Alloaromadendrene	204	25246279	.989
A18	Beta caryophyllene	204	87445	.935
A19	Alpha copaene	204	3856255	.987
A20	Gamma cadinene	204	39029419	.995
A21	Alpha thujene	136	2867052	.982
A22	Beta phellandrene	136	555102	.986
A23	Alpha cubebene	204	17699148	.998
A24	Beta cubebene	204	17699148	.975
A25	Alpha gurjunene	204	489407	.995
A26	Alpha elemene	204	5951677	.941
A27	Gamma muurolene	204	30021740	.965
A28	Naphthalene, 1,2,3,4,6,8a-hexahydro-1-isopropyl-4,7-dimethyl-	204	16728997	.971

* Structure probably very similar to this compound. This was determined by a library search and further analyses by Stirs, a computer program to determine structure and probable molecular weight.

Table 2.—–Compounds found in the chloroform fraction

Peak number	Name of compound	MW	CAS number	Correlation
B01		204	483761	0.972
B02	Gamma cadinene	204	39029419	.974
B03	1,4-cyclohexadiene,3-ethenyl-1,2-dimethyl-	136	62338572	.951
B04	Alpha muurolene	204	31983229	.946
B05	Bicyclo[4,4,0]dec-1-en,2-isoproyl-5-methyl-9-methylene-	204		.670
B06	Gamma muurolene	204	30021740	.973
B07	Naphthalene,1,2,3,4,6,8a-hexahydro-1,isopropyl-4,7-dimethyl-	204	16728997	.989
B08	1,4,-cyclohexadiene, 3-ethenyl-1,2-dimethyl-	134	62338572	.959
B09	1-methoxy-4-chloro-naphthalene *	192		.580
B10	Nonacosane	408		
B11	Hentriacontane	436		
B12	C28 branched hydrocarbon	394	638368	
B13	C30 branched hydrocarbon	422		
B14	Beta patchoulene	204	514512	.640
B15	Beta pinene	136	127913	.985
B16	Menogene	136	586630	.980
B17	Delta-3-carene	136	13466789	.982
B18	Alpha cubebene	204	17699148	.977

* Structure probably very similar to this compound. This was determined by a library search and further analyses by Stirs, a computer program to determine structure and probable molecular weight.

Table 3.--Compounds found in the methanol fraction

Peak number	Name of compound	MW	CAS number	Correlation
C01	Dioctyl phthalate			0.972
C02	Beta Cadinene	204	523477	.985
C03	Oxacycloheptadec-8-en-2-one	252	123693	.950
C04	(E)-2,3-dimethyl-4-(2',6',6'-trimethyl-1,2'-epoxy clohex-1'-YL)-buta-1,3-diene *	220		.410
C05	Tetradecanonic acid,methyl ester(isomer)	242	124107	.986
C06	Alpha muurolene	204	31983229	.960
C07	Polycyclic hydrocarbon	236		
C08	Polycyclic hydrocarbon	304		
C09	Polycyclic hydrocarbon	264		
C10	Gamma cadinene	204	39029419	.490
C11	Polycyclic hydrocarbon	238		
C12	isomer of C14	235		
C13	Beta cadinene(isomer)	204	523477	.961
C14	1H-indene,2,3-dihydro-1,1,3-trimethlyl-3-phenyl- *	236	3910358	.610
C15	Benzeneacetic acid,4-nitro-,4-chlorophenyl ester	291	53218114	.931
C16	Benzene,1,1'-(1,4-dimethyl-1-butene-1,4-diyl)bis-	236	52161543	.936
C17	Polycyclic hydrocarbon	238		
C18	Alpha cubebene	204	17699148	.978
C19	3-cyclohexene-1-ethanol,.alpha.-ethenyl-.alpha.,3-di methyl-6-(1-methylethylidene)- *	220	55780933	.420
C20	similar to C19	220		
C21	Polycyclic hydrocarbon	304		
C22	1,2-benzenedicarboxylic acid, dibutyl ester	278	84742	.988
C23	Decanedioic acid, bis(2-ethylhexyl) ester *	426	122623	.640
C24	Phenol,2,6-bis(1,1-dimethylethyl)-4-methyl-	220	128370	.976
C25	Ethanol,2-[(3-methylphenyl)methoxy]-	166	54411119	.981
C26	silane,tetrafluoro-	104	7783611	.963
C27	Tetradecanonic acid,methyl ester(isomer)	242	124107	.987
C28	1-phenanthrenecarboxylic acid,1,2,3,4,4a,9,10,10a-octahydro-1,4a-dimethyl-7-(1-methylethyl)-,methyl ester,[1R-(1.alpha.,4a.beta.,10a.alpha.)]	314	1235741	.964
C29	4-octanone,2,3-epoxy-2-methyl-	156	17257839	.977
C30	isomer of C22	278		.988
C31	isomer of C22	278		.977

* Structure probably very similar to this compound. This was determined by a library search and further analyses by Stirs, a computer program to determine structure and probable molecular weight.

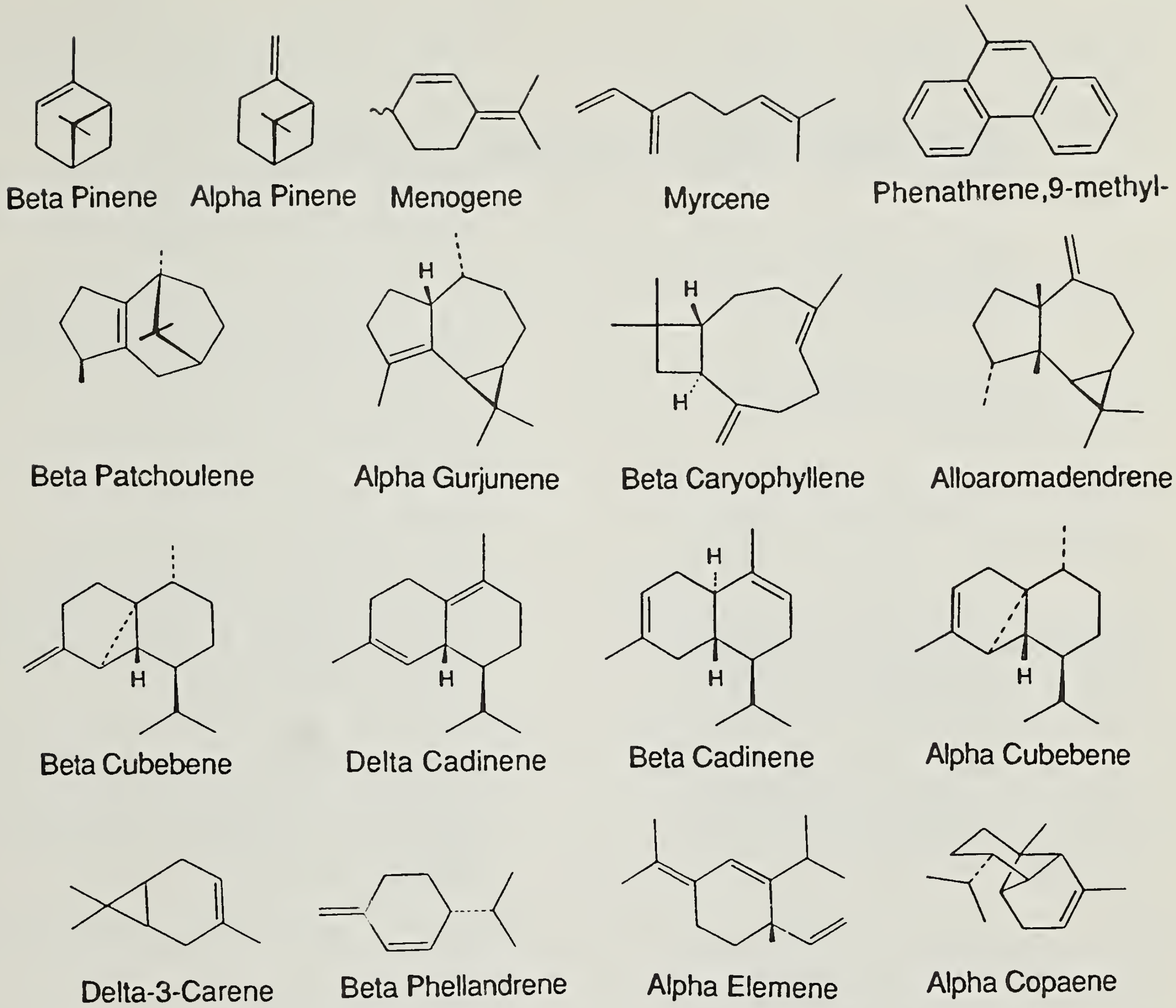

Figure 1.--Structures of some of the compounds identified in *Chrysothamnus nauseosus*.

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Section 3. Nutrition and Physiology

OVERVIEW OF POISONOUS PLANT-LIVESTOCK INTERACTION IN THE UNITED STATES

Lynn F. James and Michael H. Ralphs

ABSTRACT: Plants that are classified as poisonous are found in most range plant communities. These plants constitute a threat to the livestock grazing these areas. They also provide a challenge to management to devise strategies and procedures to prevent intoxication.

INTRODUCTION

The term "poisonous plant" infers an interaction between a plant containing a toxin and an animal. The presence of poisonous plants on a range or pasture does not mean poisoning will occur. Whether or not poisoning occurs is often dependent on range conditions, weather conditions, management practices, and the species of grazing animal (Sperry and others undated). Nearly all plant communities have plants that contain toxins, and thus are a potential threat to grazing animals. Intoxication occurs if these plants are consumed in sufficient amounts under appropriate conditions. Poisoning presently occurs with sufficient frequency to be a serious problem to livestock production and range management (James 1973).

Poisonous plants are one of the most important causes of economic loss to the livestock industry. Direct losses include death, decreased growth rate, emaciation, abortion, lowered reproductive performance, photosensitization, and birth defects. In addition, indirect costs associated with management such as altered grazing programs, fencing, increased herding costs, losses of forage, supplemental feeding programs, and veterinary fees increase. Poisonous plants on our ranges and pastures also often interfere with the systematic and efficient utilization of forage resources (James 1978).

The dollar loss from deaths and abortions caused by poisonous plants has been estimated to exceed \$199 million annually in the Western United States (Nielsen 1986). If all direct and indirect losses were considered, the total would be much greater. The actual dollar value is difficult to estimate because of insidious losses such as decreased weight gains, increased management costs, and forage losses. Unfortunately, we usually become alarmed only at large catastrophic losses. Smaller individual losses, or reduced production, have been accepted in the past as part of the costs of grazing rangelands. Because of the present economic crisis in agriculture, ranchers must become more efficient; they cannot afford even a small reduction in production due to poisonous plants.

TOXINS AND TOXICITY

Poisonous plants contain toxins that produce various effects on different classes of livestock. The concentrated efforts of veterinarians, chemists, and animal and range scientists are required to solve the problems caused by poisonous plants.

Intoxication is dependent on dose and rate of consumption. For example, nutrients such as copper, vitamin A, and phosphorus are toxic at high doses. In proper amounts they function as essential nutrients; extremely low levels result in deficiency disease. Many poisonous plants, such as lupine, chokecherry, and larkspur, when grazed under appropriate conditions, are utilized as forages. Lupine is considered, by many sheep producers, an excellent forage and indeed has been utilized extensively on many ranges. Yet lupine has caused the death of many thousands of sheep that ate excessive amounts of the plant.

One must understand the conditions under which these plants can be grazed with relative safety and when they will produce toxic effects in livestock. Some plants such as water hemlock are acutely toxic and cannot be safely grazed in even small amounts. Locoweeds and many forages containing selenium produce chronic intoxication and must be grazed over a period of weeks before intoxication occurs. However, when intoxication is noticed, irreversible damage may already have occurred. These plants should not be grazed at all.

Plants such as bitterweed of the Southwest, Colorado rubberweed, and sneezeweed grow under quite different environmental conditions, yet all contain the same toxin and produce the same signs of intoxication. Intoxication usually occurs under similar management conditions and can be dealt with by the same management strategies. Although these plants can be grazed for short periods of time without serious effects, it is best that they not be grazed at all. Plants that contain low levels of cyanide, nitrate, and oxalate can be grazed in small quantities with little problem. Death occurs when hungry animals are allowed to graze these

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plants rapidly. This usually happens when plants are abundant or in relatively pure stands.

Poisonous plants indigenous to a certain range may not be a problem every year. Environmental conditions influence plant growth and may influence toxicity. Furthermore, plants may vary in toxicity among sites, plant parts, and with stage of growth.

MANAGEMENT IMPLICATIONS

In the early days of grazing in the United States, the availability of free grazing land, the belief that the abundant grass would last forever, lack of knowledge about carrying capacities, and other factors caused serious over-grazing of the range. These attitudes and inexperience resulted in the depletion of much of the natural desirable forage and an increase in less desirable plants, some of which were toxic to livestock.

Much is still unknown about forage preferences of grazing animals. Weather can influence grazing behavior. Drought, heat, cold, and precipitation may induce unusual foraging habits. Under these conditions, unpalatable toxic plants may be consumed in sufficient quantities to cause poisoning on what is normally considered a safe range (Stoddart and others 1949). To minimize losses, the rancher must know the species of poisonous plants on his range, their location and distribution, and conditions that lead to their ingestion.

Some management practices employed by the range livestock industry may be conducive to the poisoning of livestock by plants. For example, lupine is more toxic to cattle than sheep on a unit weight basis, yet thousands of sheep have died from eating this plant while few cattle deaths have been reported. Many sheep have died from halogeton poisoning, yet relatively few cattle have been affected. This plant is about equally poisonous to cattle and sheep. The difference in the number of deaths may have been due to management procedures. Range sheep are kept in large flocks and moved from place to place as deemed necessary by the sheep herder; cattle, however, are left to move freely about a range, limited only by fences and natural barriers. Sheep are watered and provided new forage only by the herder, but cattle are free to search out the necessities of life. Consequently, hungry sheep may be driven through, bedded in, or unloaded from trucks into heavy stands of poisonous plants, and thus exposed to foreign situations. In addition, sheep generally show a preference for shrubs and forbs, which have a higher propensity for accumulating toxins than grasses (James 1973).

Poisoning of livestock under pasture conditions may also occur due to overgrazing and lack of proper attention to the animals. In these situations, as on the large fenced ranges of the Southwest, sheep, like cattle, graze unrestricted; therefore, intoxication from poisonous plants follows a different pattern.

Management activities such as trucking, driving, and penning may cause animals to become hungry and then indiscriminately graze areas that often contain an abundance of poisonous plants. Drought or improper distribution of livestock may result in a deficiency of good forage, which may cause animals to graze poisonous plants. Many poisonous plants are unpalatable and eaten only under stress. On the other hand, some poisonous plants remain green and become relatively more palatable than other plants that have matured and become dry (Everest 1974). Not all poisonous plants are unpalatable, nor are they restricted to overgrazed ranges or pastures. Larkspur, for example, is a climax plant and is readily grazed by livestock (Kingsbury 1964). Whatever the conditions or the poisonous plants, poisoning usually occurs when the animal eats excessive amounts too rapidly.

DISCUSSION

There are three principal methods that might be considered to reduce economic losses caused by poisonous plants: (1) elimination or reduction of the causative plant, (2) treatment of animals, and (3) management strategies to influence the grazing of livestock on ranges and pastures.

The cost of eliminating or markedly reducing populations of poisonous plants where widespread infestations occur must be carefully considered to determine the desirability and feasibility of such an undertaking. Chemical or mechanical treatment of ranges infested with poisonous plants is not always economically feasible, and the terrain may prohibit application of treatments known to be ecologically and economically beneficial.

Medical treatment of livestock poisoned by plants is generally of limited value because of the time interval between intoxication and treatment. Under range conditions, animals cannot be readily observed and often the observations are not frequent enough to detect most problems. In addition, the number of animals poisoned is often large and facilities for handling such animals may be inadequate. Also, there often is no adequate treatment available.

It would appear that the best and most logical approach to the prevention of livestock poisoning by most plants is proper feeding and management. Correct management principles must be applied to the pastures and ranges as well as the livestock. Resource people such as veterinarians, county agents, and land managers can render assistance in identifying the problem and developing management strategies for the prevention of intoxication of livestock by plants.

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CHEMICAL DEFENSE IN A WOODY PLANT AND THE ROLE OF DIGESTIVE SYSTEMS OF HERBIVORES

R. Thomas Palo

ABSTRACT: Alcoholic extracts of birch contain the phenolic substances platyphylloside, catechin, and rhododendrol. These phenols are metabolized to a different extent, excreted via different routes and have different physiological effects in hare and domestic rabbit as compared to moose and domestic goat. The same phytochemical may affect digestibility in one type of animal and act parenterally in another.

INTRODUCTION

Diet quality for herbivores is traditionally judged from its content of nutrients and fiber. In recent years attention has been drawn to the possible antinutritional effects of plant secondary metabolites. It has thus been demonstrated that certain polyphenolic compounds may limit availability and digestibility of nutrients (Allison and Osbourn 1970; Swain 1977; Barry and Duncan 1984; Kumar and Singh 1984; Beart and others 1985).

Evidence is also accumulating that soluble cell constituents such as phenolic glucosides, terpenoids, and alkaloids may have significant effects on the nutritive value of a plant (Fairborn 1982; Jung and Fahey 1983; Jung and others 1983; Burritt and others 1984; Lindroth and Batzli 1984; Palo and others 1985; Palo 1985; Risenhoover and others 1985).

The present theory of plant chemical defense against herbivores divides substances into two general categories dependent on their main way of action (Feeny 1976; Cates and Orians 1975; Rhoades 1979). The first category includes substances that depress digestibility and reduce the nutrient availability for the consumer by affecting the digestive process in the gut. The other category contains substances that are readily absorbed in the gastrointestinal tract and act within the body by interfering with various physiological processes.

To what extent and in which way each particular plant substance exerts its biological activity depends on its molecular size and structure (Rosenthal and Janzen 1979; Scheline 1978; Zucker 1983). In addition, the effectivness of a defense substance is largely dependent on physiological, behavioral, and ecological adaptions of herbivores to plants (Freeland and Janzen 1974; Janzen 1978; Bernays and others 1980; Rosenthal and others 1977, 1978). The tolerance of xenobiotics by a herbivore is limited by such factors as body size, microsomal activity, feeding strategy, nutritional status, and detoxification capacity (Freeland and Janzen 1974; Fowler 1983; Hanley 1983; Smith and Watkins 1984).

Some thoughts will be presented here about possible differences between the ruminant digestive system compared to the hindgut system of fiber digestion with reference to consumption of Scandinavian birch by moose and hares. Special attention will be given to the excretion pathways of birch phenols by goat, moose, hare, and rabbit. The study is a part of the aim to characterize the chemical defense mechanisms of birch in relation to attack by mammalian herbivores in boreal forest.

MATERIAL AND METHODS

Winter twigs of birch were collected at a clipping point of 1.5 mm and used in different experiments. Feces from goat, moose, rabbit, and hare were collected from caged animals fed twigs as their only feed. The twigs and feces were dried, milled to pass a 1 mm sieve, and then extracted with 95 percent ethanol (EtOH). The extract was filtered through a glass filter and evaporated to dryness. The residue was dissolved in EtOH(1) or water.

The glucosides of the water phase were hydrolyzed with pectinase (D4625, Sigma Co., St. Louis).

Conjugated phenols of the urine were hydrolyzed by treating the urine with sulfatase (S9626, Sigma Co.). The water phase and the urine were then acidified and extracted with ethylacetate (EtOAc). The organic phase was saved, evaporated to dryness, and redissolved in EtOH(2).

Rumen liquor was filtrated and then treated like urine, excluding the enzymatic step.

The samples obtained from step (1) and (2) were purified on sep-pak Silica cartridges (Waters Assor.) and applicated on thin-layer chomatography plates (TLC; HPTLC 100 x 100 mm silica gel plates 60, layer thickness 0.25 mm, Merck). The following

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mobile phases were used:
A; chloroform:metanol:water 80:15:1,
B; chloroform:2-butanone:acetic acid 10:7:2 and
C; chloroform:EtOAC 4:1

Spots were visualized by spraying with diazotized sulfanilic acid (Fluka AG. CH. 9470) dissolved in 20 percent sodium carbonate, followed by spraying with 50 percent sulfuric acid.

Identification of compounds was made against isolated pure compounds. Substances are presented by their relative front (Rf x 100) values in each mobile phase.

Catechin was obtained from Sigma Co.

RESULTS

The extract from birch twigs contained three principal phenolic compounds. These are platyphylloside (1.7-di(p-hydroxyphenyl)-heptan-3one-5ol-5-o-glucoside), rhododendrol (4-(p-hydroxylphenyl)-2-butanol), and catechin (3,5,7,3^1,4^1,-flavan-pentol) (fig. 1) (Sunnerheim and others, unpubl.). The Rf values in different mobile phases are presented in table 1.

The corresponding analyses of feces, rumen content, and urine show different degrees of metabolism of the substances depending on type of animal and compound (table 2). The TLC chromatograms of feces are identical for moose and goat fed birch. Here one principal metabolite is found. The metabolite was identified by H-NMR data as 1.7-diparahydroxy-phenyl-heptan. Incubation of platyphylloside with rumen liquor of goat showed that it is hydrolyzed and metabolized by rumen microorganisms into this final compound.

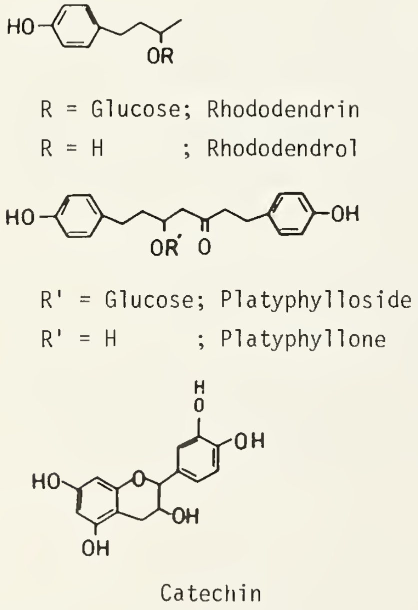

Figure 1.-- Structural formulas for the studied substances (from Tarasawa 1973, 1984; Haslam 1979).

Table 1.-- Rf values for some birch substances in different mobile phases

	Rf x 100		
	A	B	C
Platyphylloside	18	10	0
Platyphyllone	49	86	11
Rhododendrol	53	80	22
1.7-diparahydroxy-phenyl-heptan	59	89	50
Catechin	24	45	0

The analyses of feces from hare and rabbit show that these are identical with each other but differ from goat and moose. Of the studied compounds only rhododendrol is found in the feces of hare and rabbit, but only in small amounts. None of the substances platyphylloside and catechin are found in feces or urine of the animals irrespective of species. Analyses of urine obtained from rabbit and goat fed birch showed that rhododendrol and the final metabolite (Rf = 59) are present in both of the animals. Quantitatively more substances are detected in urine of rabbit than in urine from goat.

Catechin cannot be detected on TLC after incubation with rumen inocula from goat or when fed to rabbits. Catechin does not have any measurable effect on in vitro digestion in goats up to a concentration in the feed of 2 percent of the dry weight. On the other hand, the digestibility in vivo in rabbits is reduced by catechin at this concentration but the relative consumption rate is increased (Palo, unpubl. data).

Platyphylloside or one of its metabolites reduces digestibility in ruminants in vitro at a concentration below that naturally occuring in twigs (0.7 percent of dry weight). It also reduces consumption rate (at a concentration of 0.3 percent in rabbits; Palo, unpubl. data).

DISCUSSION

Very limited knowledge exists on the metabolism of phenols or other defensive chemicals in the gut system of herbivores. Some studies have been made on phenolic acids and related monomeric phenols and their metabolism and excretion in ruminants (Martin 1970, 1982; Martin and others 1983). Other studies conducted on rats, rabbits, and guinea pigs include numerous different substances (Scheline 1978). However, the authors do not emphasize differences in digestive system as a factor of importance for the metabolism and excretion of phytochemicals. Furthermore, in the discussion of plant chemical defense theory, herbivores have hitherto been regarded as static in their response to different defense categories (for example, Rhoades 1979). My data imply that differences in excretion pathways and metabolism between different types of animals could be influenced by type of digestive system of the animals.

Table 2.-- Occurrence of some birch substances in excreta of different herbivores. + = major occurrence, - = small amounts, 0 = not detected

	Hare	Rabbit		Moose	Goat		
	feces	feces	urine	feces	feces	rumen	urine
Platyphylloside	0	0	0	0	0	0	0
Platyphyllone	-	-	+	0	0	+	-
Rhododendrol	-	-	-	0	0	+	-
1.7-dipara-hydroxy-phenyl-heptan	0	0	+	+	+	+	-
Catechin	0	0	0	0	0	0	0

In this study, catechin seems to be completely metabolized in the digestive system of both rabbit and goat, but the digestibility was depressed in the former. Scheline (1978) and Harborne (1979) report that microorganisms metabolize catechin to carbon dioxide and a simple phenolic acid. This degradation pattern is common for many flavonoids and in fact all the usual phenolic acids recovered from urine of herbivores seem to originate from bacterial degradation of the feed (Harborne 1979). Furthermore, catechin may spontaneously form di- and trimeres which can form complexes with macromolecules (Haslam 1979).

These complexes may be dissolved either in the rumen or in the hindgut. The catechin is then completely metabolized by bacteria. The released macromolecules can be degraded by the rumen microbes, while in the nonruminant they may escape degradation due to a fairly short transit time through the gastro-intestinal tract. This may explain the different effects of catechin in the goat and in the rabbit.

The glucoside platyphylloside is hydrolyzed by the rumen microorganisms to its aglucone platyphyllone and then further metabolized in the rumen to 1.7-dipara-hydroxy-phenyl-heptan. The overall result of these processes is a reduced organic matter digestibility (Palo and others 1985; Sunnerheim and others, unpubl.). The appearance of the final metabolite in the feces of the goat and the moose suggests that it has either not been absorbed or more probably is being reexcreted in the bile. However, part of the platyphyllone apparently escapes degradation and is excreted in the urine.

On the contrary, the final metabolite is excreted only in the urine by rabbits and hares. Probably the hydrofilic platyphylloside passes unchanged down to the large intestine in these animals and then follows the water phase which is forced back into the caecum by the colon separation mechanism and retained (Björnhag 1972). Platyphylloside is then hydrolyzed and further metabolized to platyphyllone and the final metabolite, both of which diffuse through the gut wall and appear in the urine.

The results from studies on catechin and platyphylloside support the idea that anatomical differences in the digestive system affect the metabolism and excretion of secondary plant substances, and more important, how they exert their physiological effects. Catechin has, for instance, no effect in the goat but reduces organic matter digestibility and daily food consumption in the rabbit.

The present results, albeit preliminary, ought to allow the conclusion that one and the same secondary plant substance (or its metabolites) may exert its effect in the intestine of one species and parenterally in another.

The degradation of fibrous material in the rumen determines the rates of passage of food through the digestive tract of ruminants (Van Soest 1982; Demment and others 1985). Hares and rabbits are not to the same extent limited by particle size of food. Consequently, substances depressing digestibility would be of greater importance for the food processing capacity in the ruminant than in the nonruminant herbivore. On the other hand, the latter type of herbivore may be more sensitive to substances that are rapidly absorbed. Presumably, the herbivore will attempt to minimize the intake of certain substances that depress digestibility or that have toxic properties, depending on the particular digestive system of the animal.

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SOUTHERN TEXAS SHRUBS -- NUTRITIVE VALUE AND UTILIZATION BY HERBIVORES

L. W. Varner and L. H. Blankenship

ABSTRACT: Results of three experiments conducted over a 6-year period revealed that southern Texas shrubs were significant components of the diets of white-tailed deer (Odocoileus virginianus), jackrabbits (Lepus californicus), and beef cattle. Although 13 different shrub species were consumed by all herbivores, major competition among herbivores was for guayacan, cenizo, and mesquite. Diets of the three herbivores were most similar in winter and least similar in spring. Shrubs made up to 35, 97, and 45 percent of the winter diets of jackrabbits, white-tailed deer, and beef cattle, respectively. Among shrub species collected monthly for nutritional analyses, granjeno was the highest in overall quality with annual mean values of 73.3 percent, for in vitro digestible dry matter (DDM), 23.8 percent for crude protein (CP), and 0.18 percent for phosphorus (P). Blackbrush was the lowest in DDM of all species, averaging 31.4 percent for the entire year.

INTRODUCTION

Although southern Texas was once a savannah grassland, it is now dominated by a complex mixture of over 25 woody shrubs, trees, and cacti (Johnston 1963). A survey by the Soil Conservation Service in 1963 indicated that 93 percent of southern Texas rangelands were brush-infested, with over 70 percent having dense stands (Smith and Rechenthin 1964). The primary use of southern Texas rangeland is as livestock range; beef cattle are the primary domestic herbivores. In addition, the range provides habitat for white-tailed deer, jackrabbits, cottontail rabbits (Sylvilagus audubonii), numerous rodents, and in some areas exotic ruminants.

The shrub component of the southern Texas ecosystem is essential to both domestic and wild herbivores. It provides shade, food, and cover (Inglis 1985). The purpose of this paper is to compare (1) the dietary preferences of major herbivores for indigenous shrubs and (2) the nutritive value of these shrubs.

LOCATION AND METHODS

All three experiments reported were conducted on a 2,040-ha area 45 km southwest of Uvalde, TX, that was divided into six pastures, each with a mean size of 340 ha. Dominant soil type, covering 60 percent of the area, was clay loam.

Food habits of jackrabbits, white-tailed deer, and beef cattle were determined on a monthly basis for 14 months from March 1979 to April 1980. Approximately 10 rabbits per month were shot. Their stomach contents were collected and frozen for future diet analyses. In the immediate area where rabbits were shot, five samples each of deer and cattle feces were also collected. Microscope slides of the fecal and stomach material were prepared as described by Hansen and Flinders (1969) and Green and others (1985). Plant species in the sample were determined by the microhistological technique (Sparks and Malechek 1968). Competition for shrubs among the herbivores was evaluated using Kulczynski's similarity index (Oosting 1956). Results for the first year have been summarized and are presented on a seasonal basis. To characterize the nutritive value of an array of southern Texas shrubs, 13 native shrub species were collected monthly from four range sites (sandy loam, clay loam, clay flat, and shallow ridge). Samples from at least 10 plants per site per month were collected for analyses. Samples were separated into leaf, stem, and fruit (when available) components and analyzed for CP (Lauber 1976), DDM (Newman 1972), and P (Kallner 1975). Data from all range sites were averaged.

SHRUB UTILIZATION

Shrub species utilized by the three herbivores are shown in table 1 while scientific names of all species are given in table 2. Only two shrub species were utilized by all three herbivores. Guayacan, one of the few evergreen shrubs in southern Texas, was utilized by all herbivores in winter. Mesquite fruit was used by all herbivores in summer, and mesquite leaves were eaten by jackrabbits during seasons when they were available. Cenizo, guajillo, guayacan, Texas colubrina, and twisted acacia were all used by both deer and cattle.

Similarity in shrub utilization (fig. 1) between jackrabbits and cattle varied from almost 0 percent in spring to over 70 percent in winter. Jackrabbit and deer use of shrubs was most similar in summer and winter because both animals were using large amounts of mesquite fruit and guayacan, respectively. Deer and cattle use of shrubs was most similar in winter (76 percent) because both species used cenizo and guayacan.

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Table 1.--Percentage shrubs in diets of southern Texas herbivores

Shrub species	Spring			Summer			Fall			Winter		
	Jack-rabbits	Deer	Cattle	Jack-rabbits	Deer	Cattle	Jack-rabbits	Deer	Cattle	Jack rabbits	Deer	Cattle
Blackbrush		2.8	>1.0	1.0	10.4	>1.0		24.4			38.5	14.4
Brazil					8.5			5.9			2.9	
Cenizo		1.8				>1.0			9.0		22.8	
Feather dalea				>1.0								
Granjeno					1.3							
Guajillo					2.0	21.1			19.0			
Guayacan	>1.0	33.5	>1.0				>1.0			1.1	18.1	23.1
Lantana								1.8				
Lotebush									>1.0			
Manystem ratany	>1.0									>1.0		>1.0
Mesquite	11.0			19.4	24.9	2.3	11.1			19.9	4.9	5.5
Texas colubrina		9.0	4.7		13.4			10.0				
Twisted acacia		3.1	2.0		16.1			6.7	>1.0			
Vine ephedra			2.5									7.5
Wolfberry										3.0		

Table 2.--Common and scientific names of southern Texas shrub species

Common name	Scientific name
Blackbrush	*Acacia rigidula*
Brazil	*Condalia obovata*
Catclaw	*Acacia greggii*
Cenizo	*Leucophyllum frutescens*
Coma	*Bumelia celastrina*
Desert yaupon	*Schaefferia cuneifolia*
Feather dalea	*Dalea formosa*
Granjeno	*Celtis pallida*
Guajillo	*Acacia berlandieri*
Guayacan	*Porlieria angustifolia*
Kidneywood	*Eysenhardtia texana*
Lantana	*Lantana microcephala*
Lime pricklyash	*Zanthoxylum fagara*
Lotebush	*Condalia obtusifolia*
Manystem ratany	*Krameria ramosissima*
Mesquite	*Prosopis glandulosa*
Shrubby bluesage	*Salvia ballotaeflora*
Texas colubrina	*Colubrina texensis*
Texas persimmon	*Diospyros texana*
Twisted acacia	*Acacia tortuosa*
Vine ephedra	*Ephedra antisyphlitica*
Wolfberry	*Lycium berlandieri*

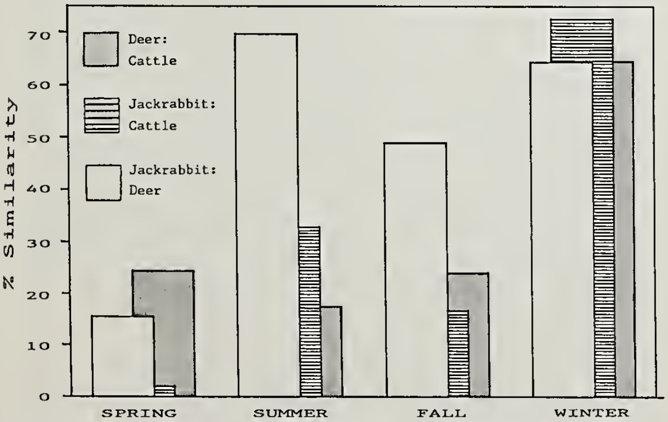

Figure 1.--Percentage similarity in seasonal shrub utilization by southern Texas herbivores.

Shrub Use By White-tailed Deer

Shrubs were the most consumed forage type for almost all months of the study (fig. 2). Shrub consumption by deer varied from 65 percent of the diet in the spring to over 95 percent in the winter. Since spring forb availability was high, shrub consumption by deer was lowest in March 1979 at 13 percent of the diet (table 3), and was highest during the fall and winter months, averaging over 94 percent from November 1979 through April 1980. The high utilization of shrubs in March 1980 compared to March 1979 was probably caused by lack of forbs in 1980 due to a dry spring. Two shrub species, blackbrush and guajillo, were consumed in significant quantities almost every month of the year. Blackbrush averaged over 12 percent of the diet per month, while guajillo averaged almost 17 percent of the diet each month. Two evergreen species, cenizo and guayacan, were particularly important during the late fall and winter months. Fruit of mesquite and Texas persimmon was particularly important during the summer months.

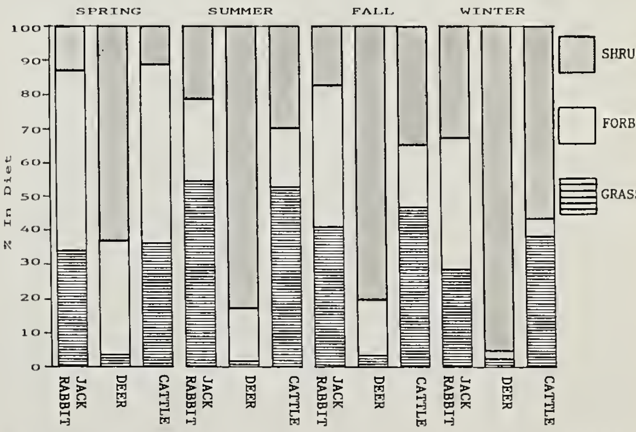

Figure 2.--Seasonal utilization of forage classes by southern Texas herbivores.

Table 3.--Percentage of southern Texas shrubs in white-tailed deer diets over a 14-month period

Shrub species	1979										1980			
	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
Blackbrush	2.4	5.8	29.8	6.9	3.1	14.0		12.9	12.6	19.5	21.6	22.7	17.9	4.1
Cenizo	1.6				4.5				20.9	20.5	12.2	10.0	5.4	23.3
Guajillo	4.0	4.3	11.2	10.8	0.8	14.8	19.5	37.1	35.0	31.6	12.4	13.2	16.6	25.9
Guayacan	3.3	34.5	5.3		17.9			0.7		4.7	6.9	35.9	46.2	23.3
Manystem ratany		2.8	4.4	11.0			7.1	5.7		2.1	3.3	1.8	2.2	
Mesquite		0.9		22.3	25.3	21.8	1.1	2.4						
Shrubby bluesage	0.3		1.9	1.3		7.1	7.9	12.8			0.3	1.2		4.1
Texas persimmon			19.6	6.0	13.0	2.3	0.8		5.4		6.2	3.6	1.3	
Twisted acacia		30.6	24.4		4.6	3.5		0.7	5.2	15.6	6.9	5.6	9.2	16.9
Other spp.	1.3	5.1	1.9		10.7	4.3	12.2	8.1	13.3	5.9	6.8	5.6		
Percent shrubs in diet	12.9	84.0	98.5	58.3	79.9	67.8	48.6	80.4	92.4	99.9	76.6	99.6	98.8	97.6

Over the entire study period, four shrub species; guajillo, blackbrush, guayacan, and twisted acacia, consistently made up a significant proportion of deer diets.

Shrub Use By Jackrabbits

Jackrabbits consumed mostly forbs, and grass throughout the year (fig. 2). Of the shrubs consumed, mesquite was the major species eaten during all seasons of the year, varying from 11 percent in spring to 20 percent in winter. Their heaviest utilization of shrubs (35 percent) was during the winter. This agrees with data reported by Westoby (1980) for jackrabbits in Utah.

Shrubs Use By Cattle

Utilization of shrubs by cattle (fig. 2) increased as the year progressed and was 9, 24, 29, and 45 percent of the diet for spring, summer, fall and winter, respectively. Guajillo, and guayacan were the most frequently used shrub species. Three other species, blackbrush, Texas colubrina, and cenizo made up substantial portions of cattle diets during some seasons of the year.

NUTRITIVE VALUE OF SOUTHERN TEXAS SHRUBS

Table 4.--Seasonal *in vitro* dry matter digestibility of southern Texas shrub species[1]

Shrub species	Season				
	Spring	Summer	Fall	Winter	Mean
Blackbrush	34.1^{f}	29.0^{f}	37.0^{e}	25.6^{f}	31.4
Brazil	61.4^{cd}	42.3^{de}	47.8^{c}	60.4^{b}	53.0
Catclaw	62.2^{c}	36.7^{e}	42.0^{de}	47.3^{d}	47.0
Coma	47.9^{e}	47.0^{d}	47.7^{c}	40.3^{e}	45.7
Desert yaupon	61.4^{cd}	56.0^{c}	58.8^{b}	55.5^{c}	57.9
Granjeno	71.7^{a}	73.3^{a}	75.2^{a}	73.0^{a}	73.3
Guajillo	46.4^{e}	38.9^{e}	41.1^{e}	35.5^{e}	40.5
Guayacan	58.0^{D}	56.6^{c}	60.2^{b}	54.9^{c}	57.4
Kidneywood	62.4^{c}	60.2^{b}	49.8^{c}	54.1^{c}	56.6
Lime pricklyash	56.2^{d}	48.1^{d}	73.2^{a}	69.3^{a}	61.7
Lotebush	47.7^{e}	50.7^{d}	38.8^{e}	44.4^{d}	45.4
Twisted acacia	32.9^{f}	36.9^{e}	31.9^{f}	28.0^{f}	32.4
Vine ephedra	66.4^{bc}	54.4^{c}	57.5^{b}	61.2^{b}	60.4
Mean	54.5	48.5	51.0	49.9	51.5

[1] Means followed by unlike letters are different ($P<0.05$).

On a seasonal basis DDM of all shrub species was greater in spring and fall than either summer or winter (table 4). Among the shrubs, blackbrush and twisted acacia were the lowest in DDM (≤ 37.0 percent) during all seasons of the year. Granjeno, the most digestible of all browse species, was never less than 71 percent DDM with an overall mean for the year of 73.3 percent. Guajillo, which was used extensively by both white-tailed deer and cattle, averaged 46.4, 38.9, 41.1, and 35.5 percent DDM during spring, summer, fall, and winter, respectively. Guayacan, which was heavily used by jackrabbits, deer and cattle during winter, was 54.9 percent DDM during this time.

Monthly analyses of CP of leaves of major shrub species are shown in figure 3. CP of leaves varied from a low of 11 percent for desert yaupon in January to 40 percent for lotebush in March. Granjeno leaves were among the highest in CP every month of the year, averaging 23.6 percent for the entire year. In southern Texas, because of generally mild winters, even deciduous species such as guajillo, granjeno, and blackbrush keep their leaves longer in the fall, and leaves appear earlier in late winter or spring than forbs or grasses. This accounts for the heavy use of these shrubs and the evergreen shrubs (guayacan and cenizo) by herbivores in winter.

Soils in southern Texas are generally low in P (Fisher 1974). This is reflected in the P content

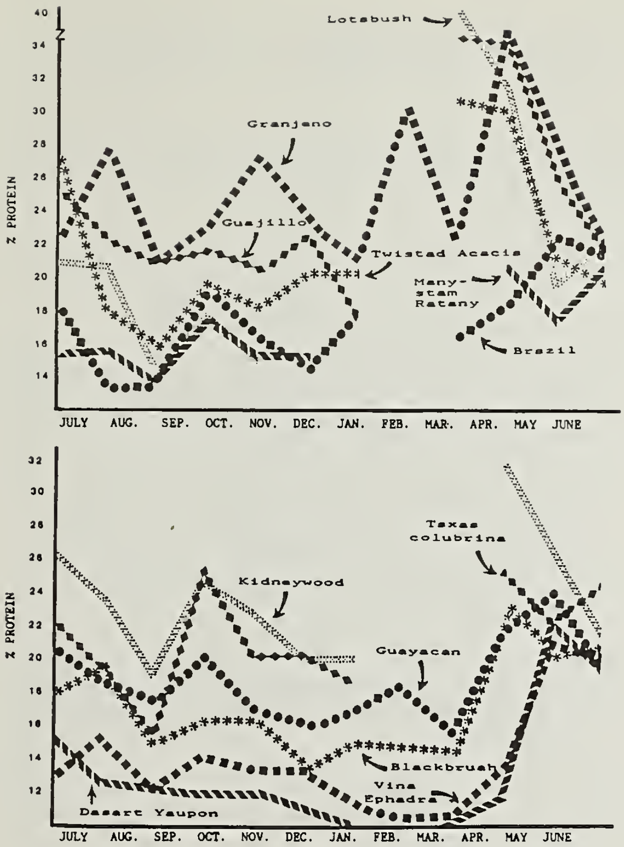

Figure 3.--Monthly protein content of southern Texas shrubs.

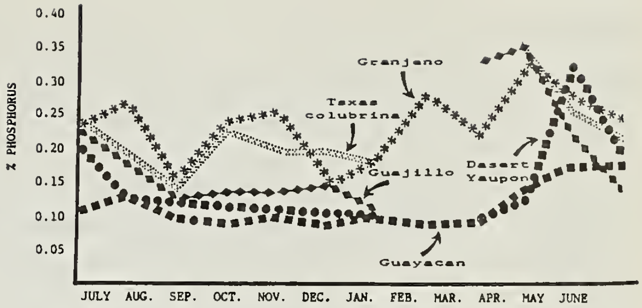

Figure 4.--Monthly phosphorus content of southern Texas shrubs.

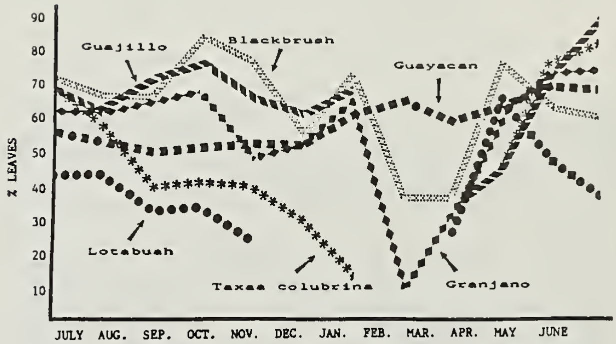

Figure 5.--Leaves as a percent of dry matter of southern Texas shrubs.

of shrub leaves (fig. 4). Over the entire year shrub leaves averaged 0.22 percent P. Guajillo and granjeno were the highest in P of the shrubs, averaging $\geq$ 0.35 percent in March and April. Guayacan was the lowest in P of shrubs during most months with a mean of 0.14 percent for the entire year.

DISCUSSION

In addition to quality, both quantity and availability of forage during the year are important to herbivores (Wallmo and others 1977). Plants, such as lotebush, that are very high in CP (40 percent) for a short period of time may not greatly improve total nutrient availability to herbivores. In March the twigs of lotebush were approximately 30 percent leaves and 70 percent stems (fig. 5). Stems are less nutritious than leaves (Sullivan 1969). Therefore, not only the quality of a particular forage species, but the quantity of leaves in relation to stems should be considered when determining which species to manage for to improve the nutrient intake of rangeland herbivores.

Knowledge of herbivore food habits must be correlated to knowledge of the nutritional quality of species consumed before we can coordinate deer and livestock management with vegetation changes. Plants that do not appear, in laboratory analyses, to be extremely high in nutritive value (such as blackbrush or twisted acacia) still may be important sources of nutrient to herbivores. They may, for reasons that are not apparent from routine laboratory analyses, be highly palatable to a particular herbivore. We need a better understanding of why some species are selected at certain times of the year and not at others and why some species that appear to be good sources of nutrients are rarely selected.

These data demonstrate that a diversity of plant species in the habitat allows herbivores to select a diet that is both nutritious and palatable. In addition, both numbers and kinds of herbivores may have to be manipulated to reduce competition for available high-quality forage species.

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THE RELATIONSHIP OF TETRADYMIA SPECIES AND ARTEMISIA NOVA TO PHOTOSENSITIZATION IN SHEEP

A. Earl Johnson

ABSTRACT: Photosensitization of sheep caused by toxins in Tetradymia canescens and T.glabrata is widespread in the Great Basin. The toxins damage animal livers in such a way that phylloerythrin, a photosensitizing byproduct of chlorophyll-rich food, is not removed from the bloodstream before it reaches the peripheral circulation. Although utilization of Tetradymia as a food is limited, during stressful situations it may be heavily eaten. Rapid liver and epidermal damage may cause death or abortion. Efforts to produce secondary photosensitization experimentally in sheep were frustrated until it was discovered that ingestion of Artemisia nova produced greater sensitivity to Tetradymia phototoxins. Possible mechanisms of interaction between the two plant species are explored.

INTRODUCTION

Tetradymia spp. are spinescent or glabrous, generally canescent shrubs that begin growth early in the spring and bloom in spring or summer. They are found scattered throughout the Great Basin and extend into southern California and British Columbia. There are 10 to 20 species of Tetradymia depending on the method of classification. Of the two species of concern here, T. canescens (spineless horsebrush) (fig. 1) is the more far-ranging and may be found throughout the Great Basin. Tetradymia glabrata (littleleaf horsebrush or coal oil brush) (fig. 2) is also widespread but occurs in greater numbers in the more central portions of the Great Basin. Both species are utilized as food by sheep but generally are grazed sparingly, with young shoots and buds having the greatest palatability. Tetradymia glabrata often becomes green well before other more palatable plants and is more heavily utilized at these times and during stormy periods when sheep may alter their grazing habits.

Fleming (1922) in Nevada alerted the livestock industry to the fact that T. glabrata (then called spring rabbitbrush) was poisonous to sheep but not harmful to cattle. He determined, through experimental feeding, that sheep could be seriously damaged or killed with relatively small daily doses of the plant within a 3- to 4-day period. Sheep fed larger doses became sick almost immediately and died within 24 hours. He noted that the liver was severely affected as evidenced by discoloration and friability grossly, and by hepatic necrosis, fibrosis, and fatty degeneration microscopically.

Figure 1.--Tetradymia canescens (spineless or little grey horsebrush) is often found in the more semiarid regions of the Great Basin. It has a distinctly grey color compared to sagebrush and other plants that usually accompany it. Its leaves are larger and softer than those of T. glabrata and their odor is not as distinct.

Fleming did not mention photosensitization and it was not until 15 years later that Clawson and Huffman (1937) incriminated, through field observation and experimental feedings, both T. glabrata and T. canescens as causative agents in "bighead," a photosensitization syndrome in sheep characterized mainly by swelling of the sheep's head.

PHOTOSENSITIZATION

Photosensitization Versus Sunburn

Photosensitization is sometimes referred to as "sunburn," but there is a distinct difference between sunburn and photosensitization. Sunburn is caused by undue exposure to ultraviolet radiation of light wavelengths shorter than 320

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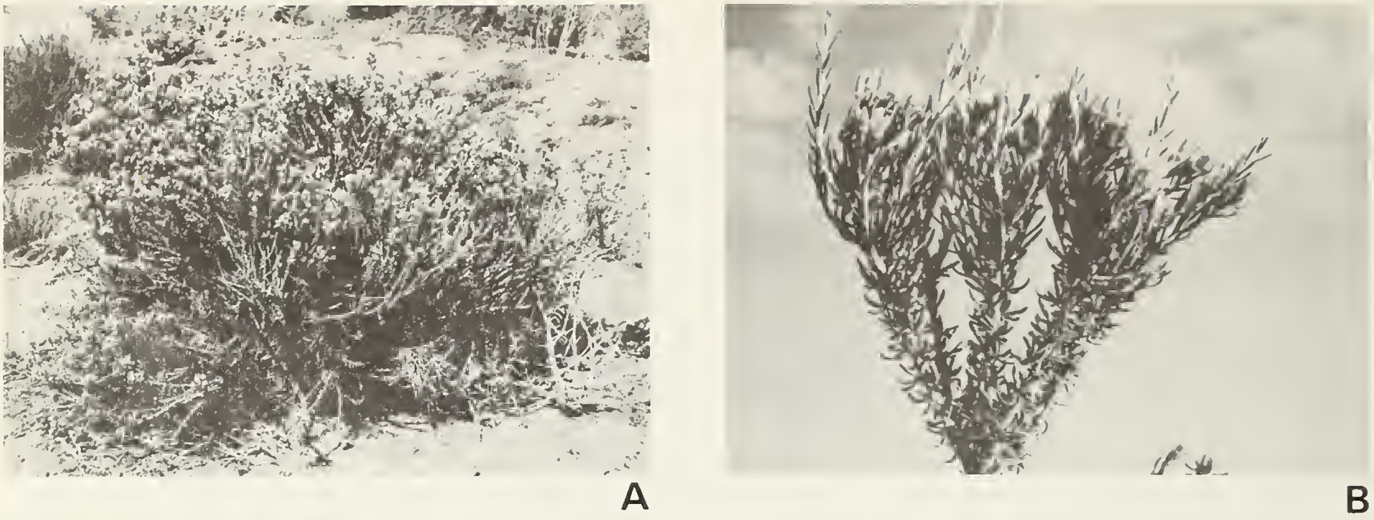

Figure 2.--Tetradymia glabrata (littleleaf horsebrush or coal oil brush) is a woody plant usually 1 to 2 feet tall (A) that grows in the more arid parts of the Great Basin. It is named for its small, dark-green leaves (B) that emit a pungent coal oil-like odor.

nanometers (nm) and results from the direct action of these ultraviolet rays on epidermal cells (Daynes and Spikes 1983). It is a normal reaction in unprotected, unpigmented skin, and the reaction is usually delayed for several hours after exposure to light. On the other hand, photosensitization involves a reaction to light of a specific photosensitizing compound that has been eaten by livestock and found its way to the skin through peripheral blood circulation. The photosensitizing compound may be found in plants or in food contaminants. In the skin it absorbs large amounts of damaging ultraviolet rays of specific wavelengths from the sun, and becomes activated or converted into a highly excited state. In this excited state, molecules of the photosensitizing agent transfer damaging energy to adjacent cellular components, disrupting a variety of cellular activities. Without light the agent is nontoxic, but on exposure to light the reaction is immediate and usually more devastating than sunburn.

Photosensitization Types

Plant photosensitizing reactions are of two types, primary and secondary. In primary photosensitization the sensitizing compound is in a plant, and as the plant is eaten the compound is absorbed and reaches the skin unchanged (Clare 1955). St. John's wort (Hypericum perforatum) and spring parsley (Cymopterus watsonii) are examples of plants containing primary photosensitizers. In secondary photosensitization, phylloerythrin is the photosensitizing agent (Clare 1955). Phylloerythrin is a byproduct of chlorophyll and is formed in the digestive tract of any ruminant eating green feed. In a normal animal, phylloerythrin is removed from the blood by the liver and secreted in the bile before it can reach the peripheral circulation. Any plant toxin or other agent that damages the liver in such a way that it loses its ability to remove the phylloerythrin may then cause secondary or hepatogenous photosensitization. Thus, there are two requirements for secondary photosensitization to occur: the animal must be eating chlorophyll-rich food, and the liver of the animal must be damaged in such a way that it cannot remove and secrete phylloerythrin formed from the chlorophyll. Most livestock photosensitizations are of this secondary type.

Photosensitization Effects in Sheep

Liver damage caused by Tetradymia and the accompanying photosensitization is often a devastating occurrence. When sheep have grazed sufficient Tetradymia, the problem can develop rapidly with several hundred sheep becoming affected in a 2- to 3- hour period. In the early stages of photosensitization the sheep become uncomfortable and seek places to rub or scratch their heads. Restlessness, swollen lips, and heavy drooping ears are usually the first signs noted by the herder, and some sheep may assume an uncharacteristic stance with the head elevated and nose pointed upward. They lose their herding instinct, begin to seek shade, and may scatter over an area of several square miles. Facial tissues may swell to the extent that they crack, with serum exudation and heavy scab formation. Secondary infection may occur if treatment is not initiated. Scabbing may cause impaired vision in some sheep. In some primary photosensitizations scarring of the eye may occur with total blindness as a result. Wool in some sheep may sluff, and repair of these areas may not occur. Sheep that have consumed larger Tetradymia doses may become sick from liver injury and may abort fetuses that are usually in the last trimester of development. The only means of treating affected sheep is to provide good food and shade and treat the symptoms. This usually requires transporting sheep to the home ranch which may be many miles away. Sheep thus treated may survive depending on the degree of liver damage and photosensitization.

The loss of a ewe also involves the loss of the full fleece that she is carrying and the loss of her fetal lamb. If she survives, she is often a nonproductive animal.

EXPERIMENTAL AND FIELD OBSERVATIONS

Even though the textbook explanation of secondary photosensitization seems rather straightforward and simple, our early attempts to experimentally produce this photosensitization quickly revealed that it was not simple. We experienced failure after failure (Johnson 1974a). A review of the literature, meager though it was, gave no clues; neither did frequent consultations with livestock owners who had had the problem. Observation of grazing habits of sheep on Tetradymia-infested ranges also gave no clues. We learned, however, that the problem did not occur annually, but usually only when certain environmental and management conditions meshed. Furthermore, sheep owners that had the problem in 2 or more successive years were alert and careful to manage their sheep to avoid Tetradymia, but sheep owners whose herds escaped the problem for a year or two became complacent and their herds were highly susceptible to the problem.

A greater appreciation of the severity of the problem was gained as more affected herds were observed. Tetradymia-infested areas where many outbreaks occurred were often 100 to 200 miles from the home ranch, so the herder or sheep owner had to deal with the problem as best they could with little or no means. We noted that isolated cases of Tetradymia-related photosensitization commonly occurred on Tetradymia-infested ranges, but sheep utilized very little Tetradymia as food in most situations. Many of the toxicity and photosensitization problems occurred along old trails and driveways. Here the Tetradymia grows in greatest abundance and the sheep are often exposed to more stressful situations than would normally be encountered when free ranging. Often these trailing sheep may be pushed along at a faster than desirable rate to maintain an allotted time schedule; they may be held up in undesirable areas while waiting for another herd to move on; they may be unduly hungry when they reach a water hole; and after drinking they may wish to eat immediately. Often Tetradymia is plentiful with little other feed available near these watering areas. Sheep, as do other animals, sometimes seem able to detect an impending storm and may change their grazing habits to "stock up" on food before the storm arrives; more Tetradymia than normal may be eaten under these conditions. Spring snows sometimes briefly cover low-growing food plants so that the taller growing Tetradymia is more available and thus may be grazed more heavily than desirable. In some years, moisture and temperature conditions allow palatable forage to grow as early as the Tetradymia so that Tetradymia is not a hazard.

As these observations were made, our efforts to produce photosensitization experimentally with the plant continued. We were convinced that it was just a matter of giving the right plant dosage in the right time period. But after feeding every reasonable dose at a multitude of time intervals and causing only occasional photosensitization, it became apparent that other factors must account for the failures. Liver damage and even death could be produced with relatively small Tetradymia dosages fed in a 36- to 48-hour period, but the occasional resultant photosensitization seemed to happen randomly and could not be correlated with dosage.

In seeking causes for our failure we conducted experiments to determine if the responsible toxin had volatilized or was enzymatically degraded in the time lapse between collecting the Tetradymia and feeding it (Johnson 1974a). To minimize this time interval and to assure that light conditions were similar at the laboratory and on the range areas where outbreaks occurred, sheep were transported to field areas and fed Tetradymia there. Results remained negative.

At about this stage of the investigation, reasons for Clawson's and Huffman's (1937) success and our failure became a great concern. While delving into some of Clawson's unpublished records, we noted that they also had difficulty in some experiments and that the successful experiments were on sheep taken immediately from range herds. Therefore, sheep from the laboratory were taken to the problem range area, and other sheep were obtained from herds grazing the range. Both groups were fed Tetradymia. Sheep from the laboratory were nonreactive; those from the range area were photosensitized. It seemed that progress was finally being made, but confirmation of results was needed. A repeat trial the following year produced essentially negative results, so again confusion reigned.

Further evaluation of Clawson's and Huffman's unpublished records revealed that they had also noted the correlation between the range sheep and their susceptibility to Tetradymia and had attempted to precondition their laboratory sheep by first experimentally feeding bud sage (Artemisia spinescens), black sagebrush (Artemisia nova), big sagebrush (Artemisia tridentata), hopsage (Grayia spinosa), winterfat (Eurotia lanata), shadscale (Atriplex confertifolia), and greasewood (Sarcobatus vermiculatus), and combinations of these (Johnson 1974b). They obtained some success with black sagebrush and big sagebrush. Armed with this information, we returned to the problem range to determine why we had been successful one year and failed the next. The answer came with the discovery that the sheep in our first successful experiment had been grazing range that was made up mostly of black sagebrush (fig. 3). Sheep used the following year in the unsuccessful attempt were taken from a location where there was little or no black sagebrush.

Subsequent experiments in which black sagebrush was fed prior to feeding Tetradymia have been much more successful in producing photosensitization, although it cannot be produced with complete regularity.

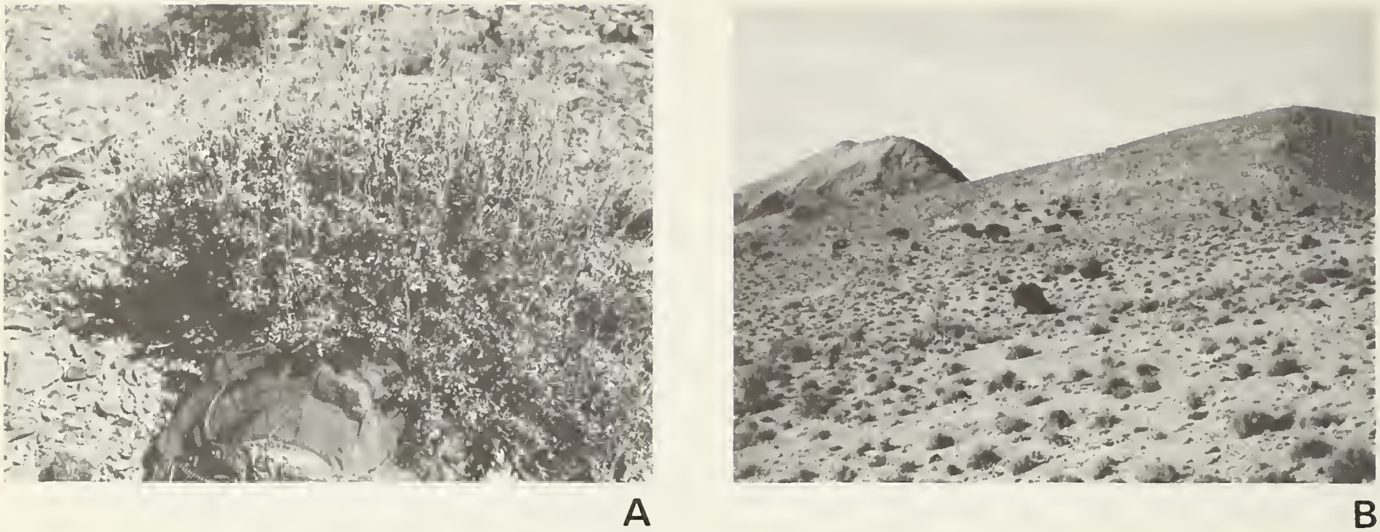

Figure 3.--*Artemisia nova* (black sagebrush) is a low-growing, dark-colored sagebrush of the tridentata type (A). It grows on well-drained gravelly or rocky slopes and is a palatable and nutritious winter food for sheep (B).

These experiments have also indicated that black sagebrush alone can be lethal to sheep when large amounts are fed without allowing the sheep to gradually adapt to the plant, and that small nontoxic doses of *Tetradymia* fed to sheep can be made toxic if black sagebrush is fed in small amounts for a few days previously.

Black sagebrush is good feed for sheep on many winter ranges in Utah and Nevada. It has a high protein content, and sheep on many of these ranges could not survive without it. However, it obviously contains toxic compounds, and at times, may be the unrecognized source of sheep problems. Some sheep owners have reported that they believe lush black sagebrush eaten by their sheep in early spring to be the source of abortion problems.

There is little doubt that there is a synergistic toxic relationship between black sagebrush and *Tetradymia glabrata* and *T. canescens*. We have conducted several experiments confirming this. *Tetradymia glabrata* is more toxic than *T. canescens*, and better success in causing photosensitization is usually obtained with *T. canescens*, probably because of its lesser toxicity. It does not kill the animal before photosensitization can occur, as *T. glabrata* often does. The precise nature of the toxic relationship of these two plants is not apparent at this time because the mechanism of absorption of phylloerythrin by liver cells and the method of its excretion into the biliary system are not known. Futhermore, the chemical nature of the toxin, in either *Tetradymia* or black sagebrush, responsible for the liver damage is not known. One of the compounds in *T. glabrata* toxic to mice has been identified, but its toxicity has not been confirmed in sheep (Jennings and others 1974). The sagebrushes contain several chemical classes of compounds, such as simple terpenes (essential oils) and sesquiterpene lactones, that could be responsible. Terpenes have been shown to alter the rumen microflora in deer (Nagy and others 1964), which might affect their ability to utilize certain feed types. If terpenes have this effect in sheep, the ability of the sheep's digestive tract to either detoxify or utilize the *Tetradymia* toxin may be altered, thus altering its toxicity.

Another possible mechanism in the relationship of these two plants may be that sagebrush induces or depletes liver microsomal enzymes that may be functional in the toxicity of *Tetradymia*.

Sagebrush toxins may injure the liver cell membrane, altering the cell's ability to absorb phylloerythrin or blocking its excretion into the biliary system. At present the histological effects on the sheep's liver of black sagebrush fed alone are being compared with the effects of *T. glabrata* fed alone and with the effects of the two plants fed in combination. Thus far, it appears that changes may be too subtle to be detected by light microscopy and may require scrutiny at the sub-cellular level by electron microscopy. The lesion may be purely biochemical and require biochemical or histochemical means of detection.

The relationship of these two plants is extremely interesting and raises questions concerning the possible ancillary relationships of other common range plants to toxicities in livestock by known poisonous plants.

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PRENATAL AND NEONATAL DEATH OF LAMBS DUE TO MATERNAL GRAZING OF VERATRUM CALIFORNICUM

Richard F. Keeler

ABSTRACT: Veratrum californicum (false hellebore), when ingested by pregnant ewes, causes prenatal and neonatal lamb mortality. Secondary compounds from the plant such as cyclopamine, jervine, and cycloposine are possibly responsible. These steroidal alkaloids exert teratogenic and embryotoxic effects. "Monkey face lamb" disease involving craniofacial defects, commonly fatal, is induced by ingestion of the plant on day 14 of gestation. Ingestion on days 19, 20, or 21 induces early embryonic deaths. Severe congenital tracheal stenosis, resulting in death of lambs immediately after parturition, along with shortening of various fore and rear limb bones are induced by daily ingestion over 2- or 3-day periods during days 27 through 33 of gestation. Collective mortality from these conditions might reduce the viable lamb crop by half. Allowing pregnant ewes to graze V. californicum before the 33d day of gestation cannot be recommended, and may be a significant factor in lamb crop losses that have been otherwise unexplained.

INTRODUCTION AND BACKGROUND STUDIES

The birth defects induced in lambs by maternal ingestion of the plant Veratrum californicum (false hellebore) (fig. 1) during gestation have been studied for several years. Cyclopia and related craniofacial deformities, called "monkey face lamb" disease by ranchers, are induced in lambs when ewes consume the plant on day 14 of gestation (Binns and others 1962, 1963, 1964, 1965). Deformities have occurred in up to 25 percent of the lambs from some range sheep flocks (Binns and others 1963, 1964). The classic expression of the disease (Binns and others 1961) is a true cyclopia (fig. 2) usually with a proboscis above the eye and severely shortened maxilla and premaxilla bones. There may be severe brain involvement with only a rind of cerebral tissue evident in some cases. Cyclopics have only one optic nerve, and the skull is altered accordingly. Lambs with mild defects show only a shortening of the maxilla and premaxilla. Severe cases die. Some mild cases may survive.


Figure 1.--The range plant Veratrum californicum.


Figure 2.--"Monkey face lamb" disease induced by maternal ingestion during gestation of Veratrum californicum.

Susceptibility to deformity is restricted to day 14 of gestation (assigning the day after breeding as day zero of gestation)(Binns and others 1965). This sharply limited period led to recommendations that pregnant sheep be denied access to the plant until 14 days after removal of rams, a practice relatively easy to follow. Ranchers commonly pursue this practice, and this has resulted in a dramatic reduction in incidence of "monkey face lamb" disease.

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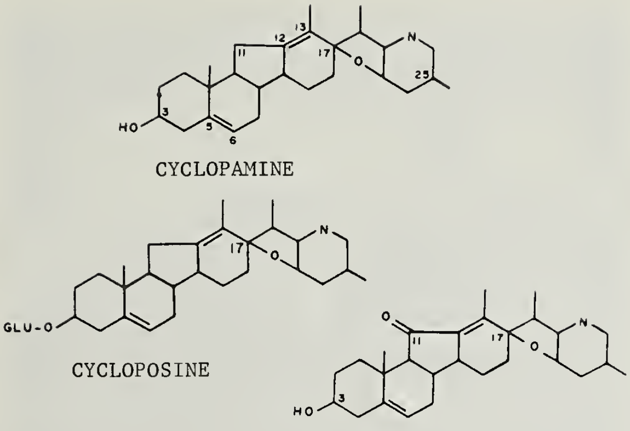

CYCLOPAMINE

CYCLOPOSINE

JERVINE

Figure 3.--Cyclopia-inducing steroidal alkaloids of Veratrum californicum.

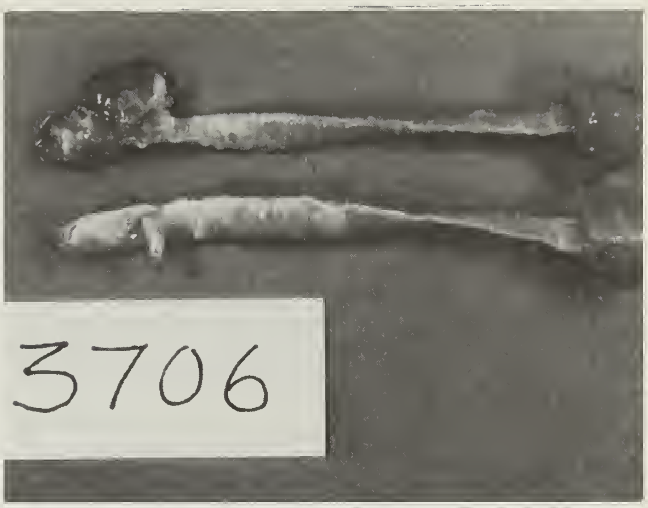

Figure 4.--Congenital tracheal stenosis in twin lambs induced by maternal ingestion of Veratrum californicum during gestation.

Certain secondary plant alkaloids proved to be responsible for the observed effects. Through extraction and isolation of alkaloids from the plant coupled with administration of the fractions and alkaloids to pregnant sheep on day 14 of gestation, it was possible to identify three alkaloids from among several dozen in the plant that could induce the condition (Keeler and Binns 1966a, 1966b; Keeler 1970, 1984). Those three alkaloids are cyclopamine, cycloposine, and jervine (fig. 3). All three are C-nor-D-homo steroidal alkaloids of the jeveratrum series with a furanopiperidine function spiro at carbon 17 of the steroid. All are closely similar--cyclopamine being 11-deoxojervine and cycloposine the 3-glucosyl glycoside of 11-deoxojervine. Both structure and configuration play essential roles in the teratogenic potency; the ether bridge is particularly critical (Keeler 1984) because of its influence on the configurational position of the essential nitrogen atom. Experiments in laboratory animals with Veratrum alkaloids, analogs, and various related model compounds suggested that the nitrogen atom had to be in an α-configurational position (fig. 4) with respect to the steroid portion of the molecule for the compound to be teratogenic (Keeler 1984).

Ranchers whose sheep flocks graze areas with abundant V. californicum, and who have experienced a high incidence of "monkey face lamb" disease, have also complained on occasion of "low lamb crops" (Binns and others 1963; Van Kampen and others 1969). Furthermore, laboratory observations of experimental sheep fed V. californicum indicated possible prenatal loss. Van Kampen and others (1969) collected and summarized data from previous experiments at our laboratory on the outcome of pregnancy in ewes gavaged (fed by stomach tube) the aerial portion of V. californicum at various gestational periods up to the 30th day. Pregnant ewes (361 from multiple breedings) had been gavaged. None cycled at regular intervals since they were multiple-bred (bred on 3 or 4 successive days) to achieve as near 100 percent conception as possible. But 60 (17 percent) came back into estrus later at irregular intervals, suggesting that embryonic death had occurred. Nineteen (5 percent) aborted, 43 (12 percent) had "monkey face" lambs, and 239 (66 percent) had normal lambs. There was a total prenatal and neonatal loss of 34 percent from embroynic death, abortion, or deformity. Among 66 single-bred controls, eight (12 percent) rebred at regular cycle intervals indicating failure to conceive to the single breeding. The other 58 controls delivered normal lambs. These observations suggested that considerable lamb loss may occur from V. californicum ingestion. The observations were consistent with the complaints by sheep ranchers of low lamb crops from ewes that had grazed areas with abundant V. californicum during gestation.

RECENT STUDIES AT THE POISONOUS PLANT LABORATORY

In recent experimental studies at our laboratory on the hazards of Veratrum ingestion in sheep, we have used groups of Columbia/Rambouillet cross ewes, single bred to Columbia rams with the day of breeding considered day zero of gestation. These ewes were then gavaged 30-50 g per ewe per dose of the root/rhizome portion of dried, ground V. californicum in water slurry at selected days of gestation. Plant material was collected in Muldoon Canyon, ID. The root/rhizome rather than aerial portion of the plant was used because concentration of the teratogenic alkaloids is about 10 times as high in the root/rhizome (Keeler and Binns 1971). Since a great deal was already known about hazards of ingestion of the plant on or about day 14 (Binns and others 1963, 1965), we conducted a preliminary study in 1980 to determine if there were hazards to the conceptus from maternal ingestion of the plant between days 19 and 42 of gestation. In groups of ewes gavaged plant material daily over 3-day periods, results suggested a prenatal death hazard related to administration on days 19 through 21, and a neonatal death hazard related to administration on days 28 through 30 or 31 through 33. In the day 28 through 30 and day 31 to 33 groups, some lambs that died shortly after birth also had limb deformities of the type previously found to occur at about that gestation period (fig. 5)(Binns and others 1972). No harmful effects were observed between days 33 and 42, and from an embryologic point of view, problems would be unlikely beyond day 42. Experiments designed to test more rigorously the mortality of concepti resulting from gavage of plant material during days 19 through 21 and 28 through 33 were clearly needed. Such experiments were performed during the next 5 years.

In one of those experiments, nine ewes were administered plant material on days 19, 20, and 21 of gestation. Two ewes lambed (22 percent), and seven (78 percent) failed to lamb. Among controls only two of nine (23 percent) failed to lamb, likely because they failed to conceive after the single breeding. Using as comparison the two of nine controls that failed to lamb, we can calculate the number and percentage of treatment ewes that probably terminated their pregnancies by early embryonic death from V. californicum ingestion as: 9 minus 2 that lambed minus 2 expected not to conceive = 5 [5 of 9 (56 percent) $P < 0.0005$]. Ingestion of the plant on days 19, 20, and 21 resulted in a high incidence of early embryonic death.

In another experiment, six pregnant ewes were administered Veratrum on days 31, 32, and 33 of gestation and six on days 28, 29, and 30. Ten of 19 lambs in these two groups died within minutes after birth. Six of the 10 that were autopsied had tracheal stenosis that prevented respiration and caused death. Only one of 12 lambs born to seven control ewes died directly after birth. It did not have tracheal stenosis. The tracheal stenosis induced by Veratrum was characterized by lateral flattening throughout the entire length of the trachea due to hypoplastic and disoriented tracheal rings. The nonpatent rings resulted in a nondistended lumen (fig. 4) through which no air could pass when the newborn lambs attempted to breathe (Keeler and others 1985). Ten of the 19 lambs born to treatment ewes also had limb defects that we had previously found to be induced at this period by either plant material or a cyclopamine preparation (Binns and others 1972; Keeler 1973), while none of the controls were so affected. Those limb defects were generally characterized by a shortening of both of the metacarpal or both of the metatarsal bones, or a shortening of all four bones (fig. 5).

A similar experiment was conducted to confirm that tracheal stenosis was induced by the plant. Plant material was gavaged to groups of pregnant ewes for 2- or 3-day intervals between the 28th and 32d days of gestation. All 12 ewes in these groups were killed 3 days prior to parturition for autopsy of fetuses. Sixteen of 24 lambs (67 percent) had tracheal stenosis and 23 of 24 (96 percent) had limb defects confirmed by autopsy of defleshed specimens. The limb defects in six of these lambs were not apparent except through careful measurements of bone lengths at autopsy and after drying of the defleshed specimens. Perhaps half of the 23 lambs with limb defects would not have been considered defective under field conditions, because limbs were only slightly shortened. Five control lambs from four control ewes had no tracheal stenosis nor limb defects.

Figure 5.--Congenital short metacarpal and metatarsal bones in a lamb induced by maternal ingestion of Veratrum californicum during gestation.

Additional experiments were conducted in 1985 that confirm all of these observations. Summarizing all experiments to date, 13 of 16 ewes (81 percent) dosed with V. californicum on days 19 through 21 of gestation failed to deliver lambs. Only two of 13 control ewes (15 percent) failed to lamb; this clearly demonstrates the ready induction of embryonic death by Veratrum ingestion. Furthermore, to date, 31 of 76 lambs (41 percent) born to 46 ewes gavaged the plant for 2- or 3-day intervals between days 27 and 33 of gestation had tracheal stenosis; none of the 32 lambs born to 21 control ewes had the condition. This clearly demonstrates the propensity of the plant to induce this defect, which is lethal within moments after birth.

Whether any or all of the three known teratogenic alkaloids are responsible for the tracheal stenosis and early embryonic death remains to be seen. They do induce "monkey face lamb" disease (Keeler 1970, 1984). Cyclopamine was tested for induction of shortened limbs and found active (Keeler 1973), although further tests were inconclusive. Preliminary experiments suggest cyclopamine may induce tracheal stenosis, although no severe cases have yet been induced. No trials have been completed with cyclopamine on days 19 through 21 to test its propensity to induce early embryonic death. But both cyclopamine and jervine induced excessive resorptions (embryonic and fetal deaths) in hamsters (Keeler 1975).

RISKS AND RECOMMENDATIONS

Table 1 summarizes lamb crop losses under experimental conditions from maternal ingestion of *Veratrum californicum* at various gestation periods, and compares them to actual or potential lamb crop losses under field conditions. Taken into consideration are losses due to "monkey face lamb" disease induced by day 14 ingestion, early embryonic deaths induced by day 19 to 21 ingestion, and neonatal deaths due to tracheal stenosis induced by day 27 to 33 ingestion. Expected incidence in the field is difficult to judge, but we estimate the field incidence of early embryonic death and tracheal stenosis would not exceed one quarter of the laboratory incidence because the highest experimental incidence (Binns and others 1965) of cephalic defects was 100 percent compared to the highest reported field incidence of 25 percent (Binns and others 1963). Consequently, potential field incidence of tracheal stenosis might reach 10 percent, and that of early embryonic death might reach 20 percent. But the figures of 25 percent, 10 percent, and 20 percent for each of the three conditions might represent a collective lamb crop loss of nearly 50 percent.

Totaling from the tables the "days at risk" (days 14, 19-20-21, 27-28-29-30-31-32-33) for the conceptus, resulting from maternal grazing of *V. californicum*, we have several days of potential hazard with some much more hazardous than others.

Table 1.--Lamb crop loss induced by *Veratrum californicum* ingestion by pregnant ewes under experimental laboratory conditions compared to actual or potential loss under field conditions

	Death from cyclopia and related defects (14th day ingestion)	Apparent embryonic deaths (19-21 day ingestion)	Deaths from trachael stenosis
	Percent		
Laboratory conditions	Up to 100	[1]81	[1]41
Field conditions	Up to 25 (actual)	[2]About 20 (potential)	[2]About 10 (potential)

[1] Collective incidence in all experiments through 1985.

[2] Potential loss based on the assumption that field cases might equal 25 percent of experimental laboratory cases as in column one.

What then is a prudent grazing policy for pregnant sheep in areas with an abundance of *Veratrum californicum*? During the 20-day period from day 14 to day 33 the conceptus is at risk from maternal grazing of the plant about half the time with a potential lamb crop loss of near 50 percent. The value of lambs lost plus attendant losses can easily exceed the value of forage consumed during the first 33 days of gestation. Consequently, a prudent recommendation must be that ranchers not allow pregnant sheep access to *Veratrum californicum* until all ewes have passed the 33d day of gestation.

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PRIMARY PHOTOSENSITIZATION IN LIVESTOCK BY RANGE PLANTS

M. Coburn Williams

ABSTRACT: Primary photosensitization is caused by skin contact or ingestion of phototoxic compounds that occur in the plant families Apiaceae, Rutaceae, Moraceae, Fabaceae, Hypericaceae, and Polygonaceae. The phototoxicity of spring parsley (Cymopterus watsonii) in ewes causes udder inflammation and sensitivity and results in significant losses of lambs from starvation and dehydration in southwestern Utah. This plant can be controlled with 2,4-D ester or 2,4-D amine applied at 2 lb/acre.

INTRODUCTION

Species of several plant genera produce photodynamic compounds that cause primary photosensitization in animals and birds (Pathak and others 1962). The photodynamic compound may reach the skin through physical contact with the plant or, if the plant is eaten, the compound is absorbed unchanged from the digestive tract and transported in the circulatory system to peripheral areas of the skin (see Johnson, this proceedings). The photodynamic compound becomes phototoxic when activated by long-wave ultraviolet radiation of a suitable wavelength.

Light-skinned animals and birds are most prone to photosensitization. All areas not protected by hair, skin pigmentation, or feathers such as eyes, ears, nose, lips, vulva, and udder (in animals), and eyes, beak, wattle, comb, feet, and legs (in birds) may be severely burned (Williams and Binns 1968). Affected areas become erythemic, swell, crack, bleed, and eventually slough. Gangrene, sloughing of toes, comb, wattle, and eyelids, and crippling have been observed in poultry. Sloughing of hair and skin and deformities of the lips, ears, and eyes have been noted in photosensitized animals. Death rarely results directly from photosensitization, but may result from secondary causes such as infection of affected areas or starvation and dehydration resulting from the inability to locate food or water due to blindness or sealed eyelids.

Species that evoke primary photosensitization are found primarily in the families Apiaceae, Rutaceae, Moraceae, Fabaceae, Hypericaceae, and Polygonaceae. Species most commonly associated with photosensitization in the United States are St. Johnswort (Hypericum perforatum) (family Hypericaceae) and buckwheat (Fagopyrum sagittatum) (family Polygonaceae) (Kingsbury 1964). The phototoxic compound in each species, hypericin and fagopyrin, respectively, has been isolated and named after the representative genus. Both compounds are napthrodianthrone derivaties. Hypericin has been shown to have two action spectra, 540 Mμ and 590 Mμ; the action spectrum of fagopyrin is 590 Mμ. Buckwheat is a minor crop in the United States and cases of photosensitization from it are rare.

St. Johnswort is an introduced plant that has spread throughout the United States. It was the first plant to be identified as a primary photosensitizer. The plant became a major invader on California ranges where it adversely affected the sheep industry. A single dose of St. Johnswort at 5 percent of the body weight (calculated on a green weight basis) was phototoxic to sheep; 1 percent of the body weight was phototoxic to cattle. The beetle Chrysolina quadrigemina, introduced in 1946 for biological control, has reduced the infestation of St. Johnswort in California by about 99 percent.

The largest single group of compounds that cause primary photosensitization are the furocoumarins (psoralens). These compounds are found primarily in the Apiaceae and Rutaceae but are also found in two genera of the Fabaceae and one genus of the Moraceae (Pathak and others 1962). Primary photosensitization from furocoumarins in the United States is usually associated with members of the carrot family (Apiaceae). The furocoumarins are complex molecules that must have a specific configuration to be photoactive. Psoralen, bergapten, xanthotoxin, isoimperatorin, and bergamotin are highly phototoxic. Many other furocoumarins have no phototoxic properties.

PHOTOTOXICITY IN THE INTERMOUNTAIN WEST

Four highly phototoxic members of the Apiaceae are found in the Intermountain West: wild parsnip (Pastinaca sativa), cowparsnip (Heracleum sphondylium), spring parsley (Cymopterus watsonii), and a related species, Cymopterus longipes. Species of three other genera, Angelica, Ligusticum, and Lomatium, are phototoxic, but these species are not indigenous to the Intermountain

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West. The foliage of cultivated parsnips, carrots, and celery is phototoxic and has evoked photosensitization in workers involved in their harvesting or processing.

Cymopterus longipes, a species common in pastures in northern Utah, does not produce phototoxic foliage, but does produce highly phototoxic seeds (Egyed and Williams 1977). The seeds contain the furocoumarin isoimperatorin.

Most livestock losses from photosensitization in the Intermountain West have been caused by spring parsley (Williams 1968). This small perennial grows in the early spring from southeastern Oregon and southwestern Idaho through Nevada to southwestern Utah. Spring parsley synthesizes the furocoumarins xanthotoxin and bergapten (Williams 1970). Xanthotoxin, which is five times more phototoxic than bergapten, occurs in greater concentrations. The appearance of the plant in southwestern Utah in late March and early April coincides with lambing. Ewes that graze the plant become photosensitized. Udders and teats become so inflammed and sensitive that the ewes refuse to let their lambs nurse. Losses of lambs from starvation and dehydration have run as high as 25 percent on some ranges in southwestern Utah and eastern Nevada.

Photosensitization in chicks fed leaves and seeds of spring parsley was characterized by erythema and swelling of scales on legs and feet, and acute erythema of the comb, beak, and eyelids. Young chicks were deformed after severe photosensitization (Van Kampen and others 1969). The upper beak failed to develop and was much shorter than the lower beak. The comb, wattle, eyelids, and other epidermal structures became gangrenous and sloughed after edema caused by the photosensitization disrupted blood circulation to those areas. Contracture of fibrous tissue in the legs resulted in deformities and sloughing of digits of the feet.

CONTROL METHODS

Spring parsley is the only primary photosensitizer in the Intermountain West for which a method of chemical control has been established (Williams and others 1970). Spring parsley was controlled 99 percent by one application of 2,4-D amine or ester applied at 2 lb/acre when plants were in early to late flower, usually from the middle of April to early May. These treatment dates are somewhat earlier than those recommended for control of big sagebrush (Artemisia tridentata); nevertheless, 2,4-D amine or ester usually controlled 50 to 70 percent of the adjacent big sagebrush when applied from the middle of April to early May.

Plots treated with 2,4-D were reevaluated three years after treatment to determine residual control of spring parsley. Little or no reinfestation occurred on these plots. Spring parsley was replaced primarily by ground smoke (Gayophytum diffusum) and common ragweed (Ambrosia artemisiifolia). No increase in grasses was noted. Downy brome (Bromus tectorum), squirreltail (Sitanion hystrix), reverchon threeawn (Aristida glauca), and Indian ricegrass (Oryzopsis hymenoides) occurred on the plots but were generally located under or adjacent to big sagebrush. Although spring parsley produced seed abundantly each year, the plants did not establish readily from seed on the test site. Long-term control was possible, therefore, with one application of herbicide.

The phototoxicity of spring parsley decreased after application of 2,4-D amine or ester. Within 4 weeks after treatment the plants were not phototoxic at the highest rate (800 mg) that could be administered in a single dose to 1-week-old chicks, whereas 150 mg of the control plant was phototoxic.

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A REVIEW OF PINE NEEDLE AND BROOM SNAKEWEED ABORTION IN CATTLE

Kip E. Panter and Lynn F. James

ABSTRACT: The ingestion of ponderosa pine (Pinus ponderosa) needles and broom snakeweed (Gutierrezia microcephala or G. serothrae) results in significant losses each year to the cattle industry because of abortion and related complications. Pine-needle-induced abortion in cattle is predominantly a problem in the Western United States. Broom snakeweed causes significant losses in the Southwest; however, the plant is spreading northward and is found in most of the Western States, Mexico, and Canada. Abortions from pine needles and broom snakeweed are characterized by weak uterine contractions, early vulvar swelling, mucous or bloody discharge, premature udder filling, birth of small, weak or nonviable calves, abortion, retained placenta, and post-abortion toxemia. Death of the cow is common if treatment is not provided.

INTRODUCTION

Ponderosa pine (Pinus ponderosa) (fig. 1) grows in every State west of the great plains, in Western Canada, and is the State tree of Montana. It has a total stand greater than any native tree in the Western United States except Douglas-fir (Pseudotsuga menziesii). It grows at elevations between 5,000 and 8,000 feet, is drought resistant, and reaches a height of over 200 feet and is 5 to 8 feet in diameter under ideal environmental conditions. It is extensively harvested for lumber. During early growth the bark is dark brown to black, thus the name blackjack pine. Older trees develop a bark color of cinnamon brown to orange yellow. Other common names include western yellow pine, western soft pine, yellow pine, and bull pine (USDA 1949; Collingwood and Brush 1955). Ponderosa pine has needles 5 to 10 inches long growing in clusters of two to three. The cones are brown, 3 to 6 inches long, and frequently grow in clusters.

A partial nutrient composition of pine needles from two different areas in Wyoming revealed values comparable to those of low quality hay (table 1) (Hamilton and Miller 1956; Kamstra and Cogswell 1975).

Figure 1.--Ponderosa pine (Pinus ponderosa) typical of the size often grazed by cattle (8 to 10 feet in height).

Table 1.--A partial nutrient composition of ponderosa pine needles

Nutrient	Unit	Amount
Carotene[1]	Mg/g	184.5
Ash[1]	Percent	2.4
Crude protein[1]	Percent	6.9
Ether extract[1]	Percent	12.1
N free extract[1]	Percent	46.3
Calcium[1]	Percent	0.34
Phosphorus[1]	Percent	0.15
Ca/P ratio[1]		2.3/1
Magnesium[1]	Percent	0.21
Manganese[1]	ppm	110.1
Nitrate[1]		Trace
Fiber content[2]	Percent	28-35
Lignin[2]	Percent	12-15
Digestibility[2]	Percent	30-42

[1] Taken from Hamilton and Miller (1956).
[2] Taken from Kamstra and Cogswell (1975).

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Figure 2.--Broom snakeweed (Gutierrezia serothrae) in flower.

Figure 3.--Heavy stands of broom snakeweed in New Mexico.

Broom snakeweed (Gutierrezia serothrae, fig. 2) is commonly called perennial snakeweed, slinkweed, turpentine weed, or matchbrush; and G. microcephala is called threadleaf broomweed. The two species are similar morphologically.

The snakeweeds are widely distributed in the Western United States, Mexico, and Canada. They extend from central Texas to California and from Saskatchewan, Canada, to northern Mexico (Lane 1985). They are widespread and invade depleted or disturbed rangeland excluding more palatable species (fig. 3). The snakeweeds are toxic to cattle, sheep, and goats. Abortion is a serious problem; losses occur every year (Mathews 1936; Dollahite and Anthony 1956; Dollahite and Anthony 1957; Dollahite and Allen 1959).

Snakeweeds are short-lived perennial shrubs ranging from 6 inches to 2 feet tall. Many unbranched erect stems originate from a woody base and die back when the plant enters dormacy. The leaves are narrow (1/8 to 1/4 inch wide) and 3/4 to 1-1/2 inches long. The flowers are yellow, in numerous clusters with three flowers per head in G. serothrae and one or two per head in G. microcephala. This is the distinguishing morphological difference between the two species (McDaniel and Loomis 1985).

The average life span of snakeweed is about 2.5 years (Parker 1982). Seedlings are sensitive to soil moisture, competition from other plants, and most die within the first year. Snakeweed rapidly increases in heavily overgrazed, burned, or disturbed sites and during and following drought. Its seeds germinate when favorable precipitation resumes and it rapidly increases as a result of reduced plant competition (Parker 1982).

TOXICITY

Pine Needles

Primary toxicological effects of pine needles in cattle are abortion and complications associated with the abortion, such as retained placenta, metritis, toxemia, and death. Abortions in cows eating ponderosa pine needles generally occur in late fall, winter, and early spring. This time corresponds to when cows in most western cow-calf operations are in the third trimester of pregnancy and when cattle are most likely to graze pine needles (Stevenson and others 1972; James and others 1977). Abortions have been induced as early as 3 months gestation and have been reported by ranchers to occur anytime. However, the closer the ingestion of needles is to the time of normal parturition, the higher the incidence of abortion. Abortion may occur any time between 24 hours and 2 to 3 weeks following the ingestion of pine needles (Stevenson and others 1972; James and others in preparation). Abortions frequently occur following a single exposure to the needles (James and others 1977; Panter and others 1985), but results from controlled experiments indicate the highest incidence of abortion is in cows eating the needles over a period of days (James and others in preparation; Panter and others 1985). Abortions have been associated with grazing green needles from trees, slash from the lumber industry, and dead, dry needles from the ground (Stevenson and others 1972; James and others 1977). Other coniferous members of the pine family, spruces, junipers, and arbor-vitae may also cause toxic effects if grazed heavily (Tucker 1961; Muenscher 1975).

Usually cows do not graze pine needles, presumably because of their resinous taste and coarse texture, but under certain circumstances needles may be eaten heavily. A number of factors are believed to cause pregnant cows to graze pine needles. Those circumstances may be stress related such as sudden weather changes that force cattle to seek the pine trees for shelter; lack of feed when cattle are hungry; changes to unfamiliar or poor quality feed; or sudden access to pine needles from windfalls or from lumbering operations; boredom or curiosity; and accidental ingestion with other feed (Stevenson and others 1972).

Abortions are characterized by weak uterine contractions, excessive uterine hemorrhage, incomplete dilation of the cervix, and often a characteristic nauseating odor. When cows graze needles over a period of time there is generally premature filling of the udder, early vulvar swelling, mucous or bloody discharge, abortion, birth of small weak calves, retained placenta, and post-abortion toxemia; death may occur (James and others 1977).

As the length of gestation increases, the vigor of the calf and the chance of survival increases. It appears that if the calf is delivered rapidly, early in the process of parturition, the calf's chance of survival is improved.

A persistent retained placenta is frequently observed regardless of the stage of gestation when the abortion occurs (Stevenson and others 1972). It has been observed that some herds of cattle that had access to pine needles, but did not abort, had a high incidence of retained placentas. Calves from these cows are often born small and weak and their survival rate is low. Some believe these calves are more susceptible to calfhood diseases.

Sheep, goats, and wildlife have been reported to abort from ingestion of pine needles (Stevenson and others 1972; McKnight 1985). However, research at our laboratory suggests that sheep are not as susceptible to the abortifacient effects of pine needles as cattle.

Toxic effects from pine needle extracts given to laboratory animals have been reported; however, toxic effects in livestock are equivocal. Pine needles fed to open cycling heifers were not toxic (Staigmiller and Panter 1985). The rapid death of many cows after abortion occurs suggests an acute toxemia resulting from the abortion and retained placenta.

The abortifacient agent(s) in pine needles are not known. Some researchers have suggested that mycotoxins may be the cause of the abortion (Chow and others 1974); others have suggested that ingestion of pine needles induces an infection with the microorganism Listeria monocytogenes, a known cause of abortion (Gray and Killinger 1966; Hether and others 1983; Hether and Jackson 1983; Adams and others 1979). Water-soluble fractions have been shown to cause resorption, stillborn kits, and reduced uterine growth in mice. The detrimental effect was lost when the aqueous fraction was autoclaved (Chow and others 1972). Similarly, pelleting of pine needles with steam eliminated the abortifacient effect of pine needles (Faulkner 1969). Cook (1960) reported that a water-soluble fraction of an acetone extract decreased the uterine weight in immature female mice, but failed to cause reproductive dysfunction. Others reported complete reproductive failure from ingesting the pine needle residue after aqueous extraction, suggesting the presence of a water-insoluble toxin (Anderson and Lozano 1977). Wagner and Jackson (1983) reported a phytoestrogenic effect in pine needles that competed with 17-β estradiol for binding to mouse uterine cytosol. Embryonic resorptions were observed in mice after hexane extracts were administered early in gestation. The active components in this extract were isolated and identified as a mixture of diterpene resin acids that included pimaric, isopimaric, sandaracopimaric, palustric/levopimaric, abietic, dehydroabietic, and neoabietic acid (Kubik and Jackson 1981). Anderson and Lozano (1979) reported a heat stable toxin soluble in methanol, ethanol, chloroform, hexanes, and 1-butanol that caused embryonic resorption in pregnant mice during the first 10 days of gestation. It is obvious from this short review that there is still much to be learned about the abortifacient element in pine needles, whether it be water soluble, water insoluble and heat stable, or heat labile.

Broom Snakeweed

Broom snakeweed causes abortion in cattle, sheep, and goats (Mathews 1936; Dollahite and Anthony 1956; Dollahite and Anthony 1957; Dollahite and Allen 1959). The abortion is similar to that from pine needles: premature udder development, early vulvar swelling, mucous and bloody discharge, abortion, birth of small weak calves, retained placenta, post-abortion toxemia, and death. There are, however, differences in toxicity. Broom snakeweed is toxic to cattle, sheep, and goats. Clinical signs of broom snakeweed toxicoses include anorexia, mucopurulent nasal discharge, crusted and sloughing skin and muzzle, listlessness, rough hair coat, hematuria, frequent painful urination, diarrhea in early stages followed by constipation, and large amounts of white mucous in foul smelling feces (Mathews 1936; Dollahite and Anthony 1956; Dollahite and Anthony 1957). The greatest losses occur from abortion in cattle. Mortality in cows is high if they do not receive supportive therapy.

Broom snakeweed varies in toxicity at different phenological stages and the site where it is growing. It is more toxic when growing rapidly, especially in the early stages of leaf growth. Although broom snakeweed grows abundantly on limestone soils, only sporadic losses are reported. Experiments have shown that abortions are much more prevalent when broom snakeweed grown on sandy soils is grazed (Dollahite and Anthony 1957).

The abortifacient and toxic elements in broom snakeweed have not been identified. Abortion and death were induced when saponins extracted from broom snakeweed were injected intravenously in cows, goats, and rabbits. Saponins administered orally to rabbits also caused abortion. However, a saponin from lechugilla (Agave lecheguilla), known to be toxic, and a supposedly nontoxic, pharmaceutical-grade saponin produced abortion and death when administered intravenously to pregnant rabbits (Dollahite and others 1962; Shaver and others 1964). Molyneux and others (1980) identified the major mono terpenes and sesquiterpenes in the essential oil fraction of Gutierrezia sarothrae. These included alpha-pinene, myrcene, linalaol, cis-verbenol, trans-verbenol, verbenone, geraniol, caryophyllene, and gamma-humulene.

ECONOMIC LOSSES

The actual economic losses from pine needle and broom snakeweed abortion and toxicity are not known, but losses occur in most areas where these plants grow. The incidence of abortion in an outbreak may vary from only a few to 100 percent. Mortality in cows is high if they do not receive supportive therapy.

Pine needle abortion occurs in the Western United States where heavy stands of ponderosa pine grow. Surveys conducted by the National Cattleman's Association and others in the Black Hills area of South Dakota, Montana, and Wyoming suggest that pine needle abortion is a serious economic problem (Robinson 1984). In addition to the economic losses due to the abortions, the costs of management such as pruning, fencing cattle away from the pines, lost forage, supplemental feeding, increased veterinary care, and increased calving intervals must be considered. In an attempt to establish monetary losses from pine needle abortion, a Crook County, SD, survey estimated that $700,000 was lost in one county from pine needle abortion (Robinson and Flinn 1984). This averaged over $10,000 per rancher and included: abortions, calf losses, increased management to avoid pines, increased veterinary care for weak calves and sick cows, and increased feed supplementation. These estimates did not include the losses from increased calving intervals that carry over for several years, decreased production in the cow due to loss of condition, decreased lactation, or the losses from small, poor-growing calves. One can easily conclude that economic loss to the livestock industry from pine needles could amount to many millions of dollars annually.

Broom snakeweed is predominantly a problem in the Southwestern United States. In 1961 the annual loss to the livestock industry in Texas alone was estimated to be between $2 and $3 million (Dollahite and Anthony 1957). A more recent estimate (McGinty 1985) put the direct annual cattle losses attributable to broom snakeweed at over $15 million. This does not include indirect losses such as underweights and loss of usable forage. If the losses occurring in New Mexico and Arizona were equal to this amount, then annual losses in the Southwest could exceed $30 million (McGinty 1985).

A conservative estimate of the combined losses to the cattle industry due to ponderosa pine and broom snakeweed is $40-50 million annually.

METHODS OF CONTROL

Ponderosa pine is important to the lumber industry. Methods of control have not been extensively studied. Suggested methods of control include clear-cutting stands in areas where cattle graze the needles, controlled burning, and experimental spraying. Spraying has been used on an experimental basis to keep young stands of pines from encroaching onto rangelands, but no methods of treatment have been published or recommended. Generally, management methods such as fencing pregnant cows away from the pines and supplemental feeding practices are used to reduce losses from pine needles.

For broom snakeweed, methods of control have been tested. One method is to apply 2,4-D at a rate of 1 lb/acre for 2 successive years. Significant control requires good soil moisture and growing conditions present (Sperry and Robinson 1963). Picloram has been effective when applied at rates ranging from 0.25 to 1 lb/acre for pellets and liquid (Schmutz and Little 1970; Gesink and others 1973). More recently low rates of picloram in combination with other herbicides have proven effective and less expensive. Picloram at 0.25 lb/acre in combination with 2,4-D at 1 lb/acre, or in combination with tryclopyr at 0.4 lb/acre, or in combination with dicamba at 0.25 lb/acre has produced kill rates greater than 95 percent (Jacoby and others 1982; Sosebee and others 1982a). A good kill rate can be obtained any time the plant is actively growing, but best results have been obtained at the end of the flowering period (Sosebee and others 1982b).

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Section 4. Foraging Behavior

DIET TRAINING: BEHAVIORAL CONCEPTS AND MANAGEMENT OBJECTIVES

Frederick D. Provenza and David F. Balph

ABSTRACT: Diet training is the manipulation of livestock dietary habits to meet a management objective. We believe diet training has the potential for making livestock production more efficient and rangelands more productive for livestock. This paper briefly describes some behavioral concepts underlying diet training and outlines potential management objectives for livestock and rangelands. These objectives include training young animals: (1) to recognize, readily accept, and efficiently harvest foods that they will encounter later in life; (2) to avoid desirable or poisonous plants; and (3) to better accept plants that have low palatability.

INTRODUCTION

Commercial success is determined by the relationship between production costs and prices received for a product. Livestock producers have relatively little control over the prices they receive for animals but can manage costs. Economic survival when profit margins are low, as they often are, necessitates a search for economical operations.

Diet training of livestock is a developing concept that may be useful in reducing costs of raising livestock. Diet training is the manipulation of an animal's dietary habits to meet a management objective. Elsewhere, we present theoretical arguments and empirical evidence supporting the concept as well as some inherent constraints on diet manipulation (Provenza and Balph in press). This paper reviews (1) behavioral principles upon which this type of management is based and (2) potential management objectives.

FEASIBILITY OF DIET TRAINING

Role of Learning

Natural selection matches an animal to its environment. This match with respect to foraging behavior of livestock probably still exists, because domestication has resulted in more quantitative than qualitative changes (Price 1984). Generalist herbivores such as livestock encounter a variety of potential foods on rangelands, some of which are appropriate while others are not. We believe the difficulty in discriminating among forages gives a selective advantage to animals whose diet selection is based on generality and flexibility. Learning what to eat and what to avoid provides generality and flexibility.

Evidence that ungulates learn what and what not to eat comes from a variety of sources. For example, animals of the same species reared in different habitats often prefer different foods when foraging in the same habitat (Arnold 1964; Leuthold 1971; Arnold and Maller 1977; Martin 1978; Frost 1981; Bartmann and Carpenter 1982). Sheep not only select foods based on their taste and texture, but also prefer foods that they can ingest quickly (Kenney and Black 1984), a factor that is probably also governed by learning. Livestock can also learn to avoid palatable foods that make them sick (Zahorik and Houpt 1977, 1981; Thorhallsdottir and others in press). These studies suggest that food habits are modified by past experience rather than determined by a presumption strategy based on energy or nutrient gain (Pyke 1984; Krebs and McCleery 1984).

Animals feeding on known foods in familiar settings (for example sheep: Arnold 1970; Arnold and Maller 1977; goats: Provenza and Malechek in press; cattle: Hodgson 1971; Hodgson and Jamieson 1981) spend less time, and hence energy (Osuji 1974), foraging but ingest more food than inexperienced animals. These differences in foraging efficiency, which persisted for as long as trials were conducted, in some cases 10 months, suggest that learning may affect foraging skills as well as food recognition and acceptance.

Learning Efficiency

The use of social models to shape dietary habits of young livestock may increase learning efficiency. Social learning may help an inexperienced animal learn from an experienced animal, thus avoiding the inefficiency and risk of testing everything itself. Social learning theory (Bandura 1977; Boyd and Richerson 1985) predicts that the best models are nurturants and respected peers. The genetic relationship between a mother and her young means that they should respond similarly to cues provided by, and consequences associated with, foods. The mother might also influence food habits of her young by transmitting odors and tastes from foods through her milk (Galef 1976; Madsen 1977).

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The evidence that social learning may be important to livestock comes from recent studies of sheep. Ewes apparently influence lambs' consumption of molasses-urea blocks (Lobato and others 1980) and whole-grain wheat supplements (Lynch and others 1983; Green and others 1984). Our research (Thorhallsdottir and others 1986) suggests that young lambs exposed to foods with their mothers consume about twice as much of the same foods after weaning as do lambs exposed with an adult ewe that is not their mother. Lambs exposed with an adult ewe consume about twice as much of the foods as do lambs exposed alone. Lambs allowed to eat the foods during exposure consume about twice as much of the foods after weaning as do lambs that only observe the foods or the mother or another adult ewe eating the foods.

Food imprinting, should it exist, may also increase learning efficiency. Imprinting is a type of learning that occurs during a sensitive period; the behavior learned during this period persists throughout life (reviewed by Hess 1973; Immelmann 1975). Imprinting helps an animal acquire important information during a specific time. Should food imprinting occur in livestock, diet training could be brief and animals would remember what they have learned. The sensitive period may be during weaning (Martin 1984). During weaning the developing animal must make the major transition from complete dependence on maternal care to independence (Galef 1981). Young herbivores initially learn about foods during this period, and can learn from their mothers. The age at which young are weaned naturally depends on the nutritional status of the mother (Arnold and others 1979), and the sensitive period may coincide with the weaning period rather than a specific age.

Limited evidence suggests that young animals learn about foods more readily than older animals, but little empirical evidence exists to suggest that the phenomenon is food imprinting. Arnold and Maller (1977) found that sheep from different environments persistently selected diets of different botanical composition, and that dietary experiences in early life had more effect on later dietary habits than when these experiences occurred at older ages. Further, Lobato and others (1980) found that sheep ate molasses-urea blocks if they had been exposed to them as lambs before about 9 months age suggesting a sensitive period. Lynch and others (1983), however, were unable to detect any difference in the response of lambs exposed to whole-grain wheat at different ages during the first 11 weeks of life. Finally, we exposed lambs as (1) monogastrics, (2) during weaning, and (3) as ruminants to the shrub Cercocarpus montanus (Squibb and others 1986). Our results are consistent with the hypothesis that a sensitive period for learning occurs during weaning, but do not rule out other explanations.

LIVESTOCK PRODUCTION OBJECTIVES

If learning affects food recognition and ingestion rates, animals such as replacement females which are reared in one environment and moved to new environments where the physical and chemical characteristics of foods are unfamiliar may forage inefficiently; they are forced to relearn what and how to eat (Zimmerman 1980). Exposing young animals to foods they will encounter later in life could increase livestock performance and thereby reduce costs. Such training might also enhance intake of supplements such as protein blocks, shrubs on grass-shrub pastures (Gade and Provenza in press), or rations in feedlots.

Animals moved to new environments also encounter unfamiliar poisonous plants and may be more vulnerable to those plants than animals familiar with them (Behnke 1980). Losses caused by poisonous plants might be reduced if we better understood how livestock detect and avoid toxic plants, and if young livestock could be trained to avoid harmful plants that are highly palatable or contain slow-acting poisons. To date, however, little research on this topic has been conducted with domestic livestock.

Most research on learned food aversions has been conducted by psychologists studying rats (Braveman and Bronstein 1985). Rats are capable of discovering a harmful food up to 12 hours after ingesting a meal of several items, only one of which was harmful (Rozin 1976). Rats respond to novel foods or foods eaten in novel places by periodically sampling the item and eating increasing amounts as long as they experience no adverse consequences. If they become ill, they immediately avoid the novel food and eat only what has been safely consumed in the past.

Ruminants may or may not fit the rat taste aversion model. As generalist herbivores, they also encounter noxious foods. Ruminants, however, have complex stomachs and may sense gastronomic distress differently from rats. Ruminants also ingest many foods during long periods of foraging, which may make it more difficult for them to discover if a food is harmful. Published literature on this topic indicates that livestock can be trained to avoid certain foods if they are simultaneously given lithium chloride (LiCl), a gastrointestinal poison (Zahorik and Houpt 1977, 1981). Our research (Thorhallsdottir and others in press) on learned food aversions suggests that sheep persistently avoid palatable foods containing LiCl; however, they sample small quantities of foods associated with illness and increase consumption when ingestion is no longer paired with illness. Additional research is required to fully determine the learning abilities of livestock and evaluate the potential management value of conditioned food aversions.

RANGE MANAGEMENT OBJECTIVES

Rangelands contain many kinds of plants, some preferred more than others by livestock. Traditionally, ranges are improved by reducing the abundance of less preferred species and planting more preferred species (reviewed by Vallentine 1971). Rather than directing all our efforts at improving rangelands for livestock, perhaps we could better match the foraging behavior of livestock to rangelands.

Selective grazing of preferred plant species by livestock can cause undesirable changes in soil stability and plant composition on rangeland (Stoddart and others 1975). To the degree that livestock can be conditioned to increase consumption of less palatable and weedy species, undesirable changes in soils and vegetation can be mitigated. Increasing utilization of less desirable species by even 10 to 20 percent might prevent, or at least delay, such changes.

Conversely, diet training might be used to prevent livestock from eating plant species desirable to foresters. Livestock grazing in forest plantations can enhance tree seedling growth and survival, but livestock often consume tree seedlings along with herbaceous species (Hsieh 1985). Aversive conditioning might be used to train young livestock to avoid tree seedlings.

Finally, managers base the carrying capacity of rangeland on the distribution of animals, and broad distribution of livestock is essential for effective use of the forage resource (Cook 1967). Learning may affect habitat selection (Hunter and Milner 1963; Cook 1967) as well as dietary habits. If so, it may be possible to train livestock to use a greater proportion of the range. Such training would enhance use of the forage resource and thereby increase carrying capacity. In addition, it may be possible to teach livestock to seek out and use sections of the range differentially. Such training could be used to increase use of upland, as opposed to riparian habitats, an important management objective in areas of the western United States where excessive use of riparian areas by livestock causes degradation of fishery resources.

CONCLUSIONS

We believe learning plays a fundamental role in the development of an herbivore's dietary habits. The likelihood that livestock learn to forage presents both problems and opportunities to livestock producers and range managers. Learning may result in inefficient or inappropriate foraging when animals are moved to new environments. Conversely, the manipulation of dietary experience may let a manager create a foraging group better suited to specific management goals.

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DOMESTIC HERBIVORE FORAGING TACTICS AND LANDSCAPE PATTERN

R. L. Senft

ABSTRACT: This paper outlines a conceptual model of large herbivore interactions with vegetation pattern. Foraging decisions by large generalist herbivores aggregate into characteristic patterns at landscape and plant community levels. At the landscape level, domestic herbivores select plant communities and certain topographic zones as feeding areas. Community preference (percent feeding time/percent pasture area) follows a modified matching pattern and is directly proportional to relative biomass of preferred plant species. At community and individual plant levels, species preference (percent in diet/percent in herbage) is an exponential function of relative palatability, where palatability is loosely correlated with nutritive quality and(or) presence of phytochemical deterrents. This is an overmatching pattern (Staddon 1983) as animals exhibit a disproportionate response to selection cues.

INTRODUCTION

What are general patterns of plant-herbivore interactions? What aspects of the forage environment provide relevant ques for habitat and diet selection? What "rules" do herbivores use to select food items? These questions are of practical as well as theoretical interest. Understanding plant-herbivore interactions would allow prediction of animal foraging behavior under a variety of management regimens and in a wide range of vegetation types. Further, elucidation of basic patterns of herbivore foraging would provide a framework within which the influence of plant secondary compounds could be evaluated.

A model of foraging behavior should include units of selection, plausible currencies and rules for discriminating among feeding options in a complex forage environment. A rudimentary model of plant-herbivore interactions is proposed. Although formulated at the level of foraging patterns (i.e., averages of many individual foraging decisions), the model may be elaborated to describe interactions with chemically complex vegetation. Further, the model may serve as a guide for predicting animal responses to changes in plant communities and to landscape-level pattern.

HIERARCHICAL FOOD RESOURCES

Vegetation may be viewed as hierarchically structured (Forman and Godron 1981). Although levels are to some extent observer-defined (Allen and Starr 1982), hierarchy concepts can provide a framework for dealing with ecological complexity in ways relevant to foraging behavior. In wildland ecosystems, individual plants aggregate in conjunction with soils to form plant communities, boundaries of which may be gradual or sharply defined. At a higher level of organization, soil-plant associations aggregate with landforms to form landscape systems (Forman and Godron 1981). For our purposes boundaries of a landscape system will be the limits of movement of an ungulate herd for some reasonable length of time. For domestic herds these boundaries may coincide with fencelines or be defined by home range behavior (Hunter 1964). At the lower end of the scale, plants themselves are hierarchically structured in ways relevant to animal nutrition and feeding behavior.

Large herbivore foraging behavior assumes different forms at different levels of the ecological hierarchy (table 1). The relevant response at a given level is preference for units comprising the next lower level. Selection of preferred feeding areas within the home range occurs at the landscape level, units of selection being plant communities or terrain types. Diet selection occurs at both plant community and individual plant levels, involving discrimination among individual plants and plant parts.

COMMUNITY-LEVEL FORAGING

Diet selection in large herbivores is based in large part on palatability of plant species and plant parts (Heady 1964). Palatability is loosely correlated with nutritive quality and may be modified by plant physical characteristics, presence of secondary compounds, and prior feeding experience. In fairly simple vegetation types, relative species preference (RP = percent in diet/percent in herbage) may be an exponential function of relative nutritive quality (RNQ):

$$RP_i = e^{k(RNQ_i - 1)}$$

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where k is a selectivity coefficient (Senft 1984). RNQ is the ratio of a positive nutritional currency in item i to the mean level in the community:

$$RNQ_i = \frac{x_i}{\sum_{j=1}^{n} b_j \cdot x_j}$$

where x is concentration of the nutrient and b is proportional biomass of a food item.

Where secondary compounds provide strong negative signals to diet selection, RP may be a negative exponential function of concentration (see other papers in this volume). Therefore, species preference may be better expressed as an exponential function of palatability rather than of nutritive quality. Palatability in this case may be a multivariate function of physical and chemical characteristics. For modeling purposes, it may be convenient to represent intrinsic palatabilities as dimensionless numbers derived from field or laboratory trials (Senft and others 1986).

Disproportionate preference for relatively nutritious items results in diets being higher in nutritive quality than the herbage on average. Exponential selection response to nutritive quality may thus result in a nutrient maximization pattern (Belovsky 1984). This is not a strict maximization response as low quality or peripheral diet items may make up significant proportions of the diet due to high relative availability. Further, nutritive properties of some items may be masked by unpalatable secondary compounds (Provenza and Malechek 1984), resulting in an apparent strategy of minimization of toxic compounds.

LANDSCAPE-LEVEL FORAGING

Large herbivores interact with landscape pattern through selection of feeding areas. In arid and semi-arid regions, domestic herbivores frequent mesic lowlands and drainages due in part to location of preferred plants and to herbage response to soil moisture (Culley 1938; Moorefield and Hopkins 1951; Peterson and Woolfolk 1955). In forested areas, grazers may concentrate on open meadow communities (Senft 1986). Browsers, on the other hand, may concentrate on patches in which preferred woody species are abundant (Hanley 1984). Correlational studies have suggested that preference for plant communities (RCP) is a linear function of relative abundance and(or) nutritive quality of food plants (Hunter 1962; Hanley 1984; Senft and others 1985; Senft 1986). This response is similar to Herrnstein's (1970) matching law, an aggregate pattern in which relative feeding effort is proportional to relative reward. Herrnstein's model can be readily modified to describe landscape level foraging patterns by:

$$RCP_i = \frac{G_i}{A_i} = \frac{B_i}{\sum_{j=1}^{n} A_j B_j}$$

where G is the proportion of total grazing time spent in a community, B is absolute biomass (kg/ha) of preferred plants and A is proportional area of a community. The quantity on the left side of the matching equation is community preference, that on the right side is relative biomass availability. To account for the effects of nutritive quality or palatability, biomass of individual species may be weighted by palatability ratios. It should be noted that the matching model describes community use as a function of a foraging currency; modifying terms must be added to account for factors such as topography or proximity to a watering point (Senft and others 1985). Nonetheless, this model may describe community use in widely divergent vegetation types (fig. 1).

IMPLICATIONS

An unexpected result of large herbivore foraging rules is an indirect relationship between preference and relative availability. In a hypothetical community composed of a palatable and an unpalatable plant, preference for either species is related to relative contribution to the herbage (dotted lines in fig. 2a). Accordingly, species preferences show wide variation when items are rare and converge to neutrality (RP approaches 1.0) when common (points in fig. 2a). A

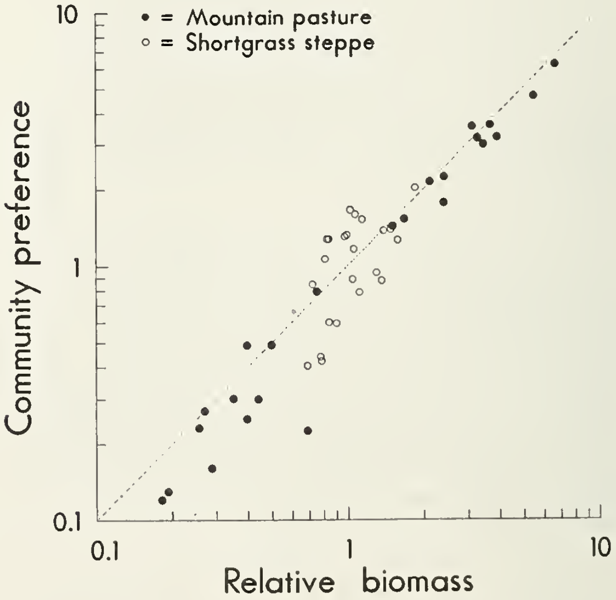

Figure 1.-- Relationship between relative community preference in cattle and relative graminoid biomass on shortgrass steppe and forested mountain pastures (Senft and others 1985; Senft 1986).

similar relationship is found between community preference and relative area (percent of total pasture area) (fig. 2b). Because of the exponential nature of the species selection rule the range in species preferences is wider than that observed for community preference.

The hierarchical foraging model may be useful in predicting large herbivore exploitation of landscape mosaics containing plants bearing anti-herbivore chemistry and the role of herbivores in succession in vegetation types where phytochemical deterrents are important. The main consequence of the community-level availability effect (fig. 2a) is that unpalatable plants will be strongly avoided until they comprise a majority of available forage in a community. At the landscape level, communities with large proportions of unpalatable plants will be avoided in favor of communities with large proportions of palatable plants. Since animals respond primarily to biomass of preferred plants, this would hold true even if the total biomass in the community comprised of palatable plants were less than that in the community comprised of unpalatable plants (see Hunter 1962). Thus, there would be strong tendency for animals to utilize plants without phytochemical deterrents, particularly in communities dominated by palatable species. The net effect would be to push the composition of plant communities and of the landscape system towards dominance by plants bearing secondary compounds (see related papers in this volume). Thus, as palatable plants become increasingly rare, pressure by herbivores will increase, thereby accelerating successional trend.

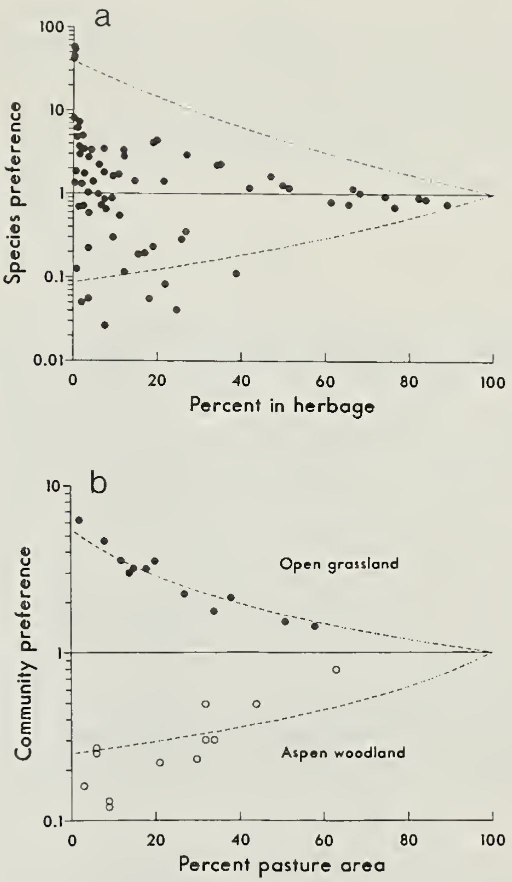

Figure 2.-- a. Effect of species relative abundance on dietary preferences. Dotted lines indicate predictions by the exponential species preference function for low- and high-quality plant species. Points indicate preferences observed on shortgrass steppe communities (Senft and others 1984).
b. Effect of proportional mix of plant communities in a landscape mosaic on community preference (Senft 1986).

CONCLUSION

The foregoing suggests that there may be basic forms or patterns to plant-herbivore interactions that are independent of vegetation type and perhaps general across species. Patterns of interaction differ with level of ecological organization. Yet, there are underlying similarities in the basic type of response (preference) and in relativistic nature of foraging currencies. Further, although details of interactions

Table 1.-- Summary of domestic herbivore interactions with landscape pattern

Level of ecological organization	Units of selection	Foraging behavior	Aggregate response pattern	Environmental influences
Plant community	Plant species Individual plants Plant parts	Diet selection	Overmatching	Nutritive quality Plant architecture Secondary compounds
Landscape	Communities	Selection of feeding areas	Matching	Forage biomass and quality

are both animal species- and vegetation type-dependent, generalized models may be useful for predicting animal response to changes in plant community composition or to landscape mosaics of differing composition. Predictions of the foraging model may be useful in interpretation of field and laboratory studies of herbivore interactions with plants bearing anti-herbivore chemistry.

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SNOWBERRY (SYMPHORICARPOS OREOPHILUS) DEFOLIATION BY SHEEP: AN EXAMPLE OF SELECTIVE BROWSING

Calvin F. Bagley, G. B. Ruyle, and James E. Bowns

ABSTRACT: Diet selection decisions made by herbivores include selection among plant species, individual plants, and plant parts. This paper describes how the shrub snowberry was selectively defoliated by sheep. Leaf-to-stem ratios were sampled using an inclined-point frame, before and after sheep browsing. Additionally, browsed snowberry stems were counted in randomly located plots and browsing method (leaves stripped from the stem or entire stems removed) was recorded. Sheep usually stripped the leaves from the stem, rarely removing any part of stem, significantly reducing leaf-to-stem ratios. Because leaves were selectively removed the traditional concept of utilization as percent removal of current year's growth may not be applicable for determining sheep grazing pressure on snowberry and similar browse species.

INTRODUCTION

Snowberry (Symphoricarpos oreophilus Gray) provides a valuable source of forage for sheep on southwestern Utah summer ranges, even when herbaceous vegetation is not limiting (Bowns 1971; Bowns and Matthews 1983; Ruyle and Bowns 1985). To determine desirable stocking rates on rangelands, accurate methods of estimating utilization of snowberry and other shrubs by livestock and wildlife are important. Many methodologies for estimating shrub utilization have been developed (Bowns 1978) but, due to the mechanics of browsing behavior in sheep and other herbivores, interpretation of the estimates from some standard sampling techniques is difficult unless these techniques are altered or qualified in some way. When browsing, sheep generally strip the leaves from the stem, leaving the stem intact. The percentage of measured biomass removed compared to total year's growth is therefore relatively low. This selective harvesting of leaves results in most of the plant's photosynthetic material being removed, and causes greater stress on the plant than would be interpreted by estimates of biomass removed.

Recent emphasis has been placed on a method of correlating browsed twig-diameter relationships to utilization (Basile and Hutchings 1966; Jensen and Urness 1981; Provenza and Urness 1981). Regression equations have been developed using this technique for snowberry on mountain pastures in southwestern Utah by Ruyle and others (1983). The inclined-point frame is another useful sampling tool that can be used for a nondestructive assessment of a shrub's vegetative structure. The point frame is used to measure the relative frequency of foliage area and a ratio of various plant parts to one another (such as, leaf:stem, green:dead; Warren-Wilson 1960, 1963, 1967). An automated point frame system can minimize errors; the fixed nature of the point diameter, which never exceeds 25 um, reduces subjectivity of the operator and increases sampling speed (Caldwell and others 1983).

Our study examined the selective browsing behavior of sheep. Our purpose was to use leaf-to-stem ratios to quantify the observed selective browsing of leaves, and to compare this measurement of selective defoliation with the regression model of twig-diameter relationships and the percentage of grazed stems.

STUDY AREA

The experiment was conducted on a mountain rangeland in southwestern Utah near Cedar City. The study area was located on a high mountain loam range site at an elevation of 2 500 m. Vegetation consisted of a mosaic of aspen (Populus tremuloides) with a snowberry understory interspersed with open areas of grassland and snowberry. Kentucky bluegrass (Poa pratensis) and Letterman needlegrass (Stipa lettermanii) were important associated grasses.

METHODS

An automated fiber-optic point frame (fig. 1; Caldwell and others 1983) with a 32.5° inclination (Warren-Wilson 1960) was used to compare changes in leaf:stem ratios resulting from grazing by sheep. The fiber-optic probe optically recognizes vegetation contacts, termed hits, as it penetrates the shrub canopy. When a plant part is detected the motorized probe stops and a record of the part hit is made. One location with 70 pin travels through the canopy was sampled in 1982 and three locations

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(replications) with 50 pin travels each, were sampled in 1983. Due to the evenness of use in the small paddock and the small variation found in the first year's sample, three locations were determined to be an adequate sample size. For each pin travel a record of each hit on a snowberry leaf or a current year's stem was recorded, before and after sheep browsed the paddock (Ruyle 1983). Leaf:stem ratios were estimated by:

$$\text{Leaf:stem} = \text{Leaf hits} : \text{Stem hits} \qquad (1)$$

In both, years snowberry utilization was estimated using a method developed by Ruyle and others (1983) in which caliper measurements of the last intact internode on browsed stems were used to predict biomass removed by browsing. Two models were used to predict the amount of biomass removed. These models distinguished between two kinds of browsing--leaf only and entire stem removal. Utilization derived from this regression technique is defined as:

$$\text{Percent biomass removed} = \frac{\text{Biomass removed}}{\text{Biomass produced}} \times 100 \qquad (2)$$

In addition to this regression procedure grazed and ungrazed stems were counted and the percentage of grazed stems calculated. Percent grazed stems is defined here as:

$$\text{Percent grazed stems} = \frac{\text{Total stems grazed}}{\text{Total stems}} \times 100 \qquad (3)$$

During 1982, 20 ewes with lambs were confined to a 0.4-ha (1-acre) paddock for 5 days. In 1983, 11 ewes with lambs were confined in the same 0.4-ha paddock for 9 days. The resulting stocking rates were 0.60 ha/AUM (animal unit month) in 1982 and 0.61 ha/AUM in 1983, where 1 AUM is the equivalent of five ewes and lambs grazing for 1 month.

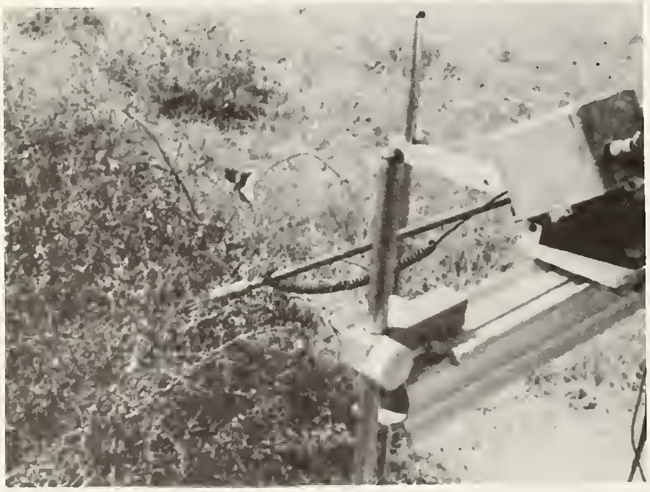

Figure 1.--Automated fiber-optic point frame system, in position to sample mountain snowberry.

RESULTS AND DISCUSSION

A comparison of the two utilization estimation methods showed a large disparity (fig. 2). The regression technique estimated biomass removed to be 33 percent, which indicates a low to moderate level of use. The grazed stems method estimated utilization to be 87 percent, indicating a heavy level of use. The selective browsing behavior of sheep provides an explanation for this disparity. When sheep browse snowberry they generally strip leaves from the stem leaving the stem intact (Ruyle and Bowns 1985) resulting in a high percentage of grazed stems but only a small amount of the plant biomass removed. In other research Ruyle and Bowns (1985) suggest that the upper limit of snowberry use by sheep, as estimated by the regression technique, is about 45 percent. A stand of snowberry that has been grazed at this intensity for several years is currently in low vigor with little or no regeneration.

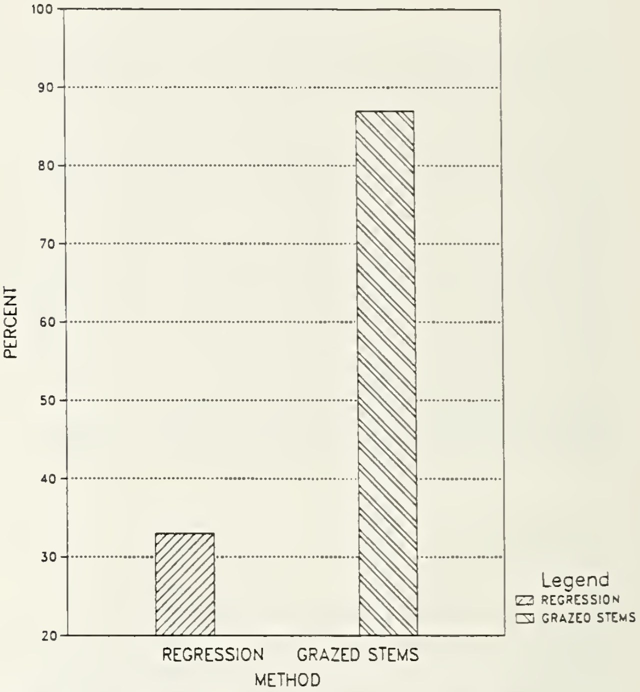

Figure 2.--Comparisons of two utilization estimation techniques. Twig-diamter regression estimate of percentage of biomass removed compared with the percentage of all stems that were grazed.

Leaf:stem ratios for pre- and postbrowsing were calculated using the point frame method and are shown in table 1. Leaf:stem ratios before browsing were 3.59 leaves per green stem and 0.34 leaves per green stem after browsing in 1982. The same paddock was grazed at similar stocking rates in 1983. The experiment yielded nearly identical results, leaf:stem ratios were 3.58 before browsing and 0.41 after browsing ($p<0.01$).

Table 1.--Leaf:stem ratios before and after browsing by sheep

	Year 1982	1983
Before browsing	3.58	[1]3.59[a]
After browsing	0.34	0.41[b]

[1] Means within columns followed by a different letter are significantly different $P < 0.01$.

In addition to the leaf:stem ratios obtained from the point frame data, we have calculated the percentage of leaves removed:

$$\text{Percent leaves removed} = \frac{\text{Leaves removed}}{\text{Total leaves}} \times 100 \qquad (4)$$

This helps describe the impact on the shrub, in terms of the amount of photosynthesizing material (leaves) harvested after a browsing event. These data are compared (fig. 3) with the percent grazed stems and the percent biomass removed. At this moderate level of biomass removed (33 percent), 87 percent of the stems were grazed and over 85 percent of the leaves were removed. The few leaves that remained on the shrub were deep within the canopy.

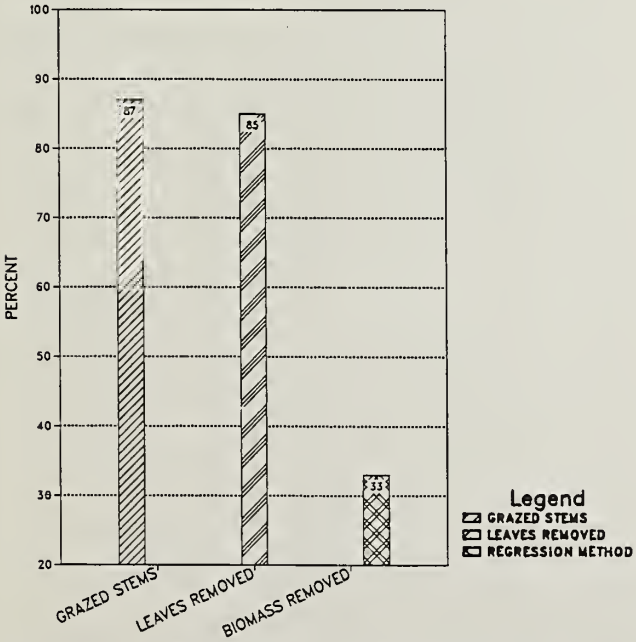

Figure 3.--Comparisons of three utilization estimation techniques. Percentage of grazed stems, percentage of leaves removed, and percentage of biomass removed.

CONCLUSIONS

Changes in leaf-to-stem ratios were compared with two utilization estimation techniques to provide insight into selective leaf removal by sheep. The true impact of this browsing behavior on the shrub is best described by the point frame data. Significant reductions in leaf:stem ratios occurred indicating high levels of photosynthetic material lost at low estimates of biomass removed as determined by traditional methods. When utilization was estimated to be 45 percent by the regression technique, the percentage of grazed stems ranged from 80 to 97 percent. Grazed-stem estimates are highly variable at levels greater than 80 percent. They have a poor correlation ($r^2 < 60$ percent; Bowns unpublished data) with biomass-removed estimates and present a greater risk for potential estimation error (Stickney 1966). Twig-diameter regression models, which account for both stems that are stripped of leaves and stems that are bitten off, provide accurate estimates of biomass removed and are a valuable sampling technique.

Careful interpretation of estimated values of biomass removed is important when selective browsing as described here is observed. Most recommended proper use levels of 50 to 60 percent or greater (Stoddart and others 1975) are based on winter use of deciduous browse species. Evaluation of the defoliation patterns is important in accurately assessing the degree of utilization of a valuable forage source such as snowberry, and other broad-leaved shrubs such as serviceberry (*Amelanchier alnifolia*), mountain mahogany (*Cercocarpus spp.*), and aspen where summer leaf stripping routinely occurs. Proper utilization levels for shrubs browsed in the summer need to be adjusted downward from recommended winter use levels when management goals require maintaining snowberry or other shrubs in good vigor and abundance.

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Section 5. Plant Response to Browsing

GROWTH, NUTRIENT, AND WATER STATUS OF JOJOBA (SIMMONDSIA CHINENSIS)

IN RELATION TO LIVESTOCK GRAZING

Bruce A. Roundy, George B. Ruyle, Albert K. Dobrenz
Van Wilson, and Don Floyd

ABSTRACT: Jojoba is a nutritious shrub of major seasonal forage value in its midelevational range in the Sonoran Desert. Its ability to regrow and maintain similar ratios of photosynthetic to nonphotosynthetic biomass, and similar water status when heavily grazed or ungrazed indicates high tolerance to grazing. Moderate grazing is recommended to maintain shrub size and forage production.

INTRODUCTION

Jojoba (Simmondsia chinensis) is a drought-tolerant, long-lived evergreen shrub of the Sonoran Desert in the southwestern United States and northwestern Mexico. It is distributed over about 26 million ha predominantly on desert foothills and washes between 600 and 1 200 m elevation (Gentry 1958). Jojoba nuts contain wax esters suited to a variety of commercial uses, especially as substitutes for sperm whale oil in the manufacture of high pressure lubricants (Scarlett 1978). Extensive research continues to be directed at potential uses and domestication of jojoba (Elias-Cesnik 1982). Jojoba is also an important component of the desert ecosystem, furnishing food for rodents (Sherbrooke 1976), birds (Thomson 1976), javelina (Pecari tajaco) (Knipe 1956), desert bighorn sheep (Ovis canadensis) (Russo 1956), and mule deer (Odocoileus heminous) (Judd 1962; Urness and others 1977), as well as forage for domestic livestock (Mills and Foster 1982). After the annual forbs and grasses senesce in early summer in central Arizona, jojoba may comprise up to 50 percent of the diet of cattle (Aguirre de Luna 1980).

The commercial and ecological value of jojoba has prompted concern over its use and management as a forage. The U.S. Department of Agriculture, Forest Service currently manages jojoba by limiting utilization to 40 percent of current year's growth under a continuous grazing system and 50 percent under a rest rotation grazing system (USDA Forest Service 1979). The effects of heavy herbage removal have not been quantified (Mills and Foster 1982) or compared with the effects of moderate utilization that is currently recommended by the Forest Service.

Caldwell (1984) recently summarized the current knowledge of factors important to grazing tolerance. Of major importance is the availability of apical meristems and ability of lateral buds to initiate regrowth and replace grazed shoots. Pruning of jojoba stimulates vegetative growth (Yermanos 1980). Jojoba may withstand heavy browsing (Judd 1962), but seed and foliage production are reportedly greatly reduced (Mills and Foster 1982). Moderately grazed jojoba shrubs may be smaller than ungrazed plants (Ruyle and Roundy 1985) but may have more stems and leaf pairs per branch than lightly grazed shrubs (Roundy and others 1986). The above observations suggest that removal of the apical buds of jojoba by grazing or pruning may stimulate twig growth from lateral buds as occurs with many other shrubs (Garrison 1971). Livestock producers have suggested that grazing of jojoba results in greater current year's growth than occurs on ungrazed plants and that new growth is more palatable and nutritious than old growth.

A major influence on persistence of plants that are grazed is the competitive environment of the associated plant community (Caldwell 1984). Defoliation of plants in semiarid and arid environments may limit their growth when soil water is available. Ungrazed plants may then use the available water and nutrients not used by grazed plants and expand their shoots or roots to preempt future resource use by grazed plants. Thus the ability of plants to maintain a favorable water balance and grow when grazed is essential for retention of competitive status in the community and is a good indication of tolerance to grazing.

The purposes of this study were to characterize the nutritional quality of jojoba and to quantify its growth and water status in relation to different grazing intensities.

Specific objectives included:

1. Compare seasonal crude protein and phosphorous levels of previous and current year's growth.
2. Compare twig initiation and growth and photosynthetic biomass percentages of ungrazed, moderately grazed, and heavily grazed shrubs.
3. Compare water stress, transpiration, stomatal resistance, and leaf temperature of ungrazed, moderately grazed, and heavily grazed plants.

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STUDY AREA AND METHODS

The study area is on a fan piedmont (Peterson 1981) south of Roosevelt Lake in southern Arizona. It is a clayloam upland range site supporting Upper Sonoran Desert shrub vegetation including paloverde (Cercidium microphyllum), wolfberry (Lycium exsertum), mesquite (Prosopis juliflora), various species of cholla and prickly pear (Opuntia) in addition to jojoba. Herbaceous vegetation is mainly restricted to annuals (Bromus rubens and Erodium cicutarium) and a few remnant perennial three-awns (Aristida spp). On the site is a 49-year-old exclosure and, nearby, a stock water pond at least as old as the exclosure. Cattle have continuously grazed the area outside the exclosure since it was built. In close proximity and on the same aspect are ungrazed jojoba plants in the exclosure, plants that are heavily grazed near the pond, and plants that are moderately grazed about 0.5 km from the pond. To determine seasonal nutritional quality, we collected samples of current and previous year's growth from four shrubs monthly from July 1978 to June 1979. Also in June 1985 samples of current and previous year's growth were collected from 20 shrubs. Samples were oven dried and ground thoroughly with a Wiley mill equipped with a 40-mesh screen. Total nitrogen was determined by the macro-Kjeldahl method (Bremner 1965). Phosphorus was analyzed following the procedure described by Chapman and Pratt (1961).

Growth patterns were determined by diagraming three branches on each of 10 ungrazed, moderately grazed, and heavily grazed shrubs. Branches were first diagramed on March 5, 1985 and rediagramed May 15, 1985. This was the period of expected maximum growth. Current year's (green) growth, old nongreen stems, leaf pairs, and grazed stems were diagramed and all internodes were measured. Twig lengths removed by grazing were estimated from measurements of stem diameter at the point of grazing using a linear regression of twig length on stem diameter calculated from 100 observations from shrubs on the study site. To determine percentages of photosynthetic biomass within the canopy, we collected two entire main branches from each of 10 ungrazed, moderately grazed, and heavily grazed plants. Branches were collected the end of June to be representative of spring growth. Branches were clipped at 5-cm increments perpendicular to the main stem. Old leaves, current year's leaves, green stems, and brown stems were separated, oven dried, and weighed.

Plant water status was quantified by measuring transpiration, stomatal resistance, and leaf temperatures with a LICOR LI-1600 steady-state porometer and by measuring xylem water potential with a pressure bomb (Sholander and others 1965) after enclosing twigs in a plastic bag (Wenkert and others 1978). Measurements were taken on four to five shrubs each that were ungrazed, moderately grazed, or heavily grazed. Measurements were taken from predawn through the day on May 15 and on July 2. In addition, carbon uptake was sampled on new and old leaves for 15 to 20 shrubs on April 12 and May 22. Measurements were taken between 10 a.m. and 1 p.m. A branch portion was enclosed in a 0.1411-L cuvette for 60 seconds and the difference in CO_2 concentration was measured from air samples taken with syringes and later injected into an infared CO_2 analyzer (Clegg and others 1978). Measurements of CO_2 taken in this manner estimate net photosynthesis or gross photosynthesis minus light and dark respiration. Leaf areas were measured with a LICOR LI-3100 area meter.

Treatments were tested for significance ($p < 0.05$) using analysis of variance with shrubs as sample units and, where appropriate, branches as subsamples. When treatments were significant, means were compared using Duncan's multiple range test.

RESULTS AND DISCUSSION

Forage Quality

Jojoba forage is high in crude protein and phosphorus during the spring (fig. 1). New growth had higher nutritive quality than old plant material, except December through March. Leaves and stems produced in the spring of 1985 were significantly higher in both crude protein (11.7 percent) and phosophorus (0.15 percent) than previous year's growth (6.7 percent and 0.07 percent, respectively), but both were adequate to satisfy dietary requirements of cows for these nutrients if intake is

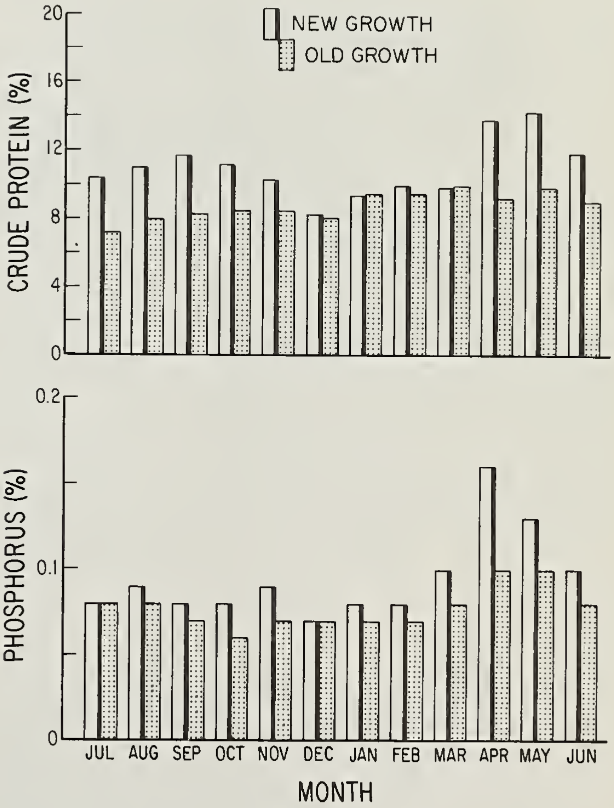

Figure 1.--Crude protein and phosphorus percentages of current and previous year's growth of jojoba shrubs sampled near Roosevelt Lake, AZ in 1978 and 1979.

normal. Jojoba clearly offers nutritive forage year round for livestock and wildlife.

Twig Initiation and Growth

Jojoba produces opposite leaves; new shoots initiate from lateral buds in the leaf axils or from apical meristems. Actively growing twigs produced this year had green stems. Percentage grazed twigs of total twigs by mid-May was 0, 38, and 63 percent for diagramed branches on ungrazed, moderately grazed, and heavily grazed shrubs, respectively. The number of new twigs initiated per centimeter of total nongreen twig length was statistically similar for all grazing treatments (table 1). Ungrazed branches had more apical buds per centimeter of nongreen twig length than grazed branches, but both grazed and ungrazed branches had similar numbers of new twigs produced per apical bud. All branches had similar numbers of lateral bud pairs per centimeter of total nongreen twig length, but grazed branches had significantly more new twigs initiated per lateral bud pair than ungrazed branches. Grazing removes apical buds, thereby stimulating new twig growth from lateral buds. New twig initiation from lateral buds compensates for loss of twigs that could have been produced from apical buds but does not necessarily result in greater total new twig initiation on grazed than ungrazed plants.

Table 1.--New twigs, buds, and twig growth of jojoba shrubs in relation to cattle grazing intensity south of Roosevelt Lake, AZ

	Grazing intensity		
Parameter	Ungrazed	Moderately grazed	Heavily grazed
New twigs per cm of non-green twig length (No.)	[1]0.35a	0.35a	0.49a
Apical buds per cm of nongreen twig length (No.)	0.15a	0.05b	0.06b
New twigs per apical bud (No.)	1.25a	1.69a	1.78a
Lateral bud pairs per cm of nongreen twig length (No.)	0.38a	0.34a	0.40a
New twigs per lateral bud pair (No.)	0.41b	0.80a	1.10a
New twig length May 15, 1985 (cm)	2.9a	3.2a	3.5a
New twig growth March 5 to May 15, 1985 (cm)	2.2a	2.9a	3.3a

[1] Means in rows followed by the same letter are not significantly different ($P < 0.05$) by Duncan's multiple range test.

The period of greatest twig growth was between March and mid-May. Mean length of current year's twigs was statistically similar for all grazing treatments on May 15. Mean twig growth between March 5 and May 15 was also similar for all treatments (table 1). In this study, grazing did not result in either increased or decreased growth of jojoba twigs.

Spring growth of twigs in this study was much greater than that reported by Guedes Almeida (1979) and Paes De Oliveira (1983). In the present study, leader growth is reported as the average length of twigs that actually elongated. Elongation occurred on about 60 percent of the more than 2,000 twigs that were measured. Measurement of fewer marked twigs, some of which may not elongate, may not be representative of active leader growth on jojoba and other woody plants (Paes De Oliveira 1983). Diagraming branches with numerous twigs is a very tedious, but more thorough, approach to quantifying woody plant growth.

Photosynthetic Biomass

Ungrazed shrubs had a higher percentage photosynthetic biomass of total biomass down through the shrub canopy than grazed shrubs (fig. 2). Total photosynthetic biomass per branch was similar for ungrazed and moderately grazed plants to a depth of 40 cm into the canopy, and to this depth was much higher for ungrazed and moderately grazed than heavily grazed plants. Grazed plants and ungrazed plants had statistically similar non-photosynthetic biomass through the canopy but ungrazed plants had a much larger woody main stem below the canopy than grazed plants. Ungrazed and moderately grazed plants had similar total photosynthetic biomass per main branch; that for heavily grazed plants was much lower (table 2). However, due to their larger woody stems below the canopy, ungrazed plants had much greater total nonphotosynthetic biomass per branch and therefore a similar percentage photosynthetic of total biomass per branch as grazed plants. Heavily grazed and ungrazed shrubs had equal ratios of photosynthetic to nonphotosynthetic biomass, but branches of heavily grazed shrubs are much smaller, so they produce much less green forage per branch than ungrazed or moderately grazed shrubs.

Heavy grazing reduced shrub size. Heights of ungrazed, moderately grazed, and heavily grazed shrubs averaged 145, 82, and 56 cm, respectively. Numbers of main branches per shrub averaged 39, 50, and 31, respectively, for ungrazed, moderately grazed, and heavily grazed shrubs. Multiplying out averages of green weight per branch, number of branches per shrub, and number of shrubs per hectare gave estimates of green forage yields of 3 382, 3 163, and 516 $kg{\cdot}ha^{-1}$ for ungrazed, moderately grazed, and heavily grazed shrubs, respectively. Although jojoba may maintain growth and sufficient photosynthetic biomass in a dense canopy to survive under heavy grazing, shrub size and forage production per shrub are greatly reduced. In contrast, moderate utilization results in almost as much green forage as that produced by ungrazed plants.

Grazed plants had a higher percentage new leaf of total photosynthetic biomass than ungrazed plants (table 2). Ungrazed plants tended to have a greater percentage old leaf of total photosynthetic biomass than grazed plants. Stem biomass was less than one-third of the total biomass, and grazed and ungrazed plants had similar stem biomass percentages.

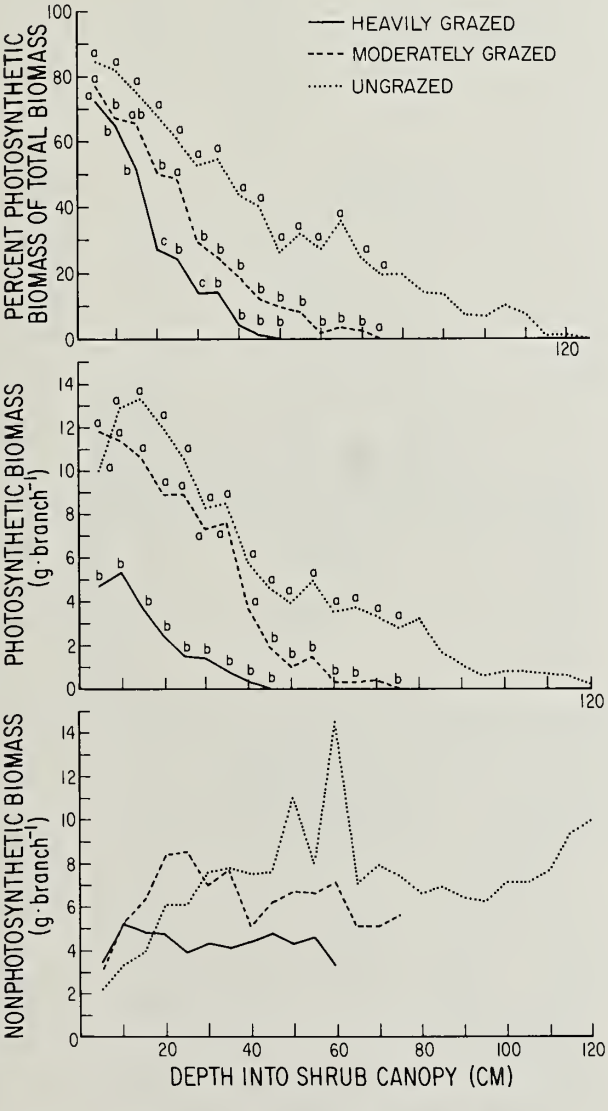

Figure 2.--Percent photosynthetic biomass of total biomass (top), photosynthetic biomass (middle), and nonphotosynthetic biomass (bottom) of jojoba shrubs in relation to intensity of livestock grazing near Roosevelt Lake, AZ. Points at the same depth with the same letter are not significantly different ($P < 0.05$) by Duncan's multiple range test. No significant differences occurred for nonphotosynthetic biomass.

Table 2.--Photosynthetic and nonphotosynthetic biomass and percentages for main branches of jojoba in relation to grazing intensity

	Grazing intensity		
Parameter	Ungrazed	Moderately grazed	Heavily grazed
Photosynthetic biomass per branch (g)	[1] 116.7a	75.9a	20.3b
Nonphotosynthetic biomass per branch (g)	168.1a	85.5b	36.3b
Percent photosynthetic of total branch biomass	44.1a	46.6a	40.8a
Percent new leaf of total photosynthetic biomass	33.9b	47.6a	49.2a
Percent old leaf of total photosynthetic biomass	38.5a	28.0a	30.4a
Percent stem of total photosynthetic biomass	27.6a	24.4a	20.4a

[1] Means in rows followed by the same letter are not significantly different ($P < 0.05$) by Duncan's multiple range test.

Photosynthetic Rates

Newly developed leaves generally had higher net photosynthetic rates than previous year's leaves especially when carbon uptake was expressed per dry weight of leaves (table 3). New leaves had a much lower specific leaf weight than previous years' leaves, and their specific leaf weight increased with age. Photosynthetic rates apparently decreased with foliage age and were low compared to those reported at similar values of plant water stress in the literature. Midday plant water stress averaged about 3.5 to 4.0 MPa on May 15 in this study (fig. 3). Net photosynthetic rates reported at these values of water stress included less than 1 to 6 mg $CO_2 \cdot dm^{-2} \cdot h^{-1}$ (Glat and others 1983), 6 to 13 mg $CO_2 \cdot dm^{-2} \cdot h^{-1}$ (Adams and others 1977), and less than 1 to 9 mg $CO_2 \cdot g^{-1}$ dry wt$\cdot h^{-1}$ (Al-Ani and others 1972). Although jojoba has low photosynthetic rates compared to many plants (Rawson and others 1977), it can photosynthesize at very low water potentials. Photosynthetic rates may vary substantially among different clones (Glat and others 1983).

Water Status

Above-normal precipitation fell in the winter of 1984-85, but little or no precipitation occurred in May through early July when plant water status was measured (fig. 4). Vapor pressure deficits and leaf temperatures were high and increased through the day (fig. 3). Leaf temperatures were usually slightly higher but within 1 °C of air temperature.

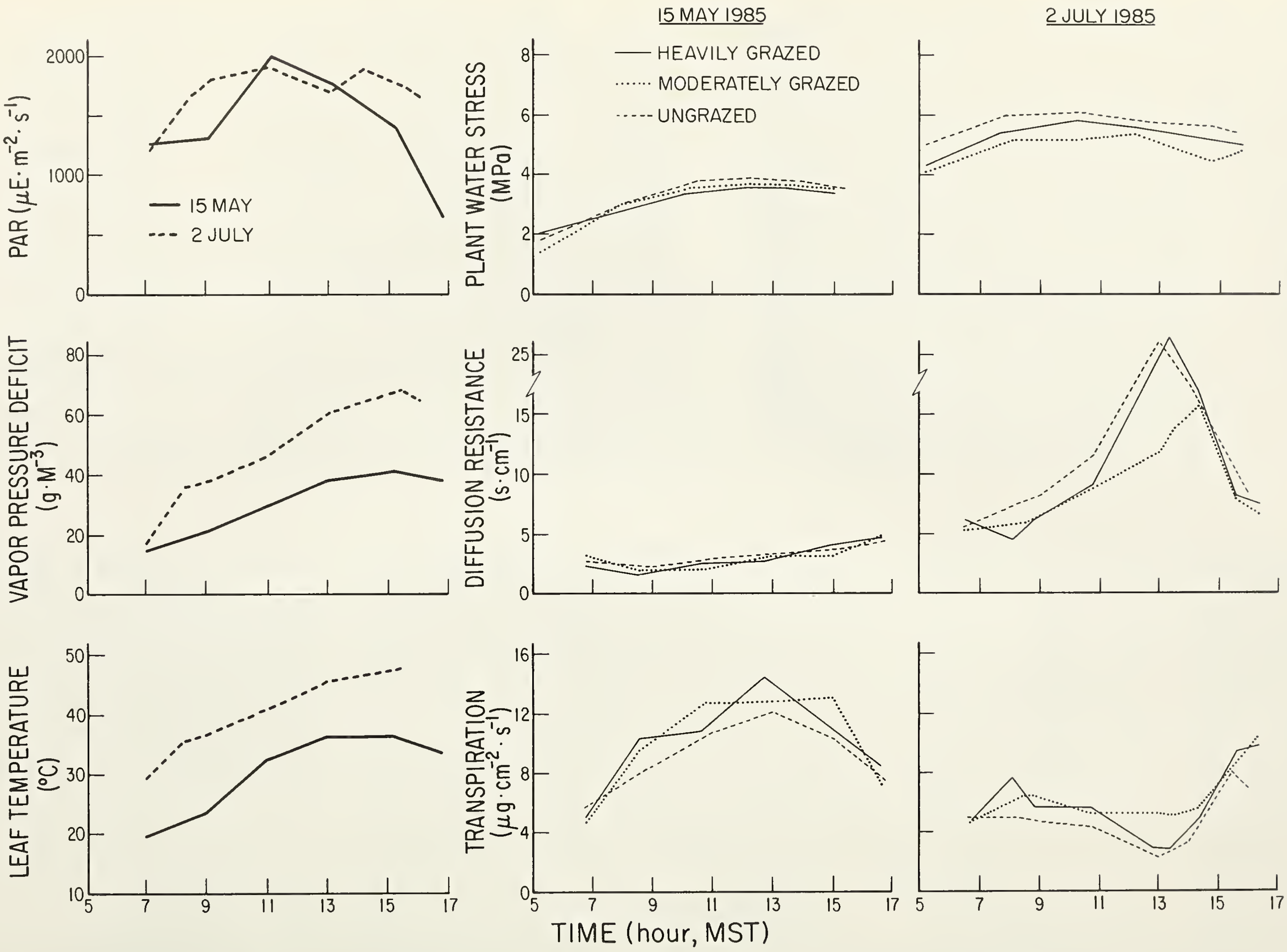

Figure 3.--Incident photosynthetically active radiation (PAR), vapor pressure deficit, leaf temperature, plant water stress, diffusion resistance, and transpiration for jojoba shrubs near Roosevelt Lake, AZ.

Table 3.--Net photosynthesis and specific leaf weights for old and new jojoba leaves sampled near Roosevelt Lake, AZ

Leaves	Net photosynthesis ($mgCO_2 \cdot dm^{-2}$ leaf area$\cdot h^{-1}$)		Net photosynthesis ($mgCO_2 \cdot g^{-1}$ dry wt$\cdot h^{-1}$)		Specific leaf weight ($g \cdot dm^{-2}$)	
	12 April	22 May	12 April	22 May	12 April	22 May
Old	[1] 1.75a	0.80c	0.49c	0.26d	3.72a	3.23a
New	1.97a	1.18b	1.72a	0.67b	1.26c	1.75b

[1] Means in the same units followed by the same letter have overlapping 95 percent confidence levels.

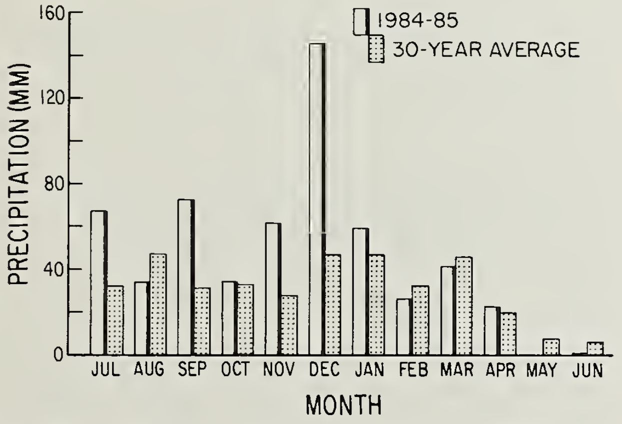

Figure 4.--Monthly precipitation at Roosevelt Lake, AZ.

In May, predawn plant water stress averaged 1.9 MPa and increased to an average maximum of 3.6 MPa at midday. Transpiration rates increased with increasing leaf temperatures and vapor pressure deficits and then decreased in the afternoon. Diffusion resistance was low and increased only slightly through the day even though plant water stress increased 1.7 MPa. By July vapor pressure deficit, leaf temperature, and plant water stress all increased markedly. Transpiration rates were low compared to May and dropped to a minimum at midday as diffusion resistance increased rapidly. Transpiration then increased as diffusion resistance decreased even though plant water stress remained high. This pattern of diffusion resistance indicates a temporary period of stomatal closure at midday.

Leaf temperatures, plant water stress, transpiration, and diffusion resistance were similar for the three grazing treatments on both sample dates (fig. 3). Only at midday on July 2 were there statistically significant differences; moderately grazed plants had higher transpiration and lower diffusion resistance than ungrazed plants. Ungrazed plants showed a trend toward slightly greater water stress than grazed plants, but differences were not statistically significant.

Indications are that grazed and ungrazed plants were able to maintain a similar water balance, even during a period of high plant water stress. Regression estimates of leaf area from biomass measurements indicated that ungrazed and moderately grazed plants had similar leaf areas and about six times the leaf area of heavily grazed shrubs. Assuming transpiration rates per leaf area are similar, ungrazed and moderately grazed shrubs could potentially transpire six times more water than heavily grazed shrubs. Provided their root systems are extensive enough to satisfy this high transpirational demand, ungrazed and moderately grazed plants could be more competitive for soil water than heavily grazed shrubs. The similar water status of grazed and ungrazed shrubs indicated a similar ability to balance transpirational water loss with water uptake through the root system. Even though heavily grazed shrubs may have smaller root systems than the larger ungrazed and moderately grazed shrubs, their lower total leaf area and probable lower transpirational water loss could allow these shrubs to maintain a water balance similar to the larger shrubs, provided the soil water available to their roots is not exploited by other plants. This is a fairly open plant community. Foliar cover of jojoba averages 14 percent inside the exclosure and 7 percent outside. Cover of all other shrubs averages 22 percent. The clayey soil has a high water holding capacity. Heavily grazed and moderately grazed plants appear to be maintaining at least as favorable a water balance as ungrazed plants. Jojoba's high drought tolerance is well evidenced by continued transpiration and photosynthesis at what is considered extremely high plant water stress for most plants.

CONCLUSIONS

Jojoba is a nutritious forage for wildlife and livestock and is of major seasonal value. Jojoba is apparently very grazing tolerant, partly because it is able to initiate new twigs from lateral buds to compensate for loss of apical buds and twigs by grazing. Heavily grazed plants maintained as high a ratio of photosynthetic to total biomass as ungrazed plants. However, heavy grazing greatly reduced shrub size and forage yield. Moderate grazing resulted in forage yields similar to those of ungrazed plants. Although grazing reduced shrub size, grazed plants maintained a water status similar to ungrazed plants, even during a period of high water stress in early summer. This indicates a comparable ability to balance transpirational water loss with water uptake through the roots. Although jojoba was tolerant of heavy grazing, moderate grazing is recommended to maintain greater shrub size and forage production.

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DIFFICULTIES IN INTERPRETATION OF LONG-TERM VEGETATION TRENDS IN RESPONSE TO LIVESTOCK GRAZING

Warren P. Clary and Ralph C. Holmgren

ABSTRACT: Grazing effects data from the Desert Experimental Range, Utah, are used to illustrate the problems of interpreting vegetation response to grazing treatment, precipitation, and site. Differences in results and analysis may be related to experience, viewpoint, plot sampling, and failure to note climatic patterns, soils, and vegetation cycles.

INTRODUCTION

Hutchings (1966), summarizing 30 years of grazing effect observations in the shadscale zone of the Great Basin Desert of western Utah, stated that "response of vegetation varied widely, depending on weather, degree of depletion, and the quality of management applied." Desert plant communities are dynamic; their floristic composition may change, sometimes dramatically, over time (West 1982). Besides current weather and livestock, some of the factors acting and interacting to effect change are climatic cycles, other herbivores including invertebrates, and the inherent attributes of plant species such as their relative longevity, palatability, resistance to disease and defoliation, seeding habits, season of active growth, and adaptability to specific sites. With these and perhaps other factors operating, range managers, as Blaisdell and Holmgren (1984) have said, "may find it difficult to judge what part of any change is due to their actions or may be under their control."

That researchers have the same problem as managers in interpreting grazing effects is clear from the varying conclusions drawn from studies made with similar objectives. Conflicting claims are notorious, and different recommendations have come from studies of season and degree of herbage removal by clipping or grazing. Studies comparing grazing systems were reviewed and summarized by Hickey (no date), who found such a divergence of conclusions he warned that a land manager "restricted to a limited amount of literature . . . is more apt to be misinformed than uninformed." Hickey suggested reasons for the differing results and conclusions; among them were: experience and viewpoint of the author, aspect of the problem stressed, duration of the study, confounding parameters, and improper or shaky extrapolation (especially from insufficiently measured aspects).

We even find disparity among separate reports from a single study that has been under way for half a century at the Desert Experimental Range (DER) in western Utah. These reports, discussed later, illustrate well the problems of interpreting data on vegetation response to grazing use. Although desert vegetation is floristically simple, and its response to applied treatments would seem straightforward, the reports from this single study provide evidence of the complexity of interpretation.

Only a part of the disparity found in the DER reports is related to a period of study or amount of data accumulated. Among the causes are some of those mentioned by Hickey. Other factors may be unique to this study. Our purpose here is threefold: to discuss briefly some previously published results and conclusions, adding information from a new data set from the same study; to look for causes of discordance among the reported findings; and to try to see if some justifiable level of harmony can be drawn.

STUDY AREA AND LAYOUT

The Desert Experimental Range, a 55,000-acre study area established in 1933, contains a set of twenty 240- or 320-acre grazing paddocks in its south-central portion. The paddocks are in an ecological zone commonly called the "salt-desert shrub" in the Great Basin Desert. We prefer the term "low-shrub cold desert" because the vegetation is generally limited to species approximately a foot or so in height, and the soils are nonsaline in the upper part of the profiles, where nearly all the roots are. The soils are calciorthids, torrifluvents, and occasionally torripsamments. The amount and timing of precipitation varies widely from year to year; the average annual amount is 6 inches. Winters are cold and summers warm. Above-ground vascular plant productivity averages about 250 pounds per acre (Holmgren 1973).

In 1935 each paddock was assigned a grazing treatment which it received annually for 50 years. A treatment is a combination of grazing

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intensity and season of use by sheep. The intensities are light use (an average of 8.5 sheep days per acre), medium use (12 sheep days), and heavy use (17 sheep days). The seasons of use are early winter, middle winter, and late winter. The first two occur during plant dormancy in cold weather; the third includes the period of thawing, warming of soil, and the beginning of plant growth. Some of the paddocks have split seasons of use, such as early-and-middle winter.

Paddock vegetation has been sampled by several different systems (fig. 1). Each 240- or 320-acre paddock has 96 or 128 permanently marked plots, 200-ft^2 in area, where live-plant cover and production have been periodically estimated at the end of the growing season. Additionally, within each of 16 of the paddocks, two pairs of 1-acre areas were established at the beginning of the study for more intensive observation. One member of each pair was grazed and one was protected from grazing by a fence. These areas, which we will refer to as "special acres," were sampled for cover and production on 40 permanent 200-ft^2 plots. These plots were sampled less frequently than the paddocks. Also, two 5- by 20-ft chart quadrats were located on each special acre; perennial plants in these quadrats were mapped at irregular intervals. Detailed community-type maps were made for the paddocks in 1935 and again in 1977. Type maps of the special acres were made in 1935 and 1967.

SOME PAST INTERPRETATIONS OF VEGETATION TRENDS

Among reports on the DER paddock grazing study, the period of study being reported has varied; the earlier ones, of course, covered only part of the period considered in later ones. The dynamic nature of the vegetation, together with time needed for following successional progress, will often result in different community compositions at different times. Other factors involved raise questions regarding the vegetation's actual response to grazing treatments; important among these are (a) variety of purpose, experience, and viewpoint of authors; (2) problems of experimental design and field layout; and (3) the fact that different data sets were used by different investigators (table 1). Here we briefly review varying interpretations of vegetation change reported from the DER grazing study and, based on our own familiarity with the area, offer explanation where possible for part of the conflict or point out insufficiency of data or differing rationale where apparent.

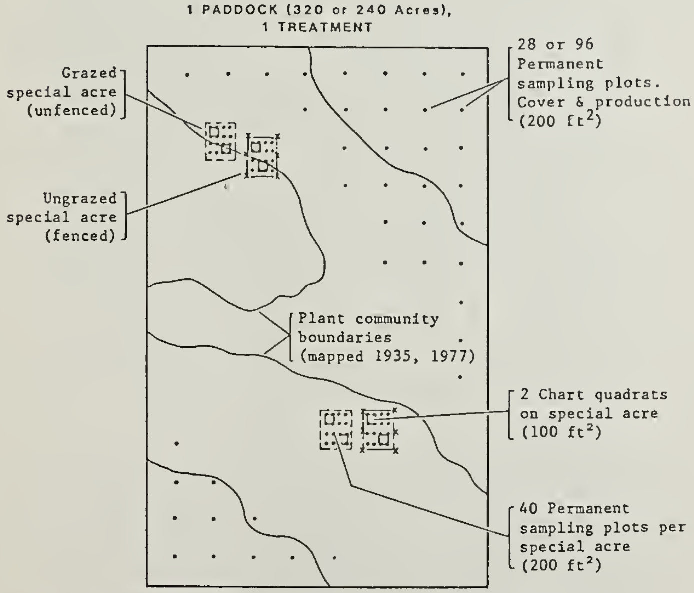

Figure 1.--A representative Desert Experimental Range paddock illustrating the different vegetation sampling systems.

Harper (1959), using quadrat-chart data, concluded that the greater amount of total plant cover mapped in 1958 than in 1935 on the special acres, both grazed and not grazed, was the result of a reduction of grazing pressure from what it had been before the beginning of the study, rather than the result of more favorable moisture conditions. Norton (1978), using a longer period of data from some of the same plots and including the time period covered by Harper, concluded that grazing had little effect on trends in the plant communities and that climate or some other environmental factor was responsible for vegetation change--an opposite interpretation.

Harper's conclusion that, even under the heavy DER grazing treatments, pressure was less than it had been prior to management of grazing cannot be verified. Harper's conclusion, however, was based in part on a very heavily grazed-not grazed comparison on nearby public lands. On the ungrazed part, plant cover increased from 1935 to 1958 in an amount similar to that on the DER. Plant cover on the grazed part decreased suggesting plant cover increases on the grazed part of the DER were a response to reduced grazing pressure.

Norton evaluated 4 years of data (1935, 1958, 1969, and 1975), and noted a "trend" in total amount of plant cover (all species together) between dates of observation, upward in the first and third intervals, and downward in the second. Although the time intervals were 23, 11, and 6 years, the changes were no greater than several of the year-to-year production changes shown in figure 2. (Cover and production have been shown to vary in a similar fashion at the DER [Hutchings and Stewart 1953]). The concept of trend involving a simple change in total plant cover is somewhat different than the concept most often used in range management; compositional makeup of cover usually is the important aspect of trend. No doubt cover

Table 1.--Reports giving differing interpretations of results from the DER paddock grazing study

Report	Data set	Years
Hutchings and Stewart (1953)	Paddock, estimated production	1935 through 1947
Smith (1984)	Paddock, estimated production	1938, 1945, 1957, 1967, 1973
Holmgren and Hutchings (1972)	Paddock, estimated cover	1935 through 1967
Holmgren and Hutchings (1972)	Special acres, estimated cover	1935, 1967
Harper (1959)	Special acres, quadrat chart cover	1935, 1958
Norton (1978)	Special acres, quadrat chart cover, individual plant presence	1935, 1958, 1969, 1975
Chambers (1979)	Special acres, quadrat chart cover, individual plant presence	1975, 1978
West (1979)	Special acres, quadrat chart, individual plant presence	1935, 1936, 1937, 1958, 1968-70
Clary and Holmgren (this paper)	Special acres, estimated cover	1935, 1967, 1983-84

was affected by climate, but the data presented by Norton do show important compositional changes related to grazing treatment that were not identified by the author. Interpretation may be conditioned by experience and viewpoint.

Several authors (Hutchings and Stewart 1953; Holmgren and Hutchings 1972; Smith 1984) have reported major die-offs of shadscale (*Atriplex confertifolia*) during specific drought periods, but another author (Chambers 1979) analyzed plant demographic data bracketing one of these periods and reported a reduction rather than an acceleration in the rate of population change. Her study was of the 1976-77 drought that closely followed the 1971-72 drought. Could earlier plant mortality have affected results in 1971-72 by removing those plants most susceptible to drought?

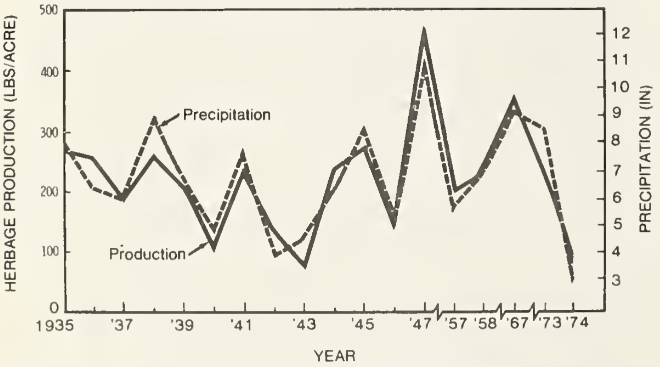

Figure 2.--Relationship of total herbage production to annual precipitation on the Desert Experimental Range.

In a major publication summarizing DER results, Hutchings (Hutchings and Stewart 1953) reported increases in winterfat even under heavy grazing, while in a later publication he reported no change in winterfat under heavy grazing after considering the effect of current year's precipitation (Hutchings 1966). However, by either approach, he found winterfat increased on the moderately and lightly grazed paddocks; these results were significantly different from those of the heavily grazed paddocks. A still later publication coauthored by the same individual reported severe losses of winterfat under heavy grazing in the spring, but gains under heavy fall-winter grazing (Holmgren and Hutchings 1972). Hutchings lumped data different ways in separate analyses. In the earlier publications he grouped pastures by intensity of use, disregarding season of grazing. In the later paper he reported on seasonal effect within intensity groups. The earlier averages or trend lines are composites of what was presented later; that is, the upward trend of winterfat in the early winter heavily grazed pastures combined with the downward trend in the late winter heavily grazed pastures are components of the trend shown for all heavily grazed pastures. So there is no conflict of data in these reported findings, but a change in analysis approach and perhaps a change in viewpoint.

Other results suggest different responses by the same plant species to grazing treatment on different soils, and sometimes to different time periods (Holmgren and Hutchings 1972; Smith 1984). Variables such as grazing intensity and timing, weather, and soils can be expected to interact differently within various plant communities with dissimilar competitive situations.

Is the DER different from other range research areas in difficulty of interpretation? Probably not. The principal difference likely lies in the fact that a number of people have studied vegetation change there over a 50-year period. Thus, the opportunity existed to examine and reexamine assumptions of vegetation change. Few other research areas have been subjected to a similar degree of repeated scrutiny.

What are some of the more obvious reasons for differences in interpretation of vegetation trends on a seemingly uniform area such as the DER? Plant community responses are known to be sensitive to annual precipitation (fig. 2). Obviously, current annual precipitation has to be accounted for in some manner if vegetation trends are to be properly interpreted. Response by individual species to seasonality of precipitation is a very real, but possibly more difficult problem, with timing of soil moisture so unpredictable and so erratic that no "average" pattern is meaningful. For instance, bud sagebrush (Artemisia spinescens) with its very restricted spring growth and reproductive period cannot respond to summer rainfall, whereas winterfat (Ceratoides lanata) has the ability to respond strongly to summer rainfall. Thus, seasonality of precipitation in the year of observation can substantially affect the apparent dominance within plant compositions. This occurs in plant cover measurements as well as plant production measurements.

Species mortalities may be differentially affected by annual and seasonal drought periods. The reported die-offs of shadscale obviously affected interpretations by different authors when their data sets were from different periods of time. The response of plant composition to release from grazing pressure on the DER has varied strikingly at different locations that appear to be similar, but apparently represent different ecological sites, or variety in attributes such as grazing histories, degree of depletion, and relative abundance of seed source. Since present knowledge does not allow one to differentiate among many of these sites at our study location, they are an obvious source of confusion. Potential interaction of climatic factors, site, and insect attacks also can cause changes that may be erroneously interpreted. The lack of good experimental design in grazing studies initiated 50 years ago has also made proper interpretation more difficult.

SOME RECENT RESULTS

The most recent data from the DER grazing paddocks contribute to a time sequence comparison which is eight to nine years greater in length than any previous comparison and, as such, provide a test of plant trend interpretations of earlier studies. The data were collected on the 200-ft^2 plots within the 64 paired 1-acre plots for paddocks numbered 1-16. These plots have been studied relatively little during the 50-year history of the DER. Although incomplete or partial sets of data were obtained in several intermediate years, the only complete sets of data were obtained in 1935, 1967, and 1983-84. The last set was obtained over a 2-year period.

Plant cover data were collected using the square-foot-density method. Plant composition expressed as a percentage of total cover was the basis of analysis, on the assumption that the proportion of total cover for a species is a more stable variable among years than absolute cover. The grazing intensity data were composited for the spring and fall-winter periods to illustrate general trends. Four major species were used to illustrate plant trends: bud sagebrush, winterfat, shadscale, and Indian ricegrass (Oryzopsis hymenoides).

Looking at the composited graphs (fig. 3) one can see that the plant composition was quite similar within groups of paired grazed and ungrazed plots in 1935 at the beginning of the study period. The ungrazed portions of both groups illustrate a similar pattern through time: an initial decline followed by a stabilization of shadscale; a slight rise and then a decline of winterfat; an apparently consistent increase in bud sagebrush to a point of community dominance in the early 1980's; and little change to 1967 followed by a modest rise for Indian ricegrass. The "others" category consisted largely of warm season grasses that reacted rather similarly among paddocks with a general increase within the composition.

Under grazed conditions (average of all grazing intensities) substantial differences in response occurred between the spring and fall-winter periods. Spring grazing resulted in a modest overall increase of shadscale in spite of the reported die-offs during dry cycles, and an elimination of bud sagebrush at all grazing intensities studied. Fall-winter grazing appeared to have a reverse effect on these two species. Shadscale experienced a decline through the period of measurement, while bud sagebrush showed little change before 1967, then increased somewhat. Winterfat showed a general decline through the period under both seasons of grazing, while Indian ricegrass showed little change before 1967, but increased later. Under both seasons of grazing each of the latter two species ended up as 10 to 13 percent of the composition.

The decline of winterfat under fall-winter grazing from 1967 to 1983-84 would not have been predicted from earlier results. Several of the researchers mentioned earlier, analyzing data sets spanning the mid-1930's through the late 1960's or early 1970's, reported winterfat increasing in importance under early winter use and under no grazing. Current data, showing substantial reductions in winterfat in the 1980's under all grazing situations including no grazing, suggest causal effects other than grazing (fig. 3). The increase of the spring-growing Indian ricegrass under spring

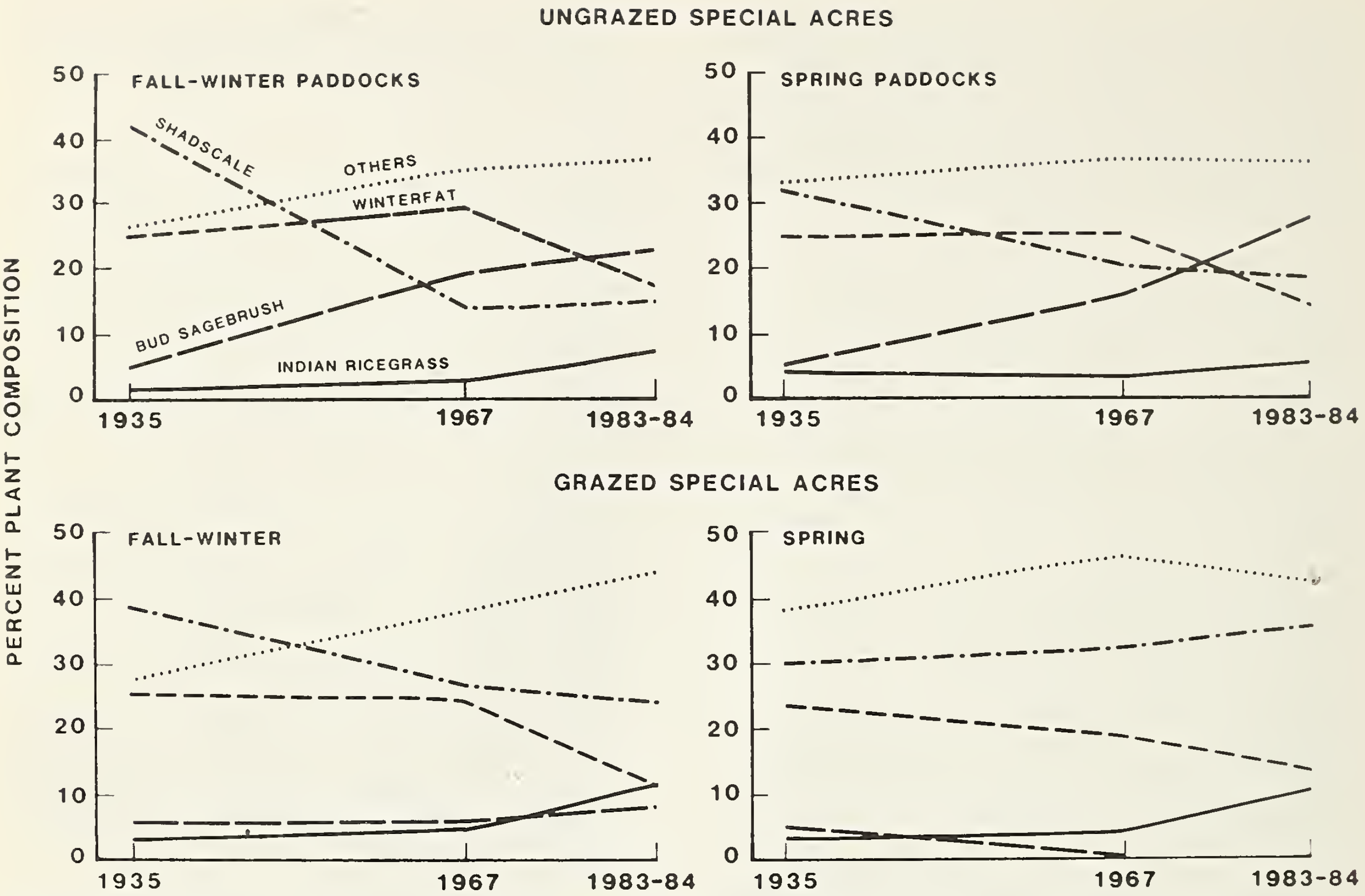

Figure 3.--Proportion of plant cover contributed by four major species and others in paddocks of all grazing intensities.

grazing use would not have been predicted from earlier results either.

As mentioned in the introduction, desert vegetation is dynamic and often reacts to factors other than grazing. The apparent increase in winterfat from 1935 to 1967 was in agreement with other published results (Holmgren and Hutchings 1972). However, precipitation in 1967 was unusual (fig. 4). Not only was the total amount (9.31 in) considerably above average (6.09 in), but most of the increase was in the summer period when winterfat could respond more to an increased moisture supply than could the other three species. Could the apparent increase in importance of winterfat have been due to the distribution of rainfall in 1967 and not to a general compositional trend?

Another of many interesting examples of divergence from anticipated response occurred on the special acres in paddocks 7 and 8 (fig. 5). These two paddocks were heavily grazed during the fall-winter period. The plant composition was determined for paddock 8 in 1983 and for paddock 7 in 1984. Water year 1983 was slightly drier than average, but the influential factor was the precipitation that occurred in the last week of water year 1982 (fig. 6). This (3.67 in) exceeded one-half of the expected total annual precipitation and was the apparent reason for luxuriant early plant growth the

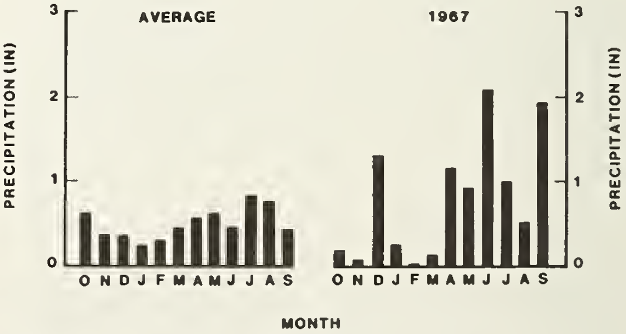

Figure 4.--Amount and monthly distribution of precipitation for water year 1967 and long-term average at the Desert Experimental Range.

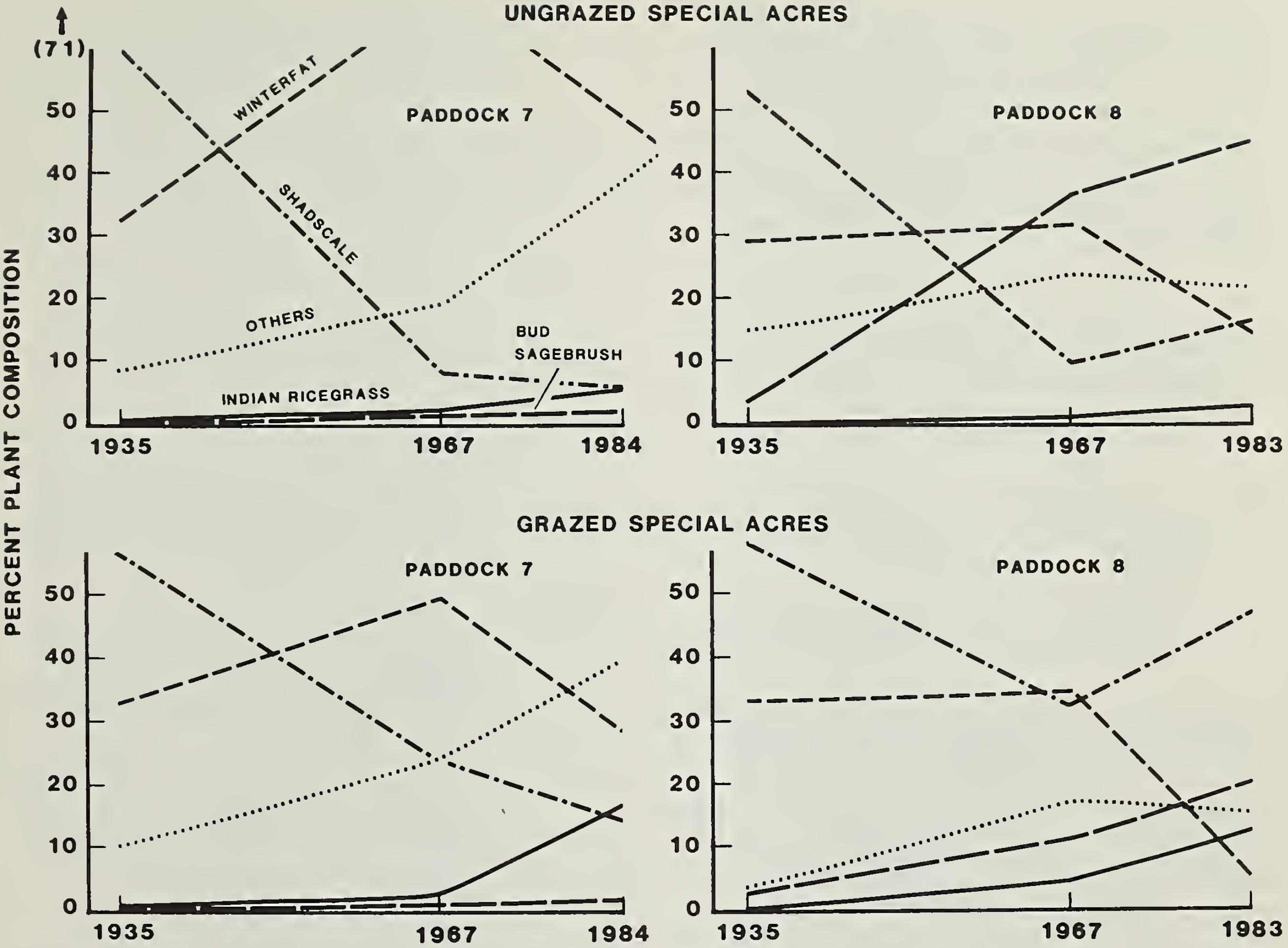

Figure 5.--Proportion of plant cover contributed by four major species and others in paddocks 7 and 8.

spring of 1983 with a strikingly profuse flowering of gooseberryleaf globemallow (Sphaeralcea grossulariaefolia) (fig. 7). This moisture supply could have caused an unusual response by the spring-growing shadscale and bud sagebrush. The summer precipitation pattern in 1984 would appear to have benefited winterfat and explain its strong dominance in the 1984 data of paddock 7.

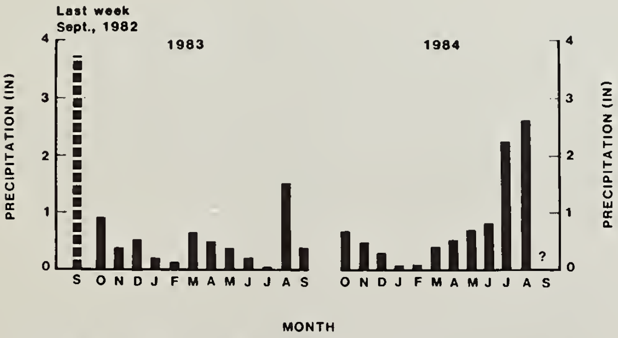

Figure 6.--Amount and distribution of precipitation for water years 1983 and 1984 at the Desert Experimental Range.

Figure 7.--Profuse growth and flowering of gooseberryleaf globemallow and other species the spring of 1983.

Moisture patterns may be the primary reason for apparent plant growth discrepancies, but there are other questions. Let us again look at figure 5. All plots were measured in 1967, therefore all were subject to the same weather patterns. These two paddocks had similar plant compositions in 1935, experienced the same grazing treatments, were located adjacent to one another, had experienced the same weather patterns, and yet were already responding very differently by 1967.

Further examination of information on paddocks 7 and 8 shows that the soils on the 1-acre plot pairs, extracted from small scale maps of the DER (Tew and others no date), were as follows:

Plot pair	Paddock 7	Paddock 8
1	Hiko Springs gravelly sandy loam	Sardo gravelly sandy loam
2	Aysees gravelly sandy loam	Hiko Springs gravelly sandy loam

The most similar responses did not occur between paddock 7 plot 1 and paddock 8 plot 2 as might be expected because of similar soils. Responses were the most similar between plots within paddocks--why? The most apparent reason for this unexpected response was an almost total lack of bud sagebrush on the 1-acre plots of paddock 7 in 1935. Thus, winterfat was able to retain general dominance in paddock 7, while bud sagebrush became dominant on the ungrazed plots and the second most dominant on the grazed plots of paddock 8. Bud sagebrush increased about six times in both paddocks--the main difference was the different starting points; paddock 7 had little more than a trace of bud sagebrush in 1935 while in paddock 8 it represented nearly 4 percent of the plant composition.

Why was bud sagebrush virtually absent from the 1-acre plots of paddock 7 at the beginning of the study period--the only paddock in which that situation occurred? Was the reason insects, disease, early day grazing concentrations, or some undefined soil or site factor? Once the occasion passes it is difficult if not impossible to reconstruct past events. This is a characteristic problem of evaluating long-term data sets.

CONCLUSIONS

It is very easy for all of us to fall into the mental trap of ascribing vegetation change to one or two simplistic factors. Nature, however, is not usually so simple. Some of the major factors that should be considered when relating vegetation reactions to grazing include:

1. Grazing treatment--including duration of years as well as season and intensity. A much different result may be witnessed if the length of a grazing trial only exceeds the average life span of shadscale compared to one that exceeds the much longer average life span of winterfat. Length of time affects (1) ability of an initially very minor component to eventually express itself; and (2) the likelihood of the low-frequency events that allow recruitment of normally infrequent new plant establishment.
2. Grazing animal species--have the differences in diet selection been fully accounted for?
3. Botanical composition--interspecies competitiveness is too often ignored. A species may actually increase even though it is being grazed during a susceptible period, if its competitors in the plant community are suffering even greater stresses of one form or another.
4. Soil and site--the same species can respond to grazing and to climate differently on different sites. Site is often confounded with treatment.
5. Weather and climate cycles--have these been fully considered when assessing effect of recent grazing management changes? Plant damaging events such as the valley-bottom floods of the mid-1970's on the DER are not predictable, and their occurrence may have to be noted at the time to properly interpret later plant death.
6. Insects and disease--have these been unnoticed agents of change? These in all probability have to be detected at the time of occurrence. One cannot go back through a long-term data set and discover their presence.
7. Realize that all of these factors can interact in different ways.

In addition to the actual biological and physical changes, the subjectivity of the method of attaining data is important. For example, quadrat charts, theoretically an objective technique, give pictures as indicative of the person who maps them as his handwriting. Cover estimates vary not only across years, but even more so as personnel change.

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INFLUENCE OF UNGULATES ON THE DEVELOPMENT OF THE SHRUB UNDERSTORY OF AN UPPER SLOPE MIXED CONIFER FOREST

Paul J. Edgerton

ABSTRACT: The role of deer and elk in forest succession was investigated in a recently harvested clearcut in the Blue Mountains, OR. Grazing prevented shrub establishment and favored development of grasses and forbs. Abundant shrubs developed within a fenced exclosure. Results suggest that by considering forage and cover requirements in silvicultural plans, managers can utilize ungulate foraging as a vegetation management tool.

INTRODUCTION

Timber harvesting characteristically changes the environment of mixed conifer forests of the interior Pacific Northwest. Disturbance resulting from logging and associated silvicultural practices creates habitats that favor the germination and establishment of numerous understory herbs and shrubs. The seral plant community mosaics that develop in these managed forests differ widely in age, size, distribution, vegetative composition, and structure. They serve as seasonal foraging areas for several kinds of wild ungulates and often livestock.

Traditionally, large ungulates, including mule deer (Odocoileus hemionus), white-tailed deer (Odocoileus virginianus), and Rocky Mountain elk (Cervus elaphus nelsoni) have been assigned a largely passive role in the development of forest ecosystems. Managers and biologists have been concerned with balancing animal numbers with available forage, and more recently, with maintaining areas of suitable cover (Thomas 1979). Little attention, however, has been given to the influence of ungulate foraging on the development of seral vegetation and to using that knowledge in the formulation of vegetation management strategies.

A long-term study has been conducted in the Blue Mountains of northeastern Oregon to provide land managers with information on secondary plant succession following timber harvest and residue treatments. This paper presents vegetation data, collected within and outside a fenced exclosure constructed for that study, that demonstrate the important function of deer and elk grazing on forest succession.

STUDY AREA AND METHODS

The study was conducted within an 8.1-ha clearcut and an adjoining unlogged stand of similar size on the Umatilla National Forest north of La Grande, OR. The area is part of the Mottet Timber Sale (lat. 45°39' N, long. 117°58' W). Elevation is 1 370 m and annual precipitation is estimated at 89-114 cm based on measurements taken at a nearby station (Fowler and others 1979). The growing season is typically warm and dry with most precipitation falling as snow during the fall and winter months. Soils have developed from volcanic ash deposited over residual basalt-derived soils and are 135 cm or more in depth. The slope is moderate and east-facing.

Forest structure and composition are characteristic of maturing mixed conifer forests in the grand fir (Abies grandis [Dougl.] Lindl.) zone in the northern Blue Mountains. The unlogged stand is a 175-year-old forest of grand fir, western larch (Larix occidentalis Nutt.), Douglas-fir (Pseudotsuga menziesii var. glauca [Beissn.] Franco), and Engelmann spruce (Picea engelmannii Parry ex Engelm.). Average tree basal area is 75.0 m^2/ha with 94 percent canopy cover.

Ecologically, the study area can be classified as the Abies grandis/Pachistima myrsinites (Pursh) Raf. habitat type of Daubenmire and Daubenmire (1968) and the white fir (Abies grandis/twinflower (Linnaea borealis L.)/forb plant community of Hall (1973). As shown in figure 1, understory vegetation cover in the undisturbed forest was relatively high. It included three grasses, 30 forbs, and 10 shrubs but was dominated by a large number of low-growing, shade-tolerant, rhizomatous forbs such as queencup beadlily (Clintonia uniflora [Schult.] Kunth), coolwort foamflower (Tiarella unifoliata Hook.), and pioneer violet (Viola glabella Nutt.). Big whortleberry (Vaccinium membranaceum Dougl. ex Torr. in Wilkes) was the only shrub of any importance, and its scattered stems appeared low in vigor.

Logging in the clearcut was completed during the summer of 1964. The forest floor was extensively disturbed by the tractor logging and a considerable

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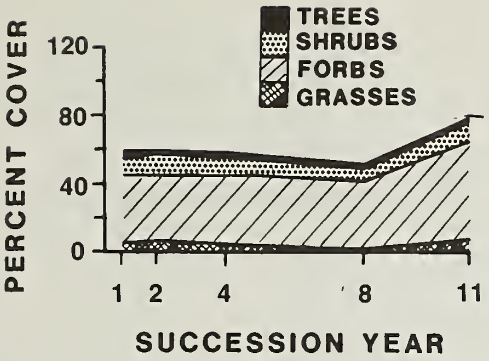

Figure 1.--Understory plant cover in an old-growth mixed conifer stand at the Mottet study area. Cover is expressed as the total layered canopy cover of each plant group and may exceed 100 percent.

amount of slash remained. To facilitate description of seral vegetation development as a result of commonly used residue treatments, one-half of the unit was broadcast burned during the fall of 1965; the remainder of the unit was left untreated. Domestic grasses were seeded on the encircling fireline but not within the unit itself. Seedlings of ponderosa pine (Pinus ponderosa Dougl. ex Laws.). Douglas-fir, grand fir, and Engelmann spruce were outplanted during the spring of 1966.

Large herds of elk and scattered, smaller groups of deer utilized the study area and surrounding forest for both forage and cover. Although their length of stay varied from year to year with the depth and persistence of the winter snowpack, animals or their signs were generally observed from early May through late November. Livestock grazed adjacent forest range but were not present within the study area.

Noting that deer and elk foraged heavily on seral vegetation developing in logged areas in nearby forests, we constructed a 1.6-ha exclosure to determine the effects of grazing on plant development and composition. The fenced area straddled burned and unburned treatments near the center of the unit.

Vegetation development was measured as percent cover using the procedure described by Daubenmire (1959). Measurements were taken in late August on 120 0.19-m^2 permanent plots located in each of the following treatments: unburned and grazed; burned and grazed; unburned and ungrazed; burned and ungrazed. Vegetation in the adjoining unlogged stand was described by the same procedure.

The number of animals utilizing the study area was not determined. An index to use during the initial 4 years of plant succession was provided by annual counts of deer and elk pellet groups on forty-eight 9.3-m^2 permanent plots in each unfenced treatment in the clearcut and the unlogged area.

The study design is a case history; hence, the data are presented as treatment means for succession years 1, 2, 4, 8, and 11 with no attempt to make statistical comparisons. In keeping with the focus of this symposium, the response of understory shrubs is emphasized in this paper. A thorough discussion of the development of all seral species at this study site and at companion study sites will be presented in another paper.

RESULTS AND DISCUSSION

Initial Plant Development

Seral vegetation developed rapidly following disturbance. Within 2 years, total vegetation cover in each treatment area of the clearcut (figs. 2 and 3) exceeded that in the unlogged forest understory (fig. 1). Increased light and moisture stimulated growth of surviving understory forbs such as sandwort (Arenaria macrophylla Hook.) and sweetscented bedstraw (Galium triflorum Michx.). Deeply churned soils and heavily burned spots were extensive and provided environments conducive to the germination and establishment of short-lived forbs such as bull thistle (Cirsium vulgare (Savi) Ten.); perennial grasses and sedges, particularly Columbia brome (Bromus vulgaris (Hook.) Shear) and Ross sedge (Carex rossii F. Boott in Hook.); and seral shrubs and trees such as blueberry elder (Sambucus cerulea Raf.), Scouler willow (Salix scoulerana Barratt ex Hook.), and western larch.

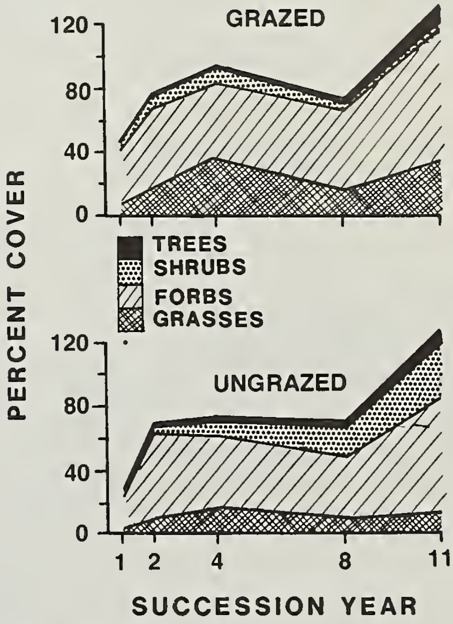

Figure 2.--Plant development in the unburned portion of the clearcut, Mottet study area. Cover is expressed as the total layered canopy of each plant group and may exceed 100 percent.

Animal Use

Pellet group counts (table 1) showed that wild ungulates, particularly elk, used the area extensively during the early years of secondary

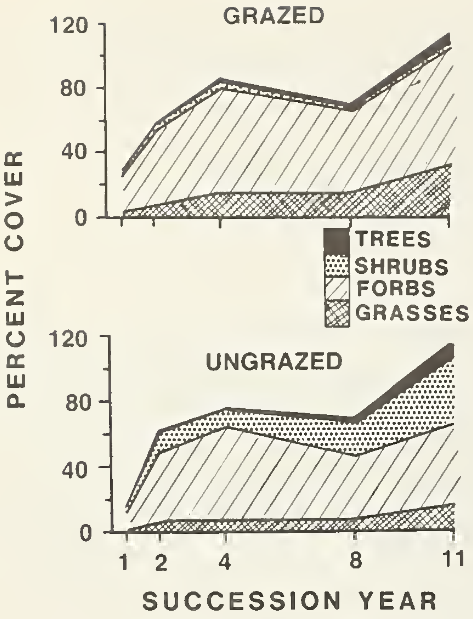

Figure 3.--Plant development in the burned portion of the clearcut, Mottet study area. Cover is expressed as the total layered canopy cover of each plant group and may exceed 100 percent.

succession. Timber sale location facilitated animal use. The unit was located approximately 1 km from the nearest, well-traveled road along a "dead-end" logging spur that was not maintained. Accordingly, as soon as harvest and residue treatment were completed, animals freely moved about the forest with minimal human disturbance.

Similar densities of deer pellet groups were found in the forest and clearcut, but elk pellet groups were more than twice as numerous in the clearcut as in the forest. These data may not, however, be a reliable index to habitat preference. Reports evaluating pellet group sampling show that activities, such as resting and foraging, are often habitat-related and may result in large variations in defecation rate (Collins and Urness 1981; Skovlin 1982). Nonetheless, it seems logical to assume that elk spent a large proportion of the time foraging in the clearcut. They also foraged in the forest, but numerous encounters with bedded animals suggest it provided essential thermal and hiding cover between foraging periods.

Table 1.--Mean annual ungulate use of the Mottet study area as determined by pellet group counts during the first 4 years following timber harvest

Treatment	Deer	Elk
	--Pellet groups/ha--	
Unlogged forest	174	270
Unburned clearcut	152	646
Burned clearcut	174	652

Grazing Effects

Figures 2, 3, and 4 allow comparison of the development of grazed versus ungrazed seral forest communities. Although grazing was noted on most plant species, its major impact was to prevent the development of shrubs while promoting the growth of grasses and sedges. Grazing obviously played a controlling role in determining vegetation composition and structure. Use was noted on many plant species, but shrubs showed the greatest impact. Seedlings of 10 species occurred throughout the clearcut during the initial 1 to 3

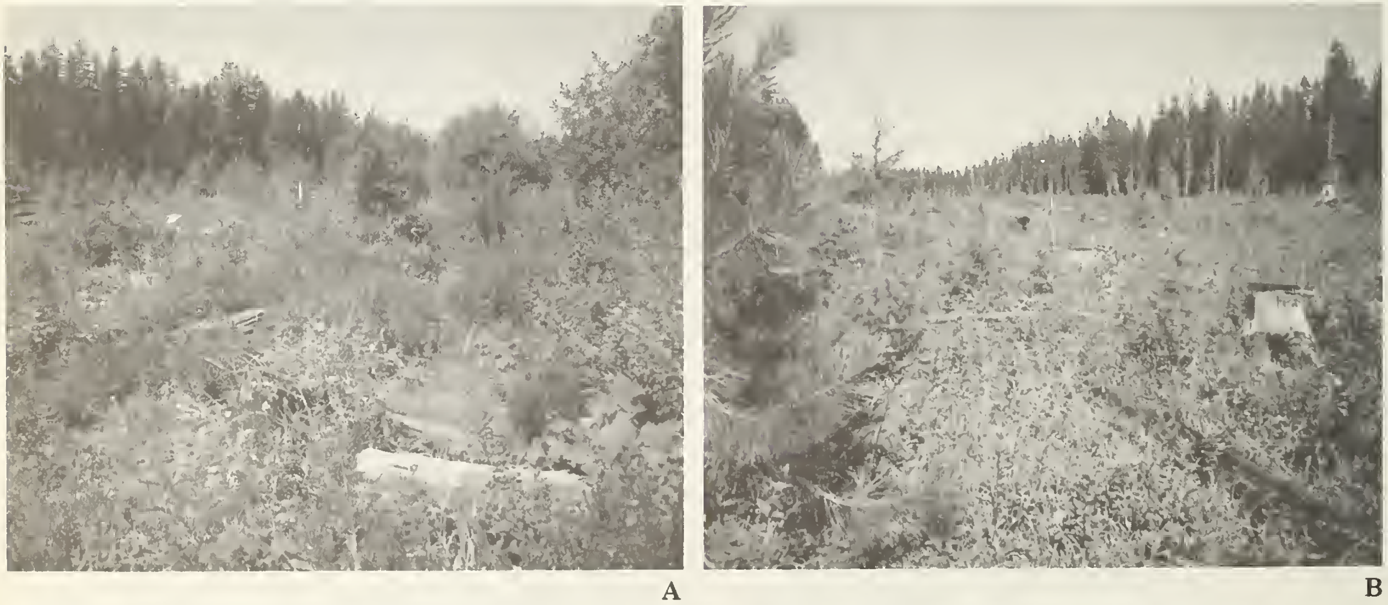

Figure 4.--Photos of seral forest communities in grazed versus ungrazed portions of the Mottet clearcut. A-burned portion after 11 seasons of grazing. B-burned portion after 11 seasons of protection. The abundant, low-growing shrubs near the center of photo B are myrtle pachistima. The taller shrubs are Scouler willows.

years after disturbance, but those accessible to deer and elk were soon heavily browsed. Repeated removal of most leaves, current twig growth, and portions of the woody stems prevented establishment and growth. By the fourth or fifth season, only those scattered, individual shrubs partially protected from overuse beneath logs or within slash piles survived. Total shrub cover averaged just 2.6 percent in the burned area and 3.7 percent in the unburned treatment after 11 years of grazing.

The photo (fig. 4a) of the area outside the exclosure illustrates the grass-forb understory that developed as a result of grazing. Composition was diverse: 11 grasses, 51 forbs, and nine shrubs in the unburned area, and 10 grasses, 40 forbs, and 10 shrubs in the burned portion. Abundant species included Columbia brome, Ross sedge, western coneflower (Rudbeckia occidentalis Nutt.), lanceleaf figwort (Scrophularia lanceolata Pursh), and bracted strawberry (Fragaria vesca bracteata [Heller] Davis. Although production of preferred shrubs had been greatly reduced by grazing, this diverse understory provided an abundance of forage until shade of the rapidly developing conifer crowns became the controlling factor.

Within the exclosure, absence of animal use favored the development of shrub seedlings. After 11 years, shrub cover totaled 35 percent in the burned portion and 41 percent in the unburned portion as compared to less than 4 percent in each of the grazed areas. In contrast, total grass and sedge cover within the exclosure was approximately one-half that occurring outside.

Twelve species of shrubs occurred within the exclosure. Several species such as baldhip rose (Rosa gymnocarpa Nutt.) and common snowberry (Symphoricarpos albus [L.] Blake) were scattered in the understory of the unlogged forest (table 2) and may have sprouted from rootstalks. Most seral shrubs were observed, however, to develop from new seedlings. Major differences in composition between treatments were expected because burning (heat) favors the germination of several widely occurring seral forest shrubs such as snowbrush ceanothus (Ceanothus velutinus Dougl. ex Hook.) (Conard and others 1982). Surprisingly, ceanothus was a minor seral species in both the unburned and burned portions of the clearcut (table 2). Myrtle pachistima (Pachistima myrsinites [Pursh] Raf.) was the only shrub whose establishment apparently benefitted from slash burning. This low-growing, evergreen shrub is found throughout the Blue Mountains but is rarely a major understory component in forest communities grazed heavily by wild and domestic ungulates. Only scattered pachistima shrubs (average cover <0.05 percent occurred in the unlogged forest. Since the seeds of this species are not carried by the wind and adjacent seed sources are not available for distribution by animals, one might speculate that the numerous seedlings found in the burned portion germinated from buried seed deposited by shrubs present during an earlier successional period.

Several individuals of black cottonwood (Populus trichocarpa Torr. I Gray) developed in the exclosure and exceeded 4 meters in height after 11 years. These deciduous trees are usually restricted to riparian environments and are not

Table 2.--Shrub cover in the Mottet clearcut study area 11 seasons after logging disturbance

	Burned clearcut		Unburned clearcut		Unlogged
	Grazed	No grazing	Grazed	No grazing	grazed
	Percent cover				
Amelanchier alnifolia Nutt.	--	--	--	--	0.2
Berberis repens Lindl.	--	--	--	--	tr[1]
Ceanothus velutinus Dougl. ex Hook.	--	1.7	tr	--	--
Chimaphila menziesii (R. Br.) Spreng.	--	--	--	--	0.2
Chimaphila umbellata (L.) Bart.	--	--	--	--	0.6
Holodiscus discolor (Pursh) Maxim.	--	--	0.3	--	--
Lonicera utahensis Wats.	--	--	--	tr	--
Pachistima myrsinites (Pursh) Raf.	0.6	19.1	--	3.3	tr
Prunus emarginata (Dougl.) Walpers	--	0.3	--	--	--
Ribes lacustre (Pers.) Poir. in Lam.	0.3	4.6	0.3	9.8	0.1
Ribes viscosissimum Pursh	0.7	6.8	0.3	4.9	--
Rosa gymnocarpa Nutt.	0.4	--	0.2	3.5	0.2
Rubus parviflorus Nutt.	0.2	2.6	1.5	3.4	--
Salix scoulerana Barratt ex Hook.	--	6.3	--	4.6	--
Sambucus cerulea Raf.	tr	tr	0.9	2.6	--
Sorbus scopulina Greene	--	--	--	--	0.1
Symphoricarpos albus (L.) Blake	0.3	--	tr	1.8	0.2
Taxus brevifolia Nutt.	--	--	--	--	7.6
Vaccinium membranaceum Dougl. ex Torr. in Wilkes	0.1	--	0.2	0.7	3.0
Total shrub cover	2.6	41.4	3.7	34.6	12.2

[1] tr = trace (<0.1 percent cover)

found in nearby forest stands; it is likely they developed from seeds widely dispersed by wind.

Establishment and growth of trees in recently harvested areas are major concerns of forest managers. In these forests, clearcut units must be satisfactorily restocked with young trees within 5 years after final disturbance. At the Mottet study area, a survey 2 years after planting showed that 7.3 ha (90 percent) of the unit was satisfactorily stocked with at least 618 trees/ha. After 11 seasons, stocking averaged 3,258 trees/ha for the entire unit. Grand fir, Engelmann spruce, and Douglas-fir occurred both as planted and naturally regenerated species. Western larch consisted entirely of seedlings established from natural seedfall. Minimal browsing or trampling damage of seedlings was noted at any time during the study.

Table 3 compares tree establishment and growth in grazed versus ungrazed vegetation that developed in the burned portion of the clearcut. Comparable data for the unburned treatment are not presented because portions of that treatment were not planted. Data for the burned area suggest that grazing was compatible with tree regeneration and may have benefited both establishment and growth. Other investigators in the Pacific Northwest have reported increased tree growth where competing understory vegetation has been reduced by carefully managed livestock grazing (Krueger 1983; Richmond 1983).

Table 3.--Stocking and height of conifers in the burned portion of the Mottet study area 11 seasons after disturbance

Species	Grazed	No grazing
	-Mean number trees/ha--	
Grand fir	1640	1363
Western larch	1195	929
Douglas-fir	889	128
Engelmann spruce	395	336
Ponderosa pine	59	198
Total	4178	2954
	---Mean height (cm)---	
Grand fir	156.0	140.1
Western larch	290.4	264.0
Douglas-fir	283.5	166.2
Engelmann spruce	162.9	191.4
Ponderosa pine	317.7	320.7

CONCLUSIONS AND IMPLICATIONS

This study has clarified the important functional role that deer and elk foraging plays in secondary succession in forests of the interior Pacific Northwest. Deer and elk altered both the pace and direction (composition) of the development of early stages of the forest succession model presented by Thomas (1979). Grazing prolonged the initial grass-forb stage while preventing shrubs from developing as the major component of the understory during seedling and sapling stages.

These effects have also been observed to be important factors influencing the composition of the understory of later successional stages. This is evidenced by Hall's (1973) description of the white fir-twinflower-forb forest community; he stated that "shrubs are conspicuously absent or very restricted in occurrence." It is obvious that patterns of past and present animal use are important factors to consider when classifying plant communities and characterizing ecosystem processes in these forests.

Knowledge of the effects of ungulate grazing on forest succession has important implications for the formulation of vegetation management strategies that may affect timber, watershed, and wildlife habitat values. During early successional stages, grazing either by wild ungulates or livestock has the potential to alter the composition and reduce the biomass of shrubs and other understory vegetation that may compete with tree seedlings for light, moisture, and nutrients. However, ungulate grazing may negatively impact watershed characteristics, not only by altering plant cover but also by causing soil compaction and surface disturbance on sensitive soils (Gifford 1981). Further, reduction in the number and size of seral shrubs simplifies understory structure and may have long-term impacts on habitat quality for dependent species of nongame wildlife (Balda 1975).

Planned or unplanned, forest harvests and other silvicultural activities create mosaics of forage and cover areas that strongly influence the distribution and degree of ungulate grazing. By understanding and considering animal needs, managers have opportunities to manipulate the size, arrangement, and structure of habitats to either minimize grazing influence or utilize it as a subtle but effective vegetation management tool.

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EFFECTS OF LIVESTOCK GRAZING AND THINNING OF OVERSTORY TREES ON UNDERSTORY WOODY PLANTS

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ABSTRACT: Two cultural treatments were employed and evaluated over 7 years to determine their effect on height increases of woody plants in decadent woodlands of southwestern North Dakota. Cultural treatments included exclusion of livestock and removing 40 percent of low-vigor trees. Shrub heights varied with species and cultural treatment. Saskatoon serviceberry (Amelanchier alnifolia), green ash (Fraxinus pennsylvanica), and Woods rose (Rosa woodsii) were taller when livestock were excluded. Green ash was taller where decadent overstory trees were removed. The response of woody plants to these cultural treatments was slow for some species and nonexistent for others.

INTRODUCTION

Woodlands on the northern High Plains are important to livestock and wildlife because they provide shade, thermal cover, and relief from wind and insects (Severson and Boldt 1978; Bjugstad and Girard 1984; Kauffman and Krueger 1984). Many woody plants provide forage during the grazing season (Holechek and others 1982; Roath and Krueger 1982; Uresk and Lowry 1984; Uresk and Paintner 1985). However, heavy grazing by livestock can result in decreased vigor of plants (Garrison 1953; Ellison 1960; Willard and McKell 1978) and alteration of species composition.

Many High Plains woodlands are becoming decadent, nearing the end of their lifespans (Boldt and others 1978), and are being replaced by grassland. These woodlands may require specific management to maintain or enhance their value for livestock and wildlife. Partial removal of the overstory trees on woodlands (increased light; less competition) influences understory production and growth of woody plants (Ehrenreicht and Crosby 1960; Jameson 1963). Some woody plants have responded to grazing and tree removal (Boldt and others 1978).

The objectives of this study were to evaluate the effects of (a) livestock grazing and (b) cutting of trees on growth of understory woody plants on the northern High Plains.

STUDY AREA AND METHODS

The study was conducted over a 7-year period from 1975 to 1981 on the Little Missouri National Grasslands, Custer National Forest, in southwestern North Dakota. A woodland system was selected in the upper reaches of Magpie Creek drainage near Belfield, ND. Trees in these prairie drainages were green ash (Fraxinus pennsylvanica) and American elm (Ulmus americana). The shrub understory included western snowberry (Symphoricarpos occidentalis), Woods rose (Rosa woodsii), spiny currant (Ribes setosum), Saskatoon serviceberry (Amelanchier alnifolia), silver buffaloberry (Shepherdia argentea), common chokecherry (Prunus virginiana), American plum (Prunus americana), hawthorn (Crataegus spp.), and raspberry (Rubus spp.).

Woodlands selected for study were located in two pastures grazed by cattle in a three-pasture range allotment under a deferred rotation grazing system. Stocking rate was 1.07 AUM/ha (animal unit months) from May 15 to October 30. Utilization of forage by late August or early September averaged 35 percent. At the beginning of this study, pastures had been managed for 2 years under this system. Before the deferred rotation grazing system was implemented, the area had been grazed season-long as a single pasture.

Twelve sample sites (0.08 ha each) were selected at scattered locations throughout a major woody draw system where site and vegetation conditions were reasonably uniform and representative (Boldt and others 1978). The experiment included two factors in a factorial design--cattle grazing versus no grazing, and tree removal versus no tree removal. The four treatment combinations were allocated at random on the 12 sites, with three replications per treatment. Fences to exclude cattle were installed in late summer and fall of 1975.

Seven species of trees and shrubs were studied over the 7-year period. These included; green ash, American elm, western snowberry, woods rose, spiny currant, Saskatoon serviceberry and common chokecherry which were common on the study areas. Other wooded species were rare on the sites.

Plots designated for tree removal (green ash; American elm) were selectively cut (40 percent of total stems) to open the canopy and stimulate sprouting in 1975 (Boldt and others 1978). Tree stems were cut to approximately 15-cm stump height

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and were removed from the site. The trees with low vigor and poorest of the growing stock as described by Boldt and others (1978) were removed. Pretreatment measurements were collected on all sites. All small live trees were measured for height (< 2.5 cm d.b.h.). Heights of all shrubs and small trees were measured on five belt transects 15.3 m by 1.2 m randomly located on each site. Height measurements (centimeters), were recorded on all sites (one sample period) during late August and early September of each year for 6 years after treatment.

Shrub height measurements were averaged by species and by site for statistical analyses. Analysis of covariance, with pretreatment data as the covariate, was employed to test treatment effects separately for each species each year (Nie and others 1975). When the covariate was not significant ($\alpha = 0.10$), an analysis of variance was used to test for treatment differences. A Bonferroni criterion of $\alpha = 0.04$ was used for individual species and year combinations. This α level was derived from an overall level of 0.25/6 years for each species (Miller 1981). However, when individual years are considered without the α level divided by 6 many more differences occur, thus the term biological trend is used in the text. The absence of interactions indicated treatments responded independently.

RESULTS

Heights of Saskatoon serviceberry were statistically greater on ungrazed compared to grazed sites during the fourth and fifth years after initial treatment (fig. 1). However, height trends (biological) from the second to sixth year indicate greater heights on the ungrazed treatment. A reduction in the number of overstory trees did not influence heights of serviceberry.

Green ash heights were statistically greater on the ungrazed than on grazed sites in the third, fourth, and sixth years after initial treatment (fig. 1). This indicates that cattle were eating green ash when not excluded from woodlands. Removal of overstory trees resulted in a significant increase in height of green ash from the third through the sixth year.

Height trends for common chokecherry were irregular, with no consistent differences between grazed and ungrazed treatments (fig. 1). However, removal of overstory trees resulted in a general but not significant trend of greater heights throughout the 6-year period.

Spiny currant plants showed no statistical differences in heights between ungrazed and grazed areas throughout the 6 years (fig. 1) However, some indications of biological trends are shown from the third through the sixth year between grazing treatments. Heights were not significantly greater on the uncut tree sites throughout the 6 years, although trends indicate that plants on the uncut site were taller.

Woods rose was taller during the fifth and sixth years on areas where livestock were excluded (fig. 1). Other years showed no differences in heights between treatments. Woods rose was significantly taller on the sites where trees were not removed than on sites with trees removed only in the second year. All heights of Woods rose were similar between treatments for the remaining 4 years when trees were removed.

Western snowberry was significantly shorter the second year on the ungrazed treatment (fig. 1). No differences were found throughout the remainder of the study. Some evidence of a trend was shown from the third through the sixth year for taller plants on the ungrazed treatment. No differences were observed for heights of snowberry as related to removal of overstory trees.

Heights of American elm saplings generally were not statistically different but were consistently higher on the ungrazed sites when compared to the grazed sites (fig. 1). Height trends for American elm were similar regardless of whether trees were removed. Taller plants were observed on the tree removal treatment, but this was not statistically different.

DISCUSSION

Height response of understory woody plants to grazing and removal of overstory trees was slow. Generally, exclusion of livestock was associated with increased height of Saskatoon serviceberry, green ash, and Woods rose. The other four species showed no response. These differences may be related to the seasonal use of woody plants by livestock (Holechek and others 1982; Uresk and Lowry 1984; Uresk and Paintner 1985). The lack of response differences between grazed and ungrazed treatments may be the result of growth stimulated by herbivore use or the lack of use (Ellison 1960; Jameson 1963).

Thinning overstory trees produced mixed results. Only heights of green ash were taller on the cut treatment. The most abundant shrub, western snowberry, did not respond to removal of overstory trees, nor did the other woody plants. Trends were evident for some species, but they were not statistically significant.

Reduced competition for light, space, and nutrients after cutting large trees may have helped ash seedlings and saplings to grow taller. Ehrenreich and Crosby (1960) reported higher production for understory plants within a hardwood forest as crown cover decreased. However, the plant species responded differently to changes in hardwood crown cover. Pase (1958), working in a ponderosa pine forest, showed that shrub production was greatest when crown canopy cover was from 0 to 19 percent. This was closely followed by shrub production in the 20 to 39 percent canopy cover. Production greatly decreased when canopy cover increased. In this study, forest canopy cover was about 58 percent on the cut sites.

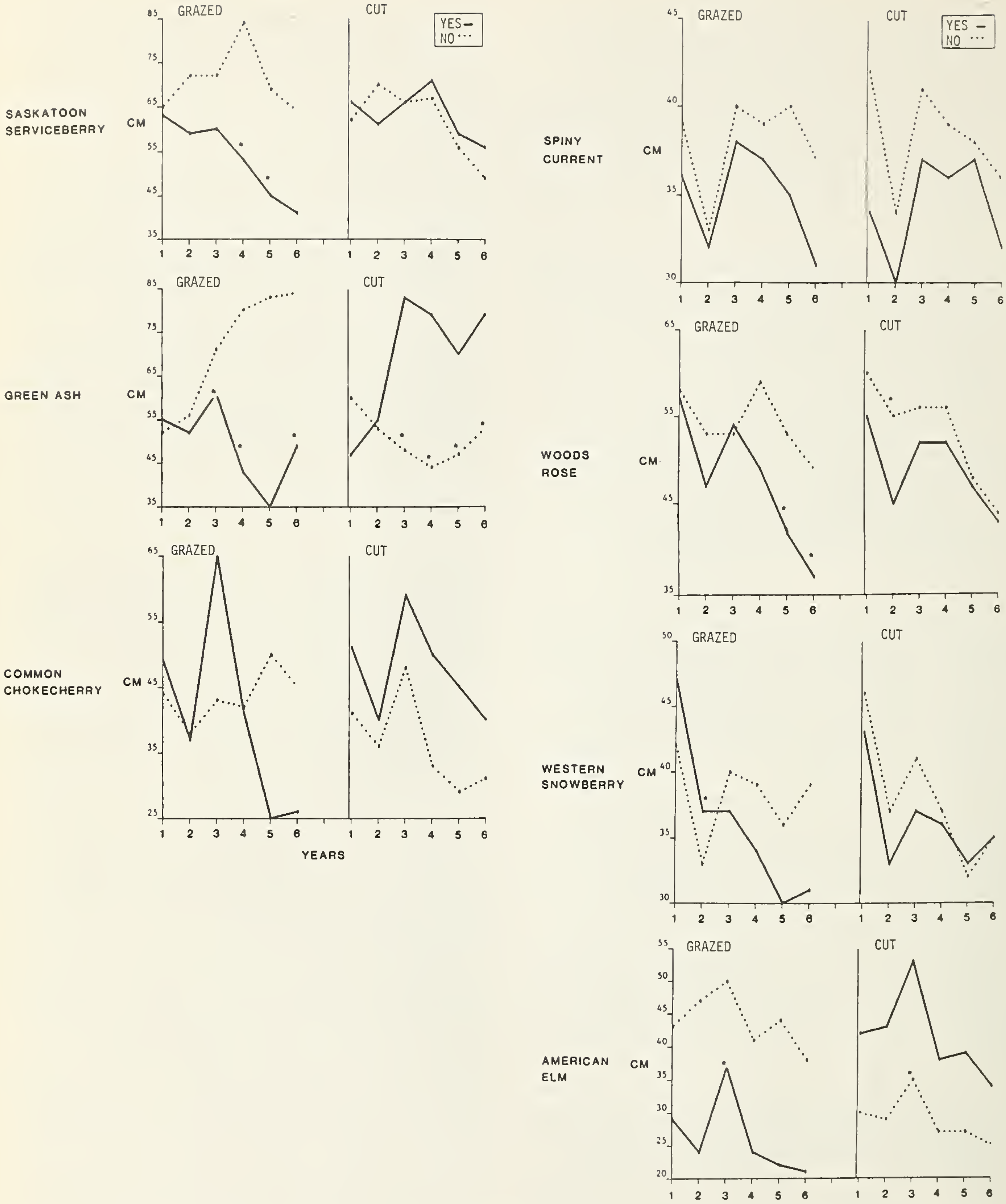

Figure 1.--Response of woody plants (cm) over a 6-year period on grazed (Yes) or ungrazed (No) pastures with 40 percent overstory trees removed (Yes) or 0 percent overstory removed (No). *Treatments are significantly different at α = 0.04.

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USING TWIG DIAMETERS TO ESTIMATE BROWSE UTILIZATION ON THREE SHRUB SPECIES IN SOUTHEASTERN MONTANA

Mark A. Rumble

ABSTRACT: Browse utilization estimates based on twig length and twig weight were compared for skunkbush sumac, wax currant, and chokecherry. Linear regression analysis was valid for twig length data; twig weight equations are nonlinear. Estimates of twig weight are more accurate. Problems encountered during development of a utilization model are discussed.

INTRODUCTION

One important aspect of managing large herbivore populations in the United States is the ability to estimate utilization of forage species. As development continues to crowd wildlife species, managing herbivore populations to maintain balance in the ecosystem has become a significant issue. Just as livestock managers should maintain proper use in pastures, game managers should strive to maintain game populations at levels that do not abuse the forage resources. Thus, managers need fast and efficient methods of estimating forage abundance and utilization.

Data on both the amount of forage available and the amount removed are needed to estimate utilization. Techniques have been developed whereby both of these parameters can be estimated from data collected in the spring after browsing has occurred. Relationships of twig diameter to weight and length have been developed for a number of shrub species (Telfer 1969; Lyon 1970; Peek and others 1971). Twig diameter-length and diameter-weight relationships have been shown to vary statistically among sites, shrub species, individual plants, and location on the shrub (Basile and Hutchings 1966; Lyon 1970; Peek and others 1971; Jensen and Urness 1981). However, variations among plants, location on the shrub, and to some extent site differences are of little practical value for estimating utilization (Basile and Hutchings 1966; Lyon 1970). Jensen and Urness (1981) showed that utilization on bitterbrush (Purshia tridentata) and cliffrose (Cowania stansburiana) could be estimated by a series of twig diameter measurements alone. Provenza and Urness (1981) demonstrated that branch and twig diameters could be used to estimate utilization on blackbrush (Coleogyne ramosissima) more accurately than measurements taken before and after browsing. Estimates of utilization based on twig diameter measurements can reduce the number of field trips necessary, and accurate estimates of utilization can be made after browsing has occurred (Jensen and Urness 1981).

The objectives of this study were: (1) to develop models from which estimates of utilization of three shrub species based on twig diameter-length and twig diameter-weight relationships could be made, and (2) to compare browse utilization estimates based on twig length with estimates based on twig weight.

METHODS

This study was conducted about 6 km north of Decker, MT, during the fall of 1984 and spring of 1985. Three shrub species, skunkbush sumac (Rhus trilobata), wax currant (Ribes cereum), and chokecherry (Prunus virginiana), were selected for study. Ten shrubs of each species were identified, and 10 twigs on each shrub were selected and marked for sampling. Twigs were selected randomly, but also to represent the full range of current year's growth. Diameters of five twigs on each shrub were measured at the budscale scar and at a point between the budscale scar and terminal bud. Values were recorded to the nearest 0.1 mm. The length from each of the diameter measurements to terminal bud of the twig was also measured. On the other five twigs, twig diameter was measured at the budscale scar and at a point between the budscale scar and the terminal bud. The twig was then clipped at both measurement points, ovendried at 60 °C for 3 days, and weighed. These measurements provided 100 data points from which to develop the regression equations to predict twig length and twig weight for each species.

Regression models of the form $Y = a + bX$ (where Y = twig length and X = twig diameter) were developed for twig diameter-length relationships using SPSS New Regression (Hull and Nie 1981). Twig diameter-weight relationships were estimated using the SPSS nonlinear regression subprogram (Robinson 1984) for the model $Y = aX^b$ (where Y = twig weight and X = twig diameter). Residuals were analyzed using SPSS New Regression.

Herbivore utilization was examined in the spring on 35 skunkbush sumac, 13 wax currant, and 18

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chokecherry plants. On each shrub, a small number of twigs on one branch were selected randomly. Diameters of browsed twigs were measured at the budscale scar and browse point with calipers, and total number of browsed twigs were counted. Utilization estimates were determined from mean diameters by plant species.

RESULTS AND DISCUSSION

Utilization Estimates

Examination of twig diameter-twig length data indicated that linear regression analyses (fig. 1) were appropriate for the three shrub species. The regression fits for twig diameter-length relationships from this study were similar to those reported for bitterbrush (Basile and Hutchings 1966) and bitterbrush and cliffrose (Jensen and Urness 1981), but less precise than those Lyon (1970) reported for serviceberry (Amelanchier alnifolia). Previous browsing activity, plant vigor, and age contributed to the variation in twig diameter-length data for chokecherry in this study, especially at the larger twig diameters.

The relationships between twig diameter and twig weights for all three species were nonlinear (fig. 2). The equations developed to predict twig weights for skunkbush sumac and wax currant were very similar (table 1). These two species exhibited similar patterns of twig growth. The nonlinear regression equations for twig diameter-weight relationships for all three species had substantially higher regression fits than did linear estimates of twig diameter-weight relationships. Ruyle and others (1983) and Telfer (1969) reported nonlinear equations for twig diameter-weight relationships. Peek and others (1971) reported high correlation coefficients for twig diameter-weight relationships for most species, and Lyon (1970) indicated that the nonlinear relationship (log transformation) between twig diameter and twig weight did not result in any improvement over the linear model.

Estimates of percent utilization based on twig weights were 24, 41, and 52 percent less than estimates based on twig lengths for skunkbush sumac, chokecherry, and wax currant, respectively (table 2). These differences result from the curvilinear relationships between twig weight and twig diameter. The longer and larger twigs had a greater portion of the total weight in the proximal portions of the twig. Browsing at the end of a twig could result in substantial removal of twig length with less proportional removal of twig weight. Therefore, estimates of twig weight are a more accurate index of utilization. Provenza and Urness (1981) also reported less utilization of browse when twig or branch weight estimates were used, compared to twig or branch length estimates, but attributed the difference to inclusion of leaves in weight estimates. These relative differences in estimates of percent utilization are probably unimportant for species such as wax currant; but, for browse species that show greater utilization, these differences become more important to managers.

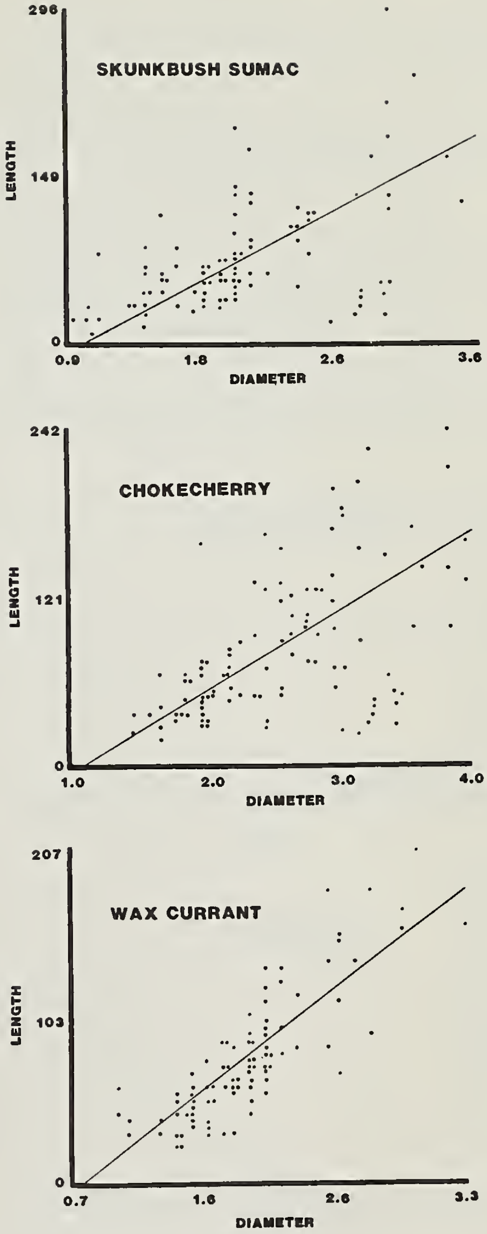

Figure 1.--Relationships of twig length (mm) to twig diameter (mm) for three shrub species in southeastern Montana.

Browsing by animals in this study did not remove large portions of individual twigs. Estimates of the percentages of individual twigs browsed (based on weight estimates) were 26, 37, and 20 percent for skunkbush sumac, chokecherry, and wax currant, respectively. Lyon (1970) suggested big game animals do not browse small percentages of individual twigs, which was contradicted by results of this study. Browsing animals on this study area were pronghorn (Antilocapra americana), mule deer (Odocoileus hemionus), and white-tailed jackrabbits (Lepus townsendii); livestock grazed portions of the study area.

When designing a study from which to develop a model to predict values, some modifications for sampling are required. Sampling in this study was pseudorandom in that a few very small and very large stems were deliberately sampled to include the extremes. However, for skunkbush sumac there was an order of magnitude difference between the three largest values and the remainder of the data. Preliminary analysis of the skunkbush sumac twig weight data with the model $Y = a + b_1X + b_2X^2$ resulted in an R^2 of 0.90. However, this regression equation was being driven by the three outlying data points (fig. 2). The resulting negative coefficient (b_1) caused the predicted weights of twigs browsed to be greater than the amount available because the function had a minima at a twig diameter larger than the mean diameter at the browse point. If the model was forced through the origin ($Y = bX^2$), the predicted weight of twigs browsed was negative, again resulting from the larger twig diameters driving the model. Other analyses that included these outliers resulted in the model $Y = aX^b$ having an exponent (b) of 5.73. The R^2 for this model also was 0.90. Examination of the residuals plot indicated the model was not appropriate. These outliers were sucker type growth and therefore were not included in the final analysis. The resulting model (table 1) and residuals plot suggested this model fit the data fairly well.

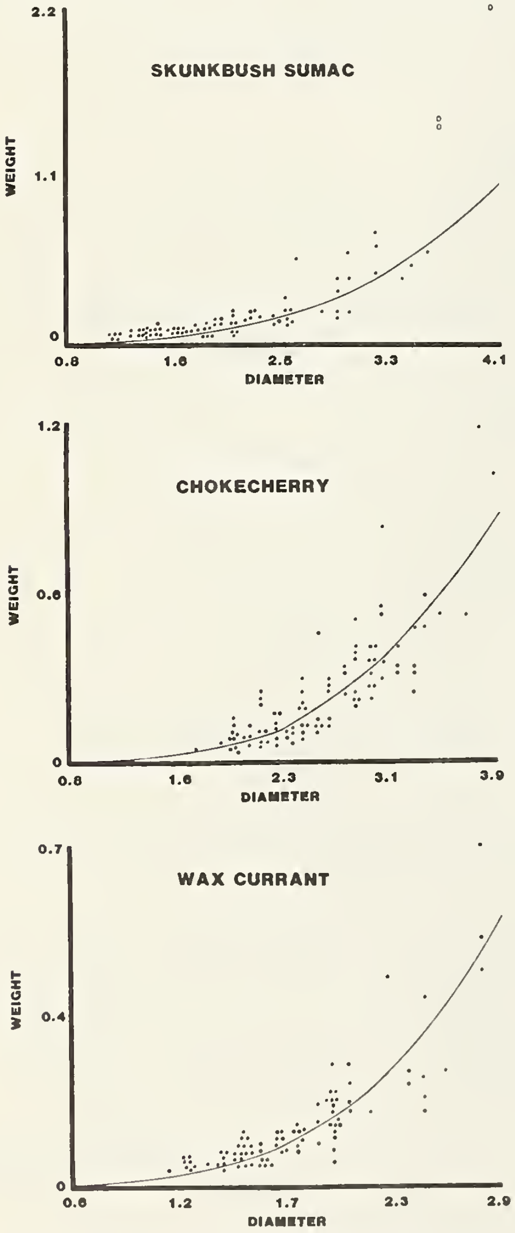

Figure 2.--Relationships of twig weight (g) to twig diameter (mm) for three shrub species in southeastern Montana.

Table 1.--Regression equations to predict length and weight of shrub twigs from twig diameter for three species of shrubs in southeastern Montana

Species	Equation	R^2
Skunkbush sumac	Length = 71.79 (6.1)[1] * (Diameter) - 64.55	0.59
	Weight = 0.007 (0.0004) * (Diameter$^{3.50}$)	0.60
Chokecherry	Length = 58.60 (5.8) * (Diameter) - 61.53	0.51
	Weight = 0.004 (0.0002) * (Diameter$^{4.05}$)	0.75
Wax currant	Length = 68.75 (5.9) * (Diameter) - 49.97	0.58
	Weight = 0.011 (0.0005) * (Diameter$^{3.69}$)	0.81

[1] The coefficient.

Table 2.--Estimates of percent utilization using length and weight equations for three shrubs species in southeastern Montana

Estimate method	Skunkbush sumac	Chokecherry	Wax currant
Length	11.1	18.9	4.2
Weight	8.4	11.2	2.0

In the future, a more selective procedure that results in a scattering of data points throughout the range of twig sizes (stratified random sampling) would be more appropriate. Random sampling of twigs concentrates the data points near the middle portions of the distribution. Without the data points at the upper and lower ends of the range (figs. 1, 2) these distributions could result in linear models that have been reported for twig diameter-weight models (Lyon 1970; Peek and others 1971).

Standardized residuals plotted against standardized twig diameters indicated that there were heterogeneous variances in these data. However, nonuniformity of variances will not introduce serious biases to regression models (National Academy of Sciences 1962: 255) provided the data are scattered throughout the range and there are no outliers. The residual plots indicated that the regression models derived were appropriate for these data. In any case, it is important to examine the residuals to see how well the model fits the data. Plots of residuals also indicate if nonlinear or weighted models should be used and they display possible outliers.

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NATURAL HISTORY OF LITTLE COTTONWOOD CANYON, UTAH: A FIELD TOUR

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INTRODUCTION

This paper is an invited account of the field trip concluding the August 7-9, 1985, Symposium on Plant/Herbivore Interactions, at Snowbird, UT. It is designed to give a vicarious or in-person visit to the site a biological, geological, and historical perspective.

GEOLOGY

The tour group traveled on the Snowbird aerial tram to its terminus at Mt. Baldy on the southern crest of the Little Cottonwood drainage basin (fig. 1). The tram terminates at a vantage point over 11,000 ft (3,353 m) above sea level. From that point one can see the Uinta Mountains to the east and several of the larger mountain systems of western Utah. As the tram made its ascent, some of the local influences of Pleistocene glaciers were readily observable. Extensive headlands along the southern wall of the canyon lie above 10,800 ft (3,292 m) elevation. Those areas accumulated enough snow during the Pleistocene to produce large glaciers that shoved their way downslope in both Little Cottonwood and American Fork Canyons. Little Cottonwood's classical U-shape owes its origin to glacial processes. Polished granitic walls and locally conspicuous moraines characterize the lower reaches of the canyon. The glacier flowed from the canyon's mouth and disgorged its ice directly into Lake Bonneville as recently as 15,000 years ago (Curry and James 1982). Bonneville's surface stood as high as 5,200 ft (1,585 m) above sea level some 13,000 yr B.P. Had we stood at the tram's upper station at that time, we would have seen an immense lake (the forerunner of Great Salt Lake) flecked with icebergs and stretching to the western horizon.

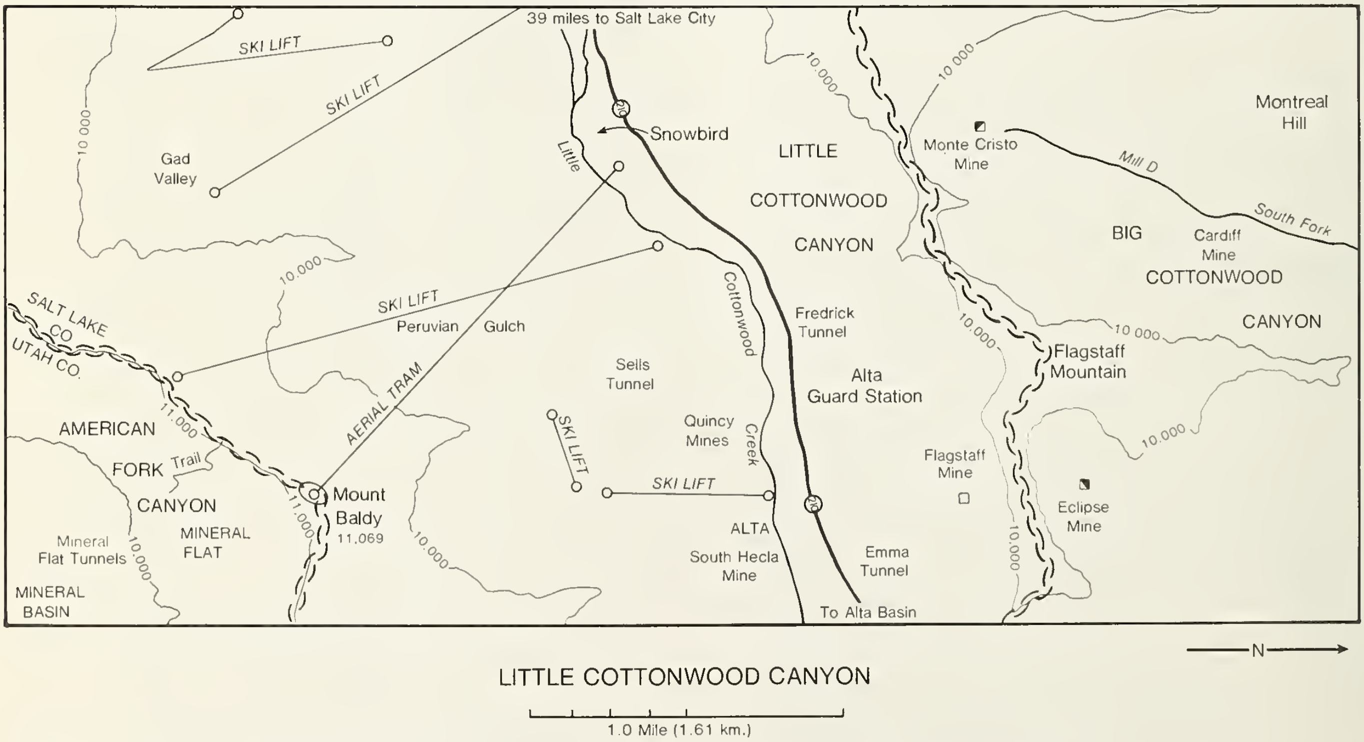

Figure 1.--Portions of Little Cottonwood and American Fork Canyons, Utah, observed on the field trip on August 9, 1985.

Little Cottonwood Canyon has complex structural features. The north wall of the canyon shows an extensive contact zone between intrusive igneous material and deep, overlying beds of sedimentary rocks. Heat and intrusive fissures of igneous material have altered both color and chemistry of sedimentary beds overlying the granitic stock. The basal sedimentary beds of quartzite, tillite, shale, and limestone appear burned and rusty for hundreds of feet above the margins of the stock. Fossils testify that the sedimentary beds in the canyon range in age from Pre-Cambrian to Jurassic. Geologists suggest that the molten stock was thrust into place in late Cretaceous or early Tertiary time (Calkins and Butler 1943). Numerous mine dumps in both Little Cottonwood and American Fork Canyons are visible from the terminus of the tram (fig. 1). They bear witness that most of the local precious metal deposits (silver, lead, copper, gold, and zinc, in order of revenue generated) occurred in fissures in the sedimentary rock just above the igneous-sedimentary contact zone.

BIOTA

Some animals and plants that are often observed in the area shown in fig. 1 are listed in table 1. Many of those species were seen as field trip participants hiked from Mt. Baldy along the trail into Mineral Basin in the American Fork drainage. Despite the fact that prevailing winds at this latitude flow from west to east, the biotas of mountains throughout the Great Basin are derived from mountains to the east. That fact is attributable to the following factors.

1) Mountain ranges between the Uintas and the Sierras are progressively younger as one moves from east to west. Thus although the Sierras now have rich biotas at high elevations, geologic evidence suggests that they did not reach elevations high enough to support subalpine and alpine taxa until after about 1.0 million yr B.P. (Axelrod and Ting 1960; Winograd and others 1985). Since all of the Great Basin ranges are older than that, their initial high-elevation colonists would have had to come from elsewhere. The Wasatch is old enough to have been such a source area: high-elevation taxa appear to have been spread westward from the Wasatch by birds or moved overland at times when lowlands were better watered (as in the Pleistocene).

2) Climates of the Wasatch are more like those of the desert mountains than those of the Sierras. Organisms adapted to the thermally moderate, high-humidity air masses of coastal California and the western slopes of the Sierras have probably been at a disadvantage as they have dispersed into the more continental and xeric climates of the Great Basin (Harper and others 1978).

3) Soils at high elevations in the Sierras are prevailingly acidic (Major and Taylor 1977), while even igneous outcrops in the Great Basin are often only weakly acidic or are nearly neutral (Harper and others 1978). Soils of the Wasatch and the sedimentary mountain ranges of eastern Nevada are basic in reaction (Holmgren 1972). Thus plants that are well adapted to the acidic soils of the Sierras tend to perform poorly in the Great Basin because of large differences in soil reaction (Harper and others 1978).

Modern distributional patterns of plants and animals in the Basin and Range Geological Province, and the Wasatch and Sierra Mountains which flank that province, were strongly influenced by environmental conditions that prevailed during the Pleistocene. Studies of biota dependent on the cool, seasonally well-watered habitats of Great Basin mountains show species richness (numbers of species per unit area) patterns reminiscent of patterns observed for oceanic islands. The species numbers tend to increase linearly with area of high-elevation habitat when both variables are expressed as logarithms (Behle 1978; Harper and others 1978). Interestingly, the steepness of the species-area regression lines differ significantly between taxonomic groups that disperse easily between modern islands of cool, moist habitat (birds and many plant species) and groups that now experience great difficulty moving between such habitat islands (many mammals now confined to high elevations). Thus mammals of boreal habitats show very steep regression lines, while birds and many plant groups display more gentle slopes for species-area regressions. Brown (1971, 1978) suggested that the steeper sloped regressions arise when a group has high extinction rates on small patches of habitat that had once been well stocked by species arriving by overland migrations during periods of better moisture relations. Alpine mammal species that appear to be representative of this group of overland dispersers are noted in table 1. As the Pleistocene waned and was followed by more xeric conditions in the Holocene, reinvasion of the small islands of suitable habitat became more difficult or impossible. Recent work has yielded much subfossil evidence that valley floors between modern islands of boreal habitat did support montane and subalpine plants in late Pleistocene times (Wells 1983). Grayson (1982) demonstrated that skeletal remains of several mammals unique to mesic montane or alpine habitats occur on a number of Great Basin ranges that are now too dry for boreal taxa. Those remains date to the late Pleistocene. Thus Brown's (1971) initial hypothesis about local extinctions on small mountain islands in the Great Basin has been supported by subfossil data from caches of biological material assembled by woodrats or prehistoric humans.

On the hike into Mineral Basin, note was taken of the fact that the flower pollinator guild at this site contained numerous dipteran insects. Pollinator guilds at low elevations in Utah are dominated by hymenopteran insects. The divergence of dipteran and hymenopteran insects with elevation seems to be the rule in

Table 1.--Animals and plants commonly seen in the vicinity of Snowbird and the terminus of the Snowbird aerial tram on Mt. Baldy. Common and scientific names (in parentheses) are listed. Mammals of alpine habitats that appear to have dispersed to high Great Basin mountains from the Sierras or the Rocky Mountains when intervening valleys were more mesic during the Pleistocene are marked with an asterisk (from Brown 1971)

Animals

Birds[1]

Broad-tailed hummingbird (*Selasphorus platycercus*)
Cassin's finch (*Carpodacus cassinii*)
Chipping sparrow (*Spizella passerina*)
Clark's nutcracker (*Nucifraga columbiana*)
Common flicker (*Colaptes auratus*)
Dusky flycatcher (*Empidonax oberholseri*)
Gray-headed junco (*Junco caniceps caniceps*)
Mountain chickadee (*Parus gambeli*)
Vesper sparrow (*Pooecetes gramineus*)
Water pipit (*Anthus spinoletta*)
Yellow-rumped warbler (*Dendroica coronata*)

Mammals[2]

Deer mouse (*Peromyscus maniculatus*)
*Ermine (*Mustela erminea*)
*Jumping mouse (*Zapus princeps*)
*Long-tailed vole (*Microtus longicaudus*)
Mt. goat (*Oreamnos americanus*)
Mule deer (*Odocoileus hemionus*)
*Pika (*Ochotona princeps*)
Red squirrel (*Tamiasciurus hudsonicus*)
Snowshoe hare (*Lepus americanus*)
*Uinta chipmunk (*Eutamias umbrinus*)
Uinta ground squirrel (*Spermophilus armatus*)
*Yellow-bellied marmot (*Marmota flaviventer*)

Plants[3]

Trees

Englemann spruce (*Picea engelmannii*)
Limber pine (*Pinus flexilis*)
Mt. alder (*Alnus incana*)
Quaking aspen (*Populus tremuloides*)
Subalpine fir (*Abies lasiocarpa*)

Grasslike Plants

Alpine bluegrass (*Poa alpina*)
Drummond rush (*Juncus drummondii*)
Letterman needlegrass (*Stipa lettermanii*)
Mt. brome (*Bromus carinatus*)
Ross sedge (*Carex rossii*)
Scribner wheatgrass (*Agropyron scribneri*)
Slender wheatgrass (*A. trachycaulum*)
Spike trisetum (*Trisetum spicatum*)
Tufted hairgrass (*Deschampsia cespitosa*)
Western sedge (*C. occidentalis*)

Shrubs

Alpine prickly currant (*Ribes montigenum*)
Blue willow (*Salix drummondiana*)
Mt. lover (*Pachistima myrsinites*)
Mt. snowberry (*Symphoricarpos oreophilus*)
Oregon grape (*Berberis repens*)
Red-berried elder (*Sambucus racemosa*)

Forbs

Arizona bluebell (*Mertensia arizonica*)
Brandegee onion (*Allium brandegei*)
Cloverhead horsemint (*Monardella odoratissima*)
Colorado columbine (*Aquilegia caerulea*)
Duncecap larkspur (*Delphinium occidentale*)
Engelmann aster (*Aster engelmannii*)
False hellebore (*Veratrum californicum*)
Fireweed (*Epilobium angustifolium*)
Leafy Jacob's ladder (*Polemonium foliosissimum*)
Marsh marigold (*Caltha leptosepala*)
Monkshood (*Aconitum columbianum*)
Parry arnica (*Arnica parryi*)
Showy goldeneye (*Viguiera multiflora*)

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[1] Bird names follow Behle and Perry (1975).

[2] Mammal nomenclature is after Brown (1971) and Grayson (1982).

[3] Plant names are from Arnow and others (1980).

mountain-valley systems throughout the earth (Warren and others, in press). Collins and others (1983) suggested that a statistically significant decline in sympetalous, yellow, tubular flowers with increasing elevation in Utah and a simultaneous rise in abundance of polypetalous, white, saucer-shaped flowers are related to strong differences in the foraging preferences of dipteran and hymenopteran pollinating insects. The differential success of dipterans and hymenopterans at high elevations seems related to basic differences in their life history patterns and behavior. Hymenopterans universally make chambers in which they deposit eggs and food for larvae, which emerge from eggs after the compartment is sealed. The food provided consists of pollen mixed with secretions from the adults. In contrast, dipterns build no nest structures and provide no parental care. Hymenopterans also thermoregulate (increase thoracic temperature) to permit flight in the colder environments of high elevations. Thermoregulation is made possible by frictional heat resulting from rapid wing movement without flight. That process uses considerable energy, since thoracic temperatures must be elevated to 18-20°C before flight is possible. Dipterans raise body temperature to levels that permit flight by passive basking in the sun. Thus dipterans have at least two energetic advantages over hymenopterans at high elevations (Arroyo and others 1981; Warren and others, in press).

The mountain goat (table 1) represents a recent introduction to the higher elevation alpine habitats of the Wasatch Mountains. Herds are thriving on both Mt. Timpanogos to the south of the area shown in fig. 1 and along the divide between Little and Big Cottonwood Canyons. Wandering animals are occasionally seen along the divide between Little Cottonwood and American Fork drainages.

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Fourth in a series of proceedings of symposia on wildland shrubs, this publication brings together current knowledge of interactions between plants and herbivores. Topics addressed by the 31 papers include plant chemistry, palatability, nutrition and physiology, herbivore foraging behavior, and plant response to browsing.

KEYWORDS: wildland shrubs, photosensitization, cattle abortion, chemistry, palatability, nutrition, foraging behavior, browsing response, physiology

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