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Ranching motivations in 2 Colorado Counties

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Abstract

The objectives of this Colorado study were to assess primary reasons ranchers choose to stay or sell the ranch, compare the motivations for ranching between a traditional agriculturally based county and a rapidly developing county, and assess whether factors such as length of tenure, fiscal dependency on ranching, and dependency on public lands play roles in decisions to sell. Personal interviews were conducted with 37 ranchers. While land use conversion occurs for a wide variety of reasons, lack of heirs and detrimental public policy were important reasons given for selling ranches. Responses showed Routt County (a rapidly developing county) ranchers were more likely to sell due to land use conversion related issues than Moffat County ranchers (p = 0.056). Ranchers with a longer legacy on their land reported that profitability, having likely heirs, and continuing tradition enhanced their reasons to stay. Groups more "at risk" of selling were non-homesteading ranchers close to retirement, larger ranches, and ranchers dependent on ranching for income with declining profits. Large ranch owners experiencing land use conflicts with non-ranchers and ranchers modestly dependent on public forage experiencing changes in public policy regulations and land use conflicts also indicated a higher proclivity to sell. Noting how groups of ranchers are impacted by different changes can help refine community efforts related to land use conversion and create more thoughtful policy measures.

Key Words: rangeland policy, regulations, survey, public lands, urban development, land use conversion

Resumen

Los objetivos, bajo este estudio en el estado de Colorado, fueron: a) determinar las razones más importantes de los productores agrícolas para continuar con su unidad de producción o venderla, b) comparar las aspiraciones de producción entre una agricultura tradicional regional y una agricultura especializada, y c) determinar si factores como el tiempo de posesión, grávamen fiscal y el uso de terrenos comunales son decisivos para vender las unidades de producción. El método de estudio fue por entrevistas personales realizándose 37 con productores agrícolas. Las razones más importantes para la venta de la unidades de producción incluyen el cambio en el uso de la tierra, la falta de herederos y una política pobre sobre el uso de terrenos comunales. Los resultados mostraron que los productores especializados del Condado Routt fueron más propensos a la venta de las propiedades que los tradicionales del Condado Moffat (P=.056). Los productores agrícolas con muchos años en la explotación reportaron que las ganancias, la existencia de herederos, y la tradición incrementa las razones para continuar produciendo. Los grupos propensos para vender fueron productores próximos al retiro, productores grandes en la escala, y productores con ganancias descendentes. Además, fueron propensos de venta los propietarios grandes con conflictos con otro tipo de productores y con productores agrícolas modestos dependientes de los cambios en la regulación de terrenos comunales para producción de forraje, y por conflictos con el uso de terrenos comunales. El factor más influyente en el ámbito de los productores agrícolas es el impacto de cambios diversos que pueden ayudar a afinar los esfuerzos comunitarios relacionados con cambios de uso de la tierra y con la creación de políticas de desarrollo más eficientes.

Colorado farm and ranch land has declined by over 600,000 ha since 1987 with over 80,000 ha lost to development and other uses in 1996 alone (Colo. Dept. of Agr. 1998). Land use conversion from agriculture to development results not only in a loss of agricultural production, but also fragments and degrades wildlife habitat and reduces open space. The current political climate advocates the conservation of ranches to protect against fragmentation and support open space, agriculture, and ecological integrity (Liffman et al. 2000). By asking ranchers why they stay or leave, we discover the underlying causes of land use conversion to better inform policy makers.

Motivations to continue ranching

Past research has indicated that factors other than profit or economic incentives influence decisions that shape a ranch family's decisions to stay on the land. Researchers have found that family, tradition, way of life, rancher image, and place attachment all motivate ranchers to retain ownership (Smith and Martin 1972, Harper and Eastman 1980, Grigsby 1980, Bartlett et al. 1989, Gentner 1999, Liffman et al. 2000). Selling the ranch itself is a market transaction, but the land may represent a way of life, livelihood, and family legacy, making the decision to sell difficult.

Previous studies indicate that for some ranchers, financial management tends to be a primary factor shaping a decision to stay in ranching. Smith and Martin (1972) identify a group characterized by their conspicuous consumption and speculative attitudes. Such individuals buy ranches as an investment and plan to sell for a higher price. These investors enjoy the "rancher image" and lifestyle, often as absentee landowners, until land values rise and reach a threshold that triggers a decision to sell. One group of 4 defined by Bartlett et al. (1989) expressed a willingness to sell the ranch, but remained due to "difficulties in selling in current market conditions." This group rated land ethic and family life

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slightly lower than the other groups. For this group it appears that economic considerations weigh more heavily in the sell or stay question. Young and Shumway (1991) support these findings, suggesting that factors including dependency on ranch income, desire to increase net worth, the perception of cattle production as a business venture, and the ability to obtain off-ranch employment all increased the probability that ranchers would perceive themselves to be profit maximizers. For these kinds of ranchers, the business tends to be a determining factor in decisions over the fate of the ranch.

Motivations to sell a ranch

Land use conversion issues, specifically, the "impermanence syndrome" and loss of "critical mass", appear related to decisions to sell or continue in ranching (Heimlich and Anderson 1987, Huntsinger and Hopkinson 1996, Hart 1991, Berry and Plaut 1978). Urbanization can lead to an "impermanence syndrome" among ranchers. This results in declining investment in agriculture and reduction in intensity of management and practices because ranchers become convinced that their land will be sold for non-agricultural uses (Heimlich and Anderson 1987). Speculation leads to idling farmlands or a conversion to other types of agriculture that are less intensive in time and capital (Berry and Plaut 1978, Conklin and Lesher 1977). Hart (1991) found that as urbanization increased around a ranch, succeeding generations were more likely to sell.

Once a ranching community loses its "critical mass" of ranchers, ranching may become less economically viable (Huntsinger and Hopkinson 1996, Hart 1991, Heimlich and Anderson 1987, Berry and Plaut 1978). As the numbers of agriculturalists declines, their political and economic clout erodes and non-farm preferences for community gain political legitimacy in local governance. New ordinances are passed designed to regulate such things as noise of machinery and tractors on roads. Demand for requisite suburban infrastructures by new residents can increase the tax load for ranchers (Berry and Plaut 1978, Lisansky and Clark 1987). Fewer ranchers in an area makes it more difficult to pool labor and resources at times of heavy work (Huntsinger and Hopkinson 1996). Furthermore, commercial businesses that provide agricultural supplies and services are more likely to go out of business as their ranching clients disappear (Flora et al. 1992, Danbom 1995, Starrs 1998).

Hart (1991, p. 35), in perhaps an overstatement to make a point, stresses the impact of urbanization on agriculture: "Urban expansion always wins, because farmers are not able to pay urban costs for land. The basic question of land conversion is not whether, but when."

Hypotheses

In the course of this research, several assumptions concerning ranchers' reasons to either stay in or leave ranching were considered. This paper addresses 5 alternative hypotheses.

1. Raising a family and maintaining tradition are primary determinants for staying in ranching.
2. Due to greater development pressure, ranchers in an area undergoing rapid development will be more likely to sell than those in a more rural, agricultural area.
3. Respondents with a longer legacy on the land will be less likely to sell.
4. Financial issues will be more important to larger ranches and for those dependent on ranch income for their livelihood.
5. Federal public land and environmental policies will affect public land dependent ranchers more than ranchers with less public land.

Methods

Thirty-seven (37) personal interviews with public land ranchers in the Colorado counties of Routt and Moffat were conducted. Ranchers were randomly selected from a compiled list of all of the federal land grazing permittees of the 2 counties.

Study area

To evaluate the effects of urbanization we compare 2 counties, one experiencing rapid development, Routt County, and the other a traditional agricultural county, Moffat County. Adjacent counties in the northwestern corner of Colorado, these 2 counties were selected for study based upon their relative proximity and similar cultural history, while differing in their growth rates and level of development. Routt County comprises 60,000 ha and 49% of its land is either state or federally owned. Moffat has 1.2 million ha with 63% of that in public ownership (Frank 1997). In 1992, Routt County had 3.4% income dependence on agribusiness, and Moffat had 1.5% (CSU Dept. of Agr. and Res. Econ. 1995).

Recreationists flock to Routt County for outdoor pursuits including skiing at the popular Steamboat Springs Ski Resort. The tourism industry in Routt County supports 147 related establishments for lodging, amusement/recreation, and eating/drinking. Moffat County has only 37 such businesses. Population growth in Routt has been double that in Moffat. Routt County had a growth rate of 18.3% between 1990 and 1997, while Moffat County increased by 8.9% (Yampa Valley Partners 1999). The overall cost of living has also risen disproportionately for the 2 counties according to a cost of living survey in Colorado. This survey composed a numeric scale using 1 as the average for the state based on the costs for 59 goods. Routt County ranks highest in the "above average" category at 1.096, whereas Moffat falls into the "low" cost of living category at .870 (Garner and Eckert 1999). Property values in Routt County have leapt from $291.2 million in 1993 to $419.2 million in 1997. For the same years, Moffat County crept from $358.7 million to $367 million (Yampa Valley Partners 1999). These county differences allow us to compare the effects of growth between rapidly developing Routt County and traditional Moffat County.

Study Sample

A sampling frame of 242 Federal permittees in the 2 counties was derived by compiling the Bureau of Land Management (BLM) and United States Forest Service (USFS) permittee lists and condensing duplicate listings. The sample size of 26 was calculated using a variance of .15 taken from Redmond et al. (1992), a study relevant to the research presented here. The sample was stratified into 7 strata based on number of AUMs and type of livestock grazed on public land, increasing the sample size. Every effort was made to interview each of these ranchers, but replacements were selected for those that refused, were not actively running their ranch, or who lived too far outside the counties. Thirty-seven personal interviews were completed.

Rancher Survey

Drawing on questionnaires of Liffman et al. (2000), Gentner (1999), Smith and Martin (1972), and Bartlett et al. (1989), the authors constructed a survey exploring motivations for staying in ranching versus leaving ranching. The survey was pre-tested on ranchers in Larimer County, Colo.

The questionnaire consisted of 7 general conceptual questions with 9 follow up questions. The general questions covered the following categories of information: quality of life, dependency on ranching for income, motivating factors for continuing to ranch, factors influential in selling the ranch, motives for staying in the area, and public policy issues. Most questions were measured on a Likert scale with 1 indicating least important, 2 less important, 3 moderately important, 4 more important, and 5 most important. The authors chose to group the Likert scale responses into either more important (4 and 5 answers) and less important (1, 2, and 3) to simplify the comparisons. Follow up questions were asked if the rancher responded with a 4 or a 5 to any of the questions in the motivations to sell category.

The Federal Policy Impacts Section of the questionnaire provided the independent variables to test hypotheses 3 through 5, including the number of animal unit months (AUMs) and private land acres, the degree of public land dependency, and whether or not the rancher's family homesteaded in that county. Since 2 ranchers did not respond to the Federal Policy Impacts Section, only 35 survey results were used to test hypotheses 3 through 5.

For Hypothesis One, simple frequencies showed which factors ranchers chose as most important for staying or leaving ranching. Hypotheses 2 through 5 required the use of the Chi-square statistic using cross tabs. Due to difficulty in finding significant differences with the small sample size and the minimal consequences of making a type I error, we considered differences of $p < 0.10$ to be significant.

Defining Groups

To cross tab the groupings, continuous data was categorized for each hypothesis including homesteading history, county, dependence on ranching for income, size of ranch by private acreage, size of ranch by number of AUMs, and dependence on public lands. Ranches were re-categorized under each group (Table 1). Private land acreages and AUMs were divided along obvious splits in the data. Public land dependency was determined by dividing the number of public land AUMs by the total number of AUMs, multiplied by a hundred. Because public land dependency had an even spread, we split it into quartiles and defined these groups as negligible, modest, moderate and high public land dependency. Homesteading and dependency on ranching for income elicited yes/no responses in the survey and were categorized as such.

The sample included a number of ranchers that had public land in 1 of the counties, but they resided either in the other county or nearby across the Wyoming border. To refine the comparison, only Routt County residents were considered in the Routt County category. Any rancher not residing in Routt was placed in the Moffat County category (Table 1).

Results and Discussion

Hypothesis One: Motivations for staying in ranching

This research partly supported the first hypothesis. Family and tradition influences came out as important for over 50% of the sample. However, way of life outranked family and tradition as reasons to continue ranching. The data also reveal that attachment to the location of the ranch influences ranchers to stay in agriculture. Profit ranked lower as a motivational factor.

Ranchers report that they stay in ranching primarily because they enjoy the work and way of life (Table 2). Over 50% of the respondents rated family and traditional reasons as most important. Family and tradition categories include: "A ranch is a good place to raise your family", consistency with family tradition, culture and values, living closer to family, "ranching is part of our Western heritage and should be preserved", "ranch has been in the family for generations and you maintain it to carry on the family tradition", and to have a business to pass on to your children (Table 2).

In addition to asking about motivations to continue ranching, we asked why ranchers stayed where they are rather than selling the ranch to buy another one elsewhere. Responses to this were grouped in 11 categories. The top answers for both counties combined (with 36 responses) indicated that tradition (50%) and attachment to the ranch setting (39%) are both important reasons to continue ranching in the area. The response "tradition" means the rancher stays here because the ranch has been in the family for 1 or more generations. "Place attachment", as defined by the survey responses, encompasses love for life style and for the natural beauty of the area as well as simply not wanting to leave. Ranchers develop a connection to their ranch, the landscape, associated wildlife, and the beauty of the area. The Likert Scale responses support this enthusiasm for place attachment; 87% of the ranchers rated living near natural beauty as more important.

Reasons for selling the ranch

The corollary to the first hypothesis, that deteriorating the quality of raising a family or altering traditions would motivate ranchers to sell, is reflected in the responses (Table 2). Ranchers say that having no one to take over the ranch would be the most compelling reason to sell the ranch (57%). Having no one to take over the ranch incorporates both loss of family and tradition, since with no one to inherit the ranch by definition indicates a severing with family tradition. Of the 21 respondents that marked this factor as more/most important, 13 (62%) responded that it is

Table 1. Ranch characteristics, Routt and Moffat Counties, Colo., 1998.

Characteristics[1]	with characteristic
	(%)
Dependent on ranching for livelihood	57
Homesteaded	58
Rate quality of life great-excellent	87
Ranch in Routt County	24
Ranch in Moffat County	76
Small ranch: owns up to 1000 acres private land	37
Medium ranch: owns 1280–8000 acres private land	43
Large ranch: own 15,000–80,000 acres private land	20
Small ranch: 90–707 total AUMs[2]/year	40
Medium ranch: 1068–8264 total AUMs/year	46
Large ranch: 14,604–39,412 total AUMs/year	14
Negligible public land dependency: 1–11%	23
Modest public land dependency: 14–34%	26
Moderate public land dependency: 35–62%	26
High public land dependency: 69–96%	26

[1] Not all ranchers answered each category; thus, n varied from 35–37.

[2] Total AUMs includes federal, private, and privately leased forage, but does not include hay fed.

Table 2. More important reasons to keep ranching or to sell responses listed in decreasing proportions, all respondents, 1999.

Survey Questions (n = 37)	Responded 4/5	n
You continue to ranch because:	(%)	
You enjoy animal husbandry	97	37
You enjoy the ranching way of life	95	37
You like ranch work	89	34
A ranch is a good place to raise your family	87	37
Allows you to live near natural beauty	87	36
Ranching allows you independence	87	37
Owning land and a ranch is consistent with your family's traditions, culture and values	81	37
Living on a ranch allows you to live closer to your family	81	37
Ranching is part of our Western heritage and should be preserved	76	37
The ranch has been in the family for generations and you maintain it to carry on the family tradition.	57	37
You continue ranching so you will have a business to pass on to your children	50	36
It would be difficult to obtain a job outside the ranch	27	37
You own land and a ranch primarily for environmental purposes	25	36
Living on a ranch allows you to live closer to your friends	22	36
Profit	19	37
Conservation easements or land trusts made the property taxes and my debt more manageable.	18	28
Other	32	12
You would sell the ranch because:		
You have no one to pass the ranch on to	57	37
Public policy regulations.	49	37
You don't like the way the community is changing.	32	37
Ranching is no longer profitable, you start losing money	32	37
Increase in property value.	30	37
Land use conflicts with non ranchers	30	36
Nearby ranches being converted to other uses.	22	37
Retirement	11	36
Prefer to improve income through selling the ranch.	11	37
Perception that society no longer appreciates ranching	5	37
Prefer to improve income through an off-ranch job	0	36
Other	30	11
Why do you choose to stay here rather than sell the ranch and buy another one elsewhere?		
Ranch has been in the family for one or more generations	49	37
Place attachment	38	
Moving does not solve problems in ranching	19	37
Good place to ranch	19	37

[1] For this open-ended question, percentages refer to response frequencies for each category.

more/most likely that a family member will take over for them in the future. Seven (33%) thought it would be moderate to very unlikely that a family member would take over and 1 (5%) did not know if it would be taken over by a family member. Thus, roughly 19% (7/37) of the sample will likely sell the ranch because they lack viable heirs.

Of particular significance to policy makers, public policy regulations were cited as the second most important reason to sell (18 respondents or 49% of the sample marked more/most important). This question clearly implied federal not local policies. The follow-up question asked these 18 respondents which policies most concerned them. Answers were categorized into 10 groups. The most frequent response was cuts in allowed grazing use on public lands (35%). Some of the fear of cuts is probably rooted in the BLM environmental impact reports being done on all allotments at the time of the interviews in summer 1999. Thirty percent of the 18 respondents indicated concern about government control over land use, usually range improvements, on both public and private lands. Twenty percent cited multiple-use as a threat. These respondents feel that recreationists and hunters would restrict their own ability to use the public lands by creating problems (trespass, vandalism, etc) and demanding more of the public land exclusively for themselves. Though not evoked in the open-ended follow-up question, the Endangered Species Act (ESA) also seems to be a concern to ranchers. Each respondent ranked a set of 5 issues according to which would most likely affect his or her ranch in the next 5 years. The ESA outranked the other issues, followed by elk management, water quality, multiple use, and water rights. Rancher comments revealed a negative undercurrent towards the ESA. Ironically these Federal policies may serve to accelerate ranch sales, creating an even greater threat to policy goals aimed at slowing land use conversion and preserving wildlife habitat.

Eleven people provided other reasons for why they would sell the ranch. Seven indicated that a loss of health would cause them to sell the ranch. Other answers were aging, county regulations, and loss of family.

Hypothesis 2: Routt County versus Moffat County

Ranchers in Routt County were more likely to sell their ranches due to land con-

Table 3. More important reasons for ranching or selling, Moffat versus Routt Counties, 1999.

Survey questions	County		p-value[1]
	Moffat (n=28)	Routt (n=9)	
Independent variables [2]:	(%)	(%)	
Did your family homestead in the area?	44	63	.329
Do you depend on ranching for your income?	64	33	.103
You continue to ranch because:			
Owning land and a ranch is consistent with your family's traditions, culture and values	75	100	.096*
Living on a ranch allows you to live closer to your family	75	100	.096*
It would be difficult to obtain a job outside the ranch	36	0	.036**
Profit	25	0	.096*
Conservation easements or land trusts made the property taxes and my debt more manageable	10	43	.046**
You would sell the ranch because:			
If you had no one to pass the ranch on to	54	67	.49
Public policy regulations	50	44	.772
You don't like the way the community is changing	29	44	.376
Ranching is no longer profitable, you start losing money	39	11	.116
Land use conflicts with non ranchers	36	11	.16
Increase in property value	32	22	.571
Nearby ranches being converted to other uses	14	44	.056*
Why do you choose to stay here rather than sell the ranch and buy another one elsewhere?			
Been in the family for one or more generations	54	33	.145
Place attachment	36	44	.783
Moving does not solve problems in ranching	11	44	.029**
Good place to ranch	22	11	.466

*, ** Significant at the 0.10 and 0.05 levels respectively.

[1] p-value results for x^2 test.

[2] For the independent variable questions, percentages refer to positive responses in each category.

version issues than in Moffat County (Table 3). Routt County residents ranked "Nearby ranches being converted to other uses" the second most common reason to sell. This marked a significant difference with Moffat, which marked this factor as seventh. Land use conversion influencing ranchers to sell supports the large body of literature indicating that urbanization causes ranchers to sell because of a lessening expectation of the persistence of agriculture as a viable use in an area, and the loss of "critical mass" (Huntsinger and Hopkinson 1996, Hart 1991, Heimlich and Anderson 1987, Berry and Plaut 1978, Conklin and Lesher 1977).

Also worthy of note were the reactions to easements and land trusts in the 2 counties. Although rated low in both counties, significantly more people rated these as important reasons to continue ranching in Routt County than in Moffat County (Table 3). Generally, only the people holding land trusts themselves considered easements important. This result is perhaps not surprising considering land trusts are more common in Routt County. Locally based conservation policies appear to have a positive influence on ranchers' willingness to keep their land from being developed.

The question "Why do you choose to stay here rather than sell the ranch and buy another one elsewhere?" elicited significantly different responses between the 2 counties (Table 4). Significantly more ranchers in Routt than in Moffat County feel that ranch difficulties may exist on any ranch, therefore moving will not resolve the problem. This finding may reveal that Routt County ranchers perceive their profession as more inherently plagued with difficulty than do their more traditional Moffat County neighbors.

Comparing the reasons ranchers continue may reveal interesting sets of characteristics for each county. Routt County ranchers focus more on the family, and less on profit (Table 3). Moffat County ranchers seem to care more about profit and are less concerned about family as a reason to ranch.

Hypothesis 3: Legacy on the Land

We hypothesized that respondents with a longer legacy on the land would be less likely to sell. Respondents with a longer legacy on the land were defined as homesteaders; their family had originally homesteaded in the area. To support this hypothesis, homesteaders would have marked fewer sell factors as more/most important and more reasons to continue as more/most important. In general this was not strongly supported by the data. However, homesteaders considered themselves less likely to sell the ranch at retirement (Table 4). Relative newcomers to ranching may view the ranch as more of a profession from which to retire rather than a way of life that continues into retirement.

Homesteaders place more importance on economics, as measured by profit and dif-

Table 4. More important reasons for homesteaders to sell or continue ranching, Routt and Moffat Counties, 1999.

Survey questions	Homesteaders (n=21)	Non-homesteaders (n=15)	p-value[1]
You continue to ranch because:	(%)	(%)	
You continue ranching so you will have a business to pass on to your children	65	33	.064*
Living on a ranch allows you to live closer to your family	67	100	.013**
It would be difficult to obtain a job outside the ranch	38	7	.032**
Profit	29	0	.023**
The ranch has been in the family for generations and you maintain it to carry on the family tradition	81	20	.000***
You would sell the ranch because:			
Retirement	0	27	.014**
Independent variable [2]			
Do you depend on ranching for your income?	62	47	.364**

*, **, *** Significant at the 0.10, 0.05 and 0.01 levels respectively.

[1] p-value results for x^2 test..

[2] For the independent variable, percentages refer to positive responses in each category.

Table 5. Significant correlations between independent variables using Pearson's r-values.

	Independent variables			
	County	Dependency on ranching for income	Homesteading	Size (number of AUMs)
Public land dependency			–.325*[3]	
Size of ranch (by number of AUMs)	.349**[2]	–.430***[3]		
Size of ranch (by number of acres of private land)	.485***[2]	–.504***[3]		.700***[4]

*, **, *** Significant at the 0.10, 0.05 and 0.01 levels respectively.

[1] Homesteaders have a higher dependency on public land than non-homesteaders.

[2] Rancher in Routt County had fewer AUMs and owned less private land than ranchers in Moffat County.

[3] Larger ranches, as defined both by number of AUMs and number of private acres, are more dependent on ranching for their livelihood.

[4] Ranches with large number of AUMs also held higher acreages of private land.

ficulty in finding a job off the ranch, as reasons to stay than do the more recent non-homesteaders (Table 4). Perhaps homesteaders ingrained in their successors the paradigm of the ranch as a business that needs to support the family needs. Members of older ranching families may have less outside work experience or professional training which keeps them tied to the ranch. Newcomers to the trade may have more job options and financial resources, allowing them to be somewhat more economically sacrificial in their attitudes towards ranching. They know they are giving up a higher standard of living for ranching and perhaps are more resigned to being "satisficers" (Smith and Martin 1972).

Not surprisingly, homesteaders also find passing the ranch on to children and maintaining tradition as reasons to stay (Table 4). Taken together, given a profit and willing heirs, homesteaders may feel more strongly about staying in ranching than their counterparts.

Hypothesis 4: Financial Concerns

The results tend to support the assumption that owners of larger ranches and ranchers more dependent on ranching for their income are more concerned with profit. Ranches with more AUMs, more private land, and ranchers who declared themselves dependent on ranching for their income (3 highly correlated variables, Table 5) stated that they would be much more likely to sell if the ranch started losing money than their counterparts (Table 6). This same set of ranchers agrees that difficulty in obtaining a job off of the ranch contributes to their reasons to continue ranching. Ranchers dependent on ranching also cited profit as a significantly more important reason to continue ranching than non-dependent ranchers.

Another finding, with strong implications for land use conversion policy, was that as size of ranch increases, land use conflicts with non-ranchers become a greater motivation to sell (Table 6). As land around large ranches is converted to non-ranching uses, resulting conflicts may influence larger ranch owners to sell.

Hypothesis 5: Public Lands Ranchers

Ranchers more highly dependent on public lands for forage did not show significantly more likelihood to sell due to public policy than those with lower dependency. It turns out, however, that it is the modestly (14–34% of their total forage is from public land) dependent ranchers who are likely to sell due to public policy regulations and land use conflicts (Table 7). This occurrence may be explained by seasonal dependence. Ranchers in the modestly dependent category have enough dependency to be affected by changes but may have fewer options in the face of such changes. These ranchers may depend on public forage for a specific period of time when no other forage is available whereas larger landholders may have more flexibility. Another possibility is that ranchers in the modestly dependent category are self-selected (i.e., their fear of being harmed by policy changes has already led them to reduce their public land).

It stands to reason that public land dependent ranchers, many of whom are homesteaders, would place more value on tradition as a reason to continue on the ranch. The data shows a correlation between homesteaders and increased dependency on public lands (Table 5). Further, public land dependent ranchers

Table 6. More important reasons to sell reported by ranches of different sizes and income dependencies, Routt and Moffat Counties, 1999.

Survey questions	AUM[1]				Dependency[3]			Acreage[4]			
	Small	Medium	Large	p[2]	Low	High	p	Small	Medium	Large	p
<u>You continue to ranch because:</u>	(%)	(%)	(%)		(%)	(%)		(%)	(%)	(%)	
Ranching is no longer profitable, you start losing money	14	25	100	.001***	13	48	.024**	15	20	86	.002***
Perception that society no longer appreciates ranching	0	0	40	.002***	—[5]	—	—	0	0	29	.014**
Land use conflicts with non-ranchers	0	44	60	.007***	—	—	—	15	20	71	.019**
Public policy regulations	21	69	60	.030**	—	—	—	—	—	—	—
<u>You continue to ranch because:</u>											
It would be difficult to obtain a job outside the ranch	21	19	80	.023**	6	43	.013**	8	33	57	.057*
You enjoy animal husbandry	100	100	80	.062*	—	—	—	—	—	—	—
Allows you to live near natural beauty	—	—	—	—	—	—	—	100	73	100	.049**
Profit	—	—	—	—	19	29	.086*	—	—	—	—

*' **' *** Significant at the 0.10, 0.05 and 0.01 levels respectively .

[1] Size of ranch categorized by the total number of AUMs, not including hay feed.

[2] p-value of given category for x^2 test.

[3] Level of dependency on ranch income for their livelihood as defined by respondents.

[4] Size of ranch categorized by the number of owned private acres on the ranch.

[5] Non-significant values not included in this table.

Table 7. More important reasons to stay or sell the ranch at different levels of dependence on public forage, Routt and Moffat Counties, 1999.

	Levels of public land dependency				
Survey questions	Negligible	Modest	Moderate	High	p-value
You continue to ranch because:					
Owning land and a ranch is consistent with your family's traditions, culture and values	50	89	100	78	.065*
The ranch has been in the family for generations and you maintain it to carry on the family tradition	0	67	89	67	.002**
Ranching is part of our Western heritage and should be preserved	50	67	100	89	.064*
You would sell the ranch because:					
Land use conflicts with non-ranchers	0	56	22	33	.083*
Public policy regulations	25	89	44	33	.036**

*' **'Significant at the 0.10, and 0.05 levels respectively.

[1]p-value results for x^2 test..

rate tradition as an important factor for staying on the ranch (Table 7).

Conclusions

Ranchers in northwestern Colorado emphasize career fulfillment, tradition, place attachment and family as reasons they intend to stay in agriculture. Profit and market factors rank relatively low as reasons to stay. Respondents list inheritance issues as the most important reason to sell, followed by public land policy regulations, economic issues, and community change. Age and loss of health may also be important reasons to sell.

Generally, this study did not find that rapid development alone would cause ranchers to sell, although land use conversion in developing counties might increase ranchers' likelihood of selling. Land use conversion can lead to conflicts with neighbors, a factor that large landowners indicated would influence them to sell. Homesteaders are less likely to sell the ranch at retirement, and profit and heirs to inherit the ranch tends to bolster their conviction to stay. Financial considerations are influential in decisions to continue in agriculture for respondents with larger ranches, dependence on ranching for an income, and with a higher dependence on public lands. Modestly dependent rather than highly dependent public land ranchers indicated an inclination to sell their ranch due to public policy regulations and conflict with non-ranchers.

This research presents a potential irony for policy makers who advocate strong environmental and other land-use programs on both public and private land. Given the finding that respondents rank changes in public policy as the second most important reason for selling a ranch, federal programs may inadvertently contribute to land use conversion by accelerating the rate of ranch sales.

The federal policies specified by ranchers as most pressing were cuts in grazing, government regulations concerning land use management, multiple use conflicts, and the Endangered Species Act (ESA). A recent study done in Routt County (American Farmland Trust 2000) described more subtle impacts that federal policies are having on ranchers' ability to continue ranching in the face of increasing land use conversion. This American Farmland Trust (2000) study found that tax incentives for buying a second home, allowing 35-acre subdivided parcels to continue to be taxed at agricultural land rates even given their weak ties to agriculture, and zoning laws that permit subdividing land into 35-acre or greater parcels without a review process hastens land use conversion from agriculture into residential properties. Federal and local policies supporting conservation easements help sustain commercial ranching but could be strengthened. The American Farmland Trust study (2000) emphasizes that policies designed to protect public lands increase development pressure on private ranchlands by luring more recreationists to the area, while also limiting the potential supply of land for development. Moreover, cutting grazing rights or substantially increasing grazing fees "will almost certainly mean additional pressure to subdivide and convert working ranches into recreational properties" (American Farmland Trust 2000, p. 14). The findings of this study in combination with the results found here should alert policy makers to the potential vulnerability of ranchers to an array of federal policies, both overt and indirect.

Decisions ranchers make about selling their ranch directly affect the use of their land and can contribute to land use conversion into subdivisions or other developments. Conversely, if ranchers do not sell their land, land use conversion is slowed. Diminished quality of ranch life, public policy regulations, the inability to pass the ranch on to future generations, land use conversion and its associated conflicts, and, for some groups, loss of profitability, may induce ranchers to sell.

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Economic analysis of using sheep to control leafy spurge

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Abstract

Leafy spurge (*Euphorbia esula* L.), a widely established exotic, noxious, perennial weed, is a major threat to rangeland and wildland in the Upper Great Plains. A deterministic, bioeconomic model, incorporating relationships between sheep grazing and leafy spurge control, grass recovery, and forage consumption by cattle, and expected costs and returns from sheep enterprises was developed to evaluate the economic viability of using sheep to control leafy spurge. Various scenarios were developed depicting likely situations facing cattle ranches adding a sheep enterprise for leafy spurge control. Two levels of flock profitability, one based on a level of proficiency achieved by established sheep ranches and one substantially lower than typically achieved in the sheep industry, were combined with debt and no-debt to represent best- and worst-case scenarios, respectively. In the best-case situations, using sheep to control leafy spurge was economical in all of the scenarios examined. In the worst-case situations, the economics of using sheep to control leafy spurge were mixed across the scenarios examined. Leafy spurge control with poor flock proficiency, high fence expense, and unproductive rangeland generally was not economical. Situations with low fencing costs, moderately productive rangeland, and poor flock proficiency resulted in less economic loss than no treatment. Actual returns from leafy spurge control for most ranchers will likely fall between the extremes examined.

Key Words: *Euphorbia esula* L., grazing, economics

Resumen

“Leafy spruge” (*Euphorbia esula* L.) Es una maleza exótica, perenne y nociva que esta ampliamente establecida y es una amenaza para los pastizales y de la parte superior de las Grandes Planicies. Se desarrollo un modelo determinístico bioeconómico incorporando las relaciones entre el apacentamiento de ovinos y el control de “Leafy spruge”, la recuperación de zacates, el consumo de forraje por bovinos y los costos y retornos esperados de la empresa de ovinos. El modelo se desarrollo para evaluar la viabilidad económica de utilizar ovinos para controlar “Leafy spruge”. Se desarrollaron varios escenarios visualizando escenarios posibles que enfrentan los ranchos de ganado bovino y agregando una empresa ovina para el control de “Leafy spruge”. Dos niveles de rentabilidad del rebaño, uno basado en el nivel de eficiencia alcanzado por ranchos borregueros establecidos y uno substancialmente menor que la eficiencia típicamente lograda por la industria de ovinos, se combinaron con deuda y no deuda para representar el mejor y peor de los escenarios respectivamente. En todos los escenarios examinados, en las situaciones que representaron el mejor de los casos, el utilizar ovinos para controlar “Leafy spruge” fue económicamente viable. En las situaciones del peor de los casos la economía de utilizar ovinos para el control de “Leafy spruge”se mezclo a través de los escenarios examinados. El control de “Leafy spruge” con una pobre eficiencia del rebaño, altos gastos de cercos y un pastizal improductivo generalmente no fue económico. Situaciones con bajos costos de cercado, pastizales moderadamente productivos y baja eficiencia del rebaño resultaron en menos perdidas económicas que el no tratamiento. Los retornos actuales del control de “Leafy spruge”en la mayoría de los ranchos probablemente caería entre los extremos examinados.

Leafy spurge (*Euphorbia esula* L.), first introduced in North America in the 19th century, was found in North Dakota in 1909, and was considered a threat to rangeland in the Upper Great Plains as early as 1933 (Hanson and Rudd 1933). The weed currently infests large amounts of untilled land in the Plains and Mountain states and creates serious economic losses for land owners and ranchers (Leitch et al. 1996). The nature of leafy spurge and the detrimental effects of the weed on untilled land have been documented (Watson 1985, Lajeunesse et al. 1995, USDA 1995).

Current control technologies are ineffective in eradicating established infestations on untillable land (Lym 1997). As a result, leafy spurge control must be approached as a long-term management problem since (1) the weed cannot be eradicated economically with current technology,[1] (2) uncontrolled infestations have detrimental long-term consequences for grazing land, and (3) time lags often exist between treatments and returns. Although several control methods are available to land managers, each control approach has limitations in its applicability and effectiveness in treating leafy spurge infestations. Grazing with sheep and goats, while known to be effective in controlling leafy spurge since the 1930s (Helgeson and Thompson 1939, Helgeson

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[1] Leafy spurge has been eradicated using tillage activities in combination with fertilization in cropland (Lym and Messersmith 1993). These techniques are not readily feasible in most grazing land situations.

and Longwell 1942), has lacked widespread adoption (Sedivec et al. 1995, Sell et al. 1999a). The apparent inability of biological agents to establish on many leafy spurge infestation sites (Bangsund et al. 1999), the economic and environmental restrictions and constraints associated with herbicides, and the ineffectiveness of cultural controls (e.g., mowing, burning) have led to a renewed interest by land owners in evaluating sheep grazing as a leafy spurge control method.

Sheep will graze leafy spurge, and if used properly, reduce infestation density and prevent infestation spread over time (Helgeson and Longwell 1942, Johnston and Peake 1960, Bowes and Thomas 1978, Lacey et al. 1985, Sedivec et al. 1995). Since sheep will not eradicate leafy spurge and controlling leafy spurge with sheep requires grazing over several years, using sheep as a leafy spurge control must be considered a long-term management strategy. Preliminary research on the economic feasibility of using sheep to control leafy spurge has not evaluated the long-term benefits or costs of grazing control strategies (Sedivec et al. 1995, Williams et al. 1996). Since leafy spurge control must be approached as a long-term management problem, information on the economic feasibility of leafy spurge control methods must also be based on long-term treatment benefits and costs (Bangsund et al. 1996).

A goal of this study was to provide economic information for assessing long-term grazing control strategies for leafy spurge. Sell et al. (1999b) identified economic information on leafy spurge controls as one of the most desired types of weed control information sought by ranchers, local decision makers, and public land managers in the Upper Great Plains.

Methods

A deterministic, simulation model was developed to evaluate the economics of using sheep to control leafy spurge and determine which variables influence the economic feasibility of various grazing strategies (Fig. 1). The economic feasibility of using sheep to control leafy spurge was evaluated using selected scenarios which reflect likely situations facing cattle ranches adding a sheep enterprise for leafy spurge control. The annual difference between treatment expenses, and the value of grazing outputs recovered and retained through treatment were discounted over 10 years to provide a long-term perspective for various control scenarios. General model design was adapted from Bangsund et al. (1996).

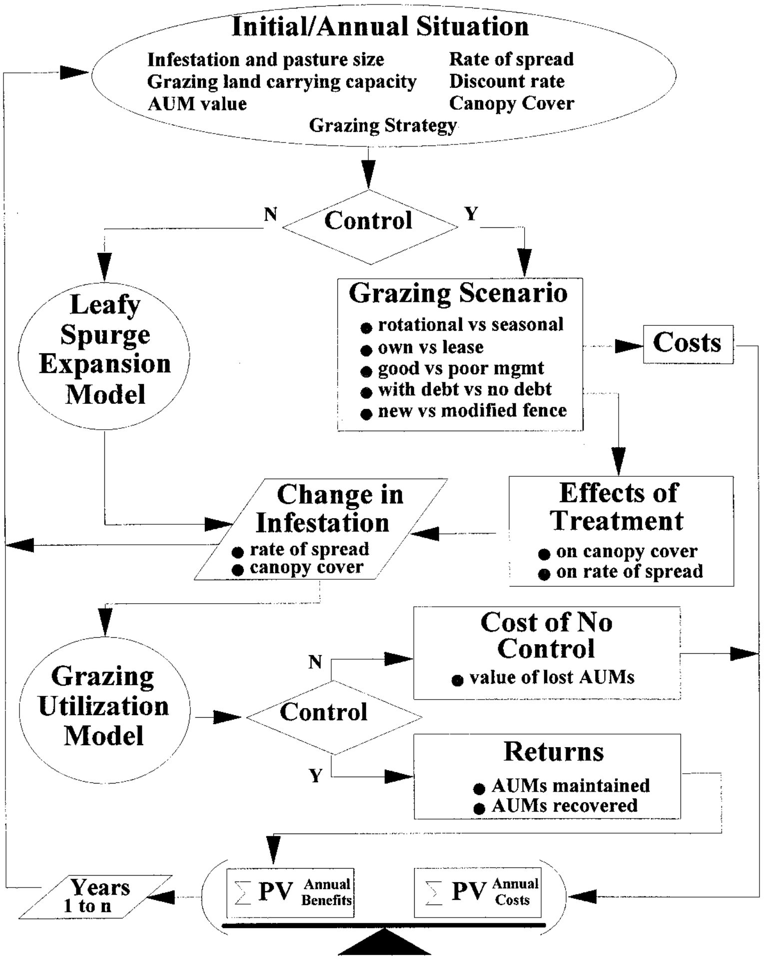


Fig. 1. Economic evaluation model of the control of leafy spurge using sheep grazing.

Model Development

Documented effects of long-term sheep grazing on infestation canopy cover, rate of spread, grass rejuvenation (i.e., increase in grass production within the infestation resulting from grazing controls), and cattle grazing recovery rates (i.e., amount of available grass cattle will consume upon reduction in leafy spurge canopy cover) were not available. The relationships used in this study were developed from a combination of short-term data from unpublished grazing trials and input from range and weed scientists. Sufficient data from grazing trials were not available to develop control relationships over a 10-year period. To conduct a long-term economic evaluation of sheep grazing, it was necessary to largely rely on the assumptions and "best estimates" of range and weed scientists. Until these relationships are refined through additional grazing trials, much of the economic analysis provided by this research remains sensitive to those key assumptions and relationships.

The model included the relationship between leafy spurge control using sheep and forage recovery by cattle, sheep enterprise budgets, leafy spurge growth (patch expansion) component, and an economic analysis component. Leafy spurge expansion was based on a model adapted from Bangsund et al. (1993). Expected control was modeled as a function of time (i.e., years grazed), assuming the same flock is used to graze leafy spurge annually, proper stocking rates are maintained, and grazing controls are properly implemented (Fig. 2) (personal communication, Lym, Kirby, Sedivec 1999). Control was defined as a percentage of the previous year's canopy cover {e.g., canopy cover(year 2)-[canopy cover(year 2) x control(year 2)] = canopy cover(year 3)}.

The rate of infestation spread under sheep grazing was modeled as a function of the number of years of control. Since the model can accommodate various rates of expansion, reduction in the rate of

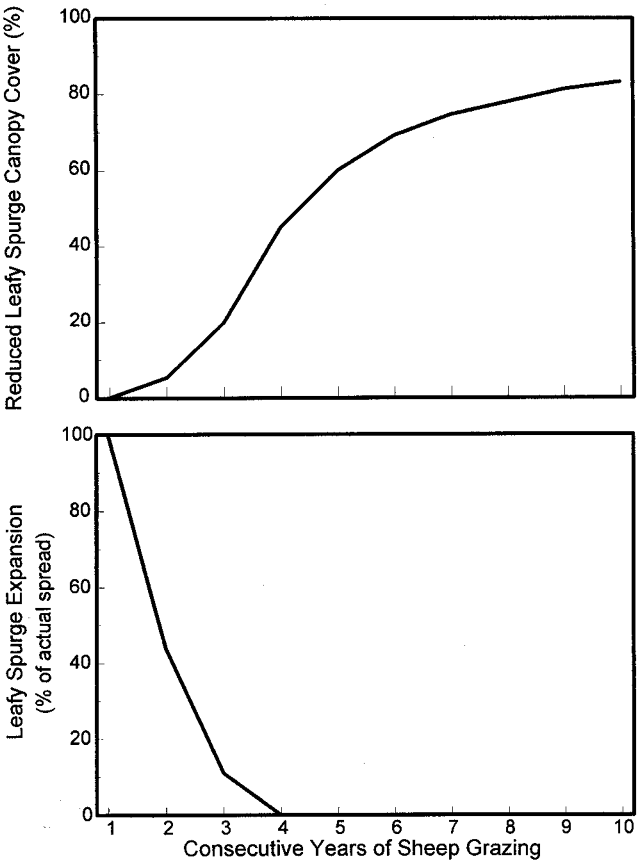


Fig. 2. Projected rate of leafy spurge expansion and leafy spurge canopy cover reduction with seasonal sheep grazing (personal communication, Lym, Kirby, and Sedivec 1999).

spread was estimated as a percentage of actual spread (Fig. 2). Infestation spread in the analysis was 0.6 m year^{-1}.

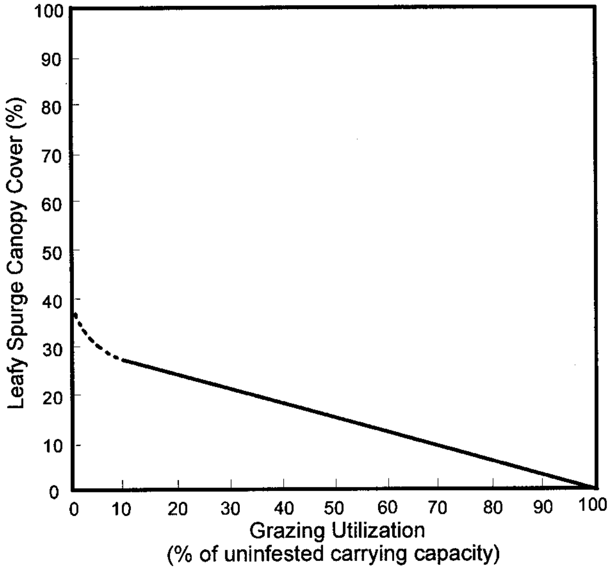
The relationship between lost cattle grazing capacity and infestation canopy cover was estimated from consultation with range scientists and was based on a linear function of canopy cover (Fig. 3). Grazing losses for cattle in leafy spurge-infested pastures stem from avoiding forage within infestations and from decreased herbage production within dense infestations (Lym and Messersmith 1985, Lym and Kirby 1987, Kronberg et al. 1993). Once a leafy spurge infestation represents about one-third of the canopy cover (top growth) within the patch, cattle grazing within the infestation has been eliminated. The model assumes that a 30% canopy cover would roughly translate to about 80 to 130 stems m^{-2}.

The approach for estimating the amount of forage consumed by cattle as a result of leafy spurge treatment was based on the amount of forage available within leafy spurge infestations (as a percentage of uninfested carrying capacity) and the amount of available carrying capacity that cattle would utilize. The model assumes that as leafy spurge infestations increase in canopy cover, grass production within those infestations decreases (Fig. 4). The relationship between leafy spurge canopy cover and grass production was based on the ability of leafy spurge to out compete native vegetation and create near monocultures (Watson 1985, Messersmith et al. 1985).

Because leafy spurge control was based on the number of consecutive years of sheep grazing, the rate of forage consumed by cattle within the infestation was also modeled as a function of the number of years of sheep grazing (Fig. 5). Since sheep will not eradicate leafy spurge, forage consumption (as a percent of carrying capacity) by cattle within leafy spurge infestations was assumed to remain below that of uninfested rangeland. Some minor avoidance to grazing within the infestation may exist and grass production within the infestation would likely remain below that of uninfested rangeland, due to competition by leafy spurge roots. Grass production within the infestation was modeled to increase over time as infestation canopy cover was reduced; however, constraints on the increase in grass production were incorporated to prevent forage production from equaling the productivity of uninfested rangeland. The model assumes that cattle are properly stocked for the carrying capacity of the pasture.

Sheep Enterprises

Several possible sheep enterprise scenarios were modeled after typical operations in western North Dakota (Nudell et al. 1998). Breeding stock was commercial Western White-faced ewes and black-faced rams. Ewes were assumed to lamb



Note: Dashed line indicates uncertainty in the relationship.

Fig. 3. Assumed reduction in cattle grazing within leafy spurge infestations (personal communication, Lym, Kirby, and Sedivec 1999).

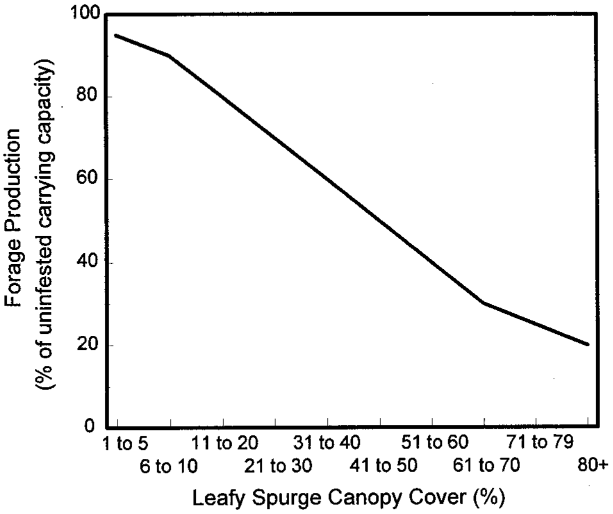


Fig. 4. Postulated relationship between grass production and leafy spurge infestation canopy cover (personal communication, Lym, Kirby, and Sedivec 1999).

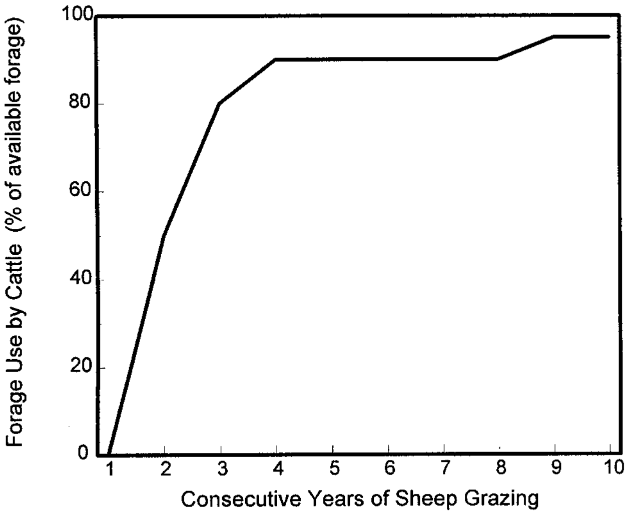


Fig. 5. Assumed carrying capacity utilization by cattle within leafy spurge infestations controlled with seasonal sheep grazing (personal communication, Lym, Kirby, and Sedivec 1999).

in February, with spring lambs fed during the summer and marketed in the fall as slaughter lambs. Replacements were raised. Only ewes and rams were used for leafy spurge control. Sheep budgets were prepared using an enterprise analysis program for sheep producers (Hughes et al. 1997).

Variations in the sheep enterprises were limited to flock proficiency (e.g., lambing rate, weaning weight, death loss), size, and debt. Because flock proficiency will likely vary depending upon the management ability, experience, animal husbandry, and willingness and ability of ranchers and producers to devote resources to flock management, 2 levels of flock proficiency were considered. The addition of a sheep enterprise for leafy spurge control was assumed to not affect the management of the existing cattle enterprise. One scenario was based on flock proficiency equal to that of established North Dakota sheep producers, whereas the other scenario was based on flock proficiency substantially less than typically achieved by established sheep producers (Table 1) (Nudell et al. 1998, N.D. Farm and Ranch Business Management 1999).

Sheep enterprises were further categorized by size and debt. Small flocks had 60 ewes and large flocks had 200 ewes. Half of the sheep enterprises had no debt, meaning that breeding stock, facilities, and equipment were either already available or purchased without financing. The enterprises with debt had 50% of the equipment and facility requirements financed for 5 years and 50% of breeding stock purchases financed for 3 years. Annual interest rate was 10%. Thus, budgets for 8 combinations of flock proficiency, size, and debt were compiled.

The number of sheep needed for leafy spurge control generally decreases after the first 3 years and again after 7 years of a seasonal grazing control program (Sedivec et al. 1995). Stocking rate reductions for sheep were estimated as a percentage of the initial stocking rate. Budgets for each production scenario were estimated annually over a 10-year period to accommodate changing flock size and corresponding changes in debt (Table 2). Production coefficients, selling prices, and variable expenses per ewe were not adjusted over the 10-year period.

Fencing expenses included modifying an existing fence or constructing new fence. Material costs were based on 1999 retail prices in western North Dakota. Modified fencing was based on adding 2 barb wires to an existing 3- or 4-wire fence. New fence was based on 6 barb wires, including requirements for line and corner posts. Pastures were assumed to be relatively flat and square. Five percent of total fencing expense was charged to the enterprises annually.

Several key assumptions were made in the preparation of the sheep budgets. Economic charges (depreciation) were not included for machinery and equipment that generally overlaps with cattle production (e.g., stock trailers, loader tractor, pickup). All pastures were assumed to have water present in sufficient quantities and available to sheep. Water maintenance and pasture expenses were not included. Selling prices for lambs, cull ewes, and

Table 1. Sheep enterprise coefficients and characteristics.

	Level of Flock Proficiency	
Characteristic/Coefficients	Good	Poor
Selling characteristics		
Market lamb price ($ kg^{-1})	1.65	1.65
Cull ewe price ($ kg^{-1})	0.77	0.77
Cull ram price ($ hd^{-1})	50.0	50.0
Wool price ($ kg^{-1})	1.10	1.10
Market lamb weight (kg hd^{-1})	54.4	47.6
Lamb weaning weight (kg hd^{-1})	22.7	20.4
Cull ewe weight (kg hd^{-1})	68.0	68.0
Wool production (kg ewe-1 year^{-1})	4.5	4.5
Flock Proficiency		
Conception rate (%)	100	100
Lambing rate (%)	150	100
Lamb death loss (%)	10	12
Ewe death loss (%)	5	5.5
Replacement rate (%)	20	20
Ewes per ram	33	33

Table 2. Annual net revenues to unpaid labor, management, and equity per ewe for various sheep enterprise scenarios over a 10-year period, western North Dakota.

	With Debt				No Debt			
	Small[1] Fencing[2]		Large[1] Fencing		Small Fencing		Large Fencing	
Years	New	Modify	New	Modify	New	Modify	New	Modify
	($)							
	Good Proficiency							
1 & 2	23.55	28.85	39.94	41.00	30.57	33.80	44.41	45.06
3	15.48	20.78	31.57	32.63	22.49	25.72	36.05	36.70
4 & 5	19.36	28.19	30.28	32.05	24.94	30.33	31.66	32.74
6	24.94	30.33	31.66	32.74	24.94	30.33	31.66	32.74
7	19.53	24.92	26.66	27.74	19.53	24.92	26.66	27.74
8–10	14.56	22.65	29.67	31.29	14.56	22.65	29.67	31.29
	Poor Proficiency							
1 & 2	–12.12	–6.82	–4.56	–3.50	–5.22	–1.99	–0.18	0.47
3	–22.99	–17.69	–15.71	–14.65	–16.08	–12.85	–11.34	–10.69
4 & 5	–14.69	–5.86	–2.96	–1.19	–9.11	–3.72	–1.58	–0.50
6	–9.11	–3.72	–1.58	–0.50	–9.11	–3.72	–1.58	–0.50
7	–17.22	–11.83	–9.37	–8.29	–17.22	–11.83	–9.37	–8.29
8–10	–16.88	–8.79	–3.64	–2.02	–16.88	–8.79	–3.64	–2.02

[1] Small flocks based on 60 ewes and large flocks based on 200 ewes. Flock reductions occurred in years 4 and 8.

[2] New fencing expenses based on constructing a 6–wire fence, with requirements for line and corner posts. Modified fence included adding 2 barb wires to an existing 3– or 4–wire fence. New fence cost was estimated at \$831 km^{-1}. Modified fence cost was estimated at \$159 km^{-1}.

wool represented a 5-year average of N.D. prices (N.D. Agricultural Statistics Service, various issues). Net returns to unpaid labor, equity, and management for the various sheep enterprises with debt ranged from (\$12.12) to \$41.00 ewe^{-1} in year 1 of the 10-year budgeting period (Table 2). Net returns for debt-free sheep enterprises ranged in year 1 of the 10-year budgeting period from (\$5.22) to \$45.06 ewe^{-1} (Table 2).

Treatment Scenarios

The model was structured to assess control scenarios by (1) comparing only control costs with control benefits (i.e., classic economic cost/benefit approach) and (2) determining potential overall losses with control (using sheep) vs losses without control (i.e., least-loss or cost-effective approach). Grazing scenarios where cumulative discounted annual benefits are greater than cumulative discounted annual costs are economically feasible[2]. In the second approach, grazing scenarios that are not economical (i.e., discounted costs greater than discounted benefits) may still result in less economic loss than incurred without control. Under those conditions, using grazing controls would be economically advisable, provided more economical control options were not available. In the event that an existing grazing strategy results in more loss than without control, a "do nothing" strategy or one employing other methods (i.e., herbicides, biological agents, combined controls) might be optimal.

A mixed-species, seasonal grazing approach was modeled based on sheep grazing leafy spurge infested pastures for 4 consecutive months. One ewe can be added per cow without reducing cattle production (Umberger et al. 1984, Glimp 1988, Nelson et al. 1992, Sedivec et al. 1995). Adding sheep at a rate of 2.5 ewes ha^{-1} of leafy spurge was assumed to not violate the rule of allowing one ewe per cow to a given pasture. The stocking rate for cattle was assumed to increase over time because of improved levels of leafy spurge control. The change in forage production for cattle was measured in AUMs and assumed (1) ranchers adjusted cattle stocking rates or grazing duration to accommodate the increase in grazing output, (2) initial cattle stocking rates were appropriate for the land before leafy spurge treatment, and (3) sheep stocking rates were reduced over time.

Although a number of scenarios were used to evaluate the economics of using sheep to control leafy spurge over a wide range of possibilities, several variables were held constant across all analyses. Pasture size was limited to 141.6 ha. Uncontrolled infestation spread was limited to 0.6 radial m year^{-1} and infestations were assumed to increase in canopy cover by 1.5% annually without treatment. Grazing outputs were valued at \$15 AUM^{-1} (N.D. Agricultural Statistics Service, various issues). Leafy spurge infestation canopy cover was limited to 5, 15, and 30%, which represented low (17% loss), moderate (50% loss), and high (100%) grazing losses within the infestation, respectively. Treatment benefits and costs were discounted annually at 4%.

Results

Results from the model provided a quantitative look at the long-term economic feasibility of adding a sheep enterprise to control leafy spurge under a variety of plausible situations facing landowners in the Upper Great Plains. The model also was used to assess the influence of the magnitudes of various economic and physical variables on returns from treatment.

Benefit-Cost Analysis

For control scenarios including good flock proficiency, positive net returns from leafy spurge control were substantial. Total net returns (discounted treatment returns less discounted treatment costs) from leafy spurge control using sheep, with rangeland carrying capacities of 0.5 AUMs ha^{-1}, ranged from \$303 to \$541 ha^{-1} of leafy spurge over a 10-year period, depending upon fencing obligations, debt, and flock size. With rangeland carrying capacities of 1.9 AUMs ha^{-1}, total discounted net returns from leafy spurge control ranged from \$339 to \$647 ha^{-1} of leafy spurge over a 10-year period (Table 3).

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[2] The concept of financial feasibility (i.e., constraints on or availability of resources and cash flow needed for flock, equipment, building, and fencing purchases) was not examined. Other constraints, such as availability of labor, were not addressed.

Table 3. Total discounted net returns per hectare over a 10-year period, control of leafy spurge using sheep under seasonal grazing.

	20.2–ha Infestation Infestation Canopy Cover (%)						101.2–ha Infestation Infestation Canopy Cover (%)					
Carrying	5	15	30	5	15	30	5	15	30	5	15	30
Capacity	Modified Fence			New Fence			Modified Fence			New Fence		
	($)											
AUMs ha^{-1}	good flock proficiency with no debt											
0.5	415	424	438	361	370	384	518	527	541	501	511	525
1.0	426	445	474	372	391	420	529	548	576	513	532	560
1.5	438	467	510	384	412	455	541	569	612	525	553	595
2.0	450	488	545	396	434	491	553	590	647	536	574	630
	good flock proficiency with debt											
0.5	376	386	400	303	313	327	488	497	511	466	475	489
1.0	388	407	436	315	334	363	499	518	547	478	496	525
1.5	400	428	471	327	355	398	511	539	582	489	517	560
2.0	412	449	507	339	377	434	523	560	617	501	538	595
	poor flock proficiency with no debt											
0.5	–68	–59	–45	–122	–113	–99	–26	–17	–2	–42	–33	–19
1.0	–57	–38	–9	–111	–92	–63	–14	4	33	–30	–12	17
1.5	–45	–17	26	–99	–70	–27	–3	25	68	–19	9	52
2.0	–33	5	62	–87	–49	8	9	46	103	–7	30	87
	poor flock proficiency with debt											
0.5	–106	–97	–82	–179	–170	–155	–55	–46	–31	–77	–67	–53
1.0	–94	–75	–47	–167	–148	–120	–43	–25	4	–65	–47	–18
1.5	–82	–54	–11	–155	–127	–84	–32	–4	39	–54	–26	17
2.0	–70	–33	24	–144	–106	–48	–20	17	74	–42	–5	52

For control scenarios including poor flock proficiency, net returns from leafy spurge control were sensitive to rangeland productivity and leafy spurge canopy cover. Total net returns from leafy spurge control, with rangeland carrying capacities of 0.5 AUMs ha^{-1}, ranged from \$(179) to \$(2) ha^{-1} of leafy spurge over the 10-year period, depending upon fencing obligations, debt, and flock size. With rangeland carrying capacities of 1.9 AUMs ha^{-1}, total net returns from leafy spurge control ranged from \$(144) to \$103 ha^{-1} of leafy spurge (Table 3).

Generally, discounted net returns from leafy spurge control were about \$30 to \$57 ha^{-1} higher for scenarios having no debt vs those with debt (Table 3). Over a 10-year period, net returns from leafy spurge control were \$64 ha^{-1} less for scenarios with new fence vs modified fence scenarios with small infestations and were \$19 ha^{-1} less with large infestations. Discounted net returns ha^{-1} from leafy spurge control were higher with large infestations (101.2 ha) vs small infestations (20.2 ha) across all scenarios. In a 10-year period, discounted net returns from large infestations compared with small infestations increased by \$42 to \$111 ha^{-1} for all scenarios with modified fence. For all scenarios with new fence over the same period, net returns from leafy spurge control improved by \$82 to \$163 ha^{-1} when comparing small with large infestations.

Least-loss Analysis

Least-loss analysis compares economic losses incurred if a leafy spurge infestation was uncontrolled to losses incurred with control. Where economic losses with treatment are more than the economic losses incurred without control, the treatment program or strategy would not be recommended.

The good flock proficiency scenarios had positive enterprise returns, which resulted in positive discounted net returns from control. Thus, least-loss analyses were not conducted for those scenarios. Least-loss analyses were conducted for the poor flock proficiency scenarios.

Over a 10-year period, most sheep grazing scenarios with high rangeland productivity and high leafy spurge canopy cover resulted in less economic loss than with no control (Table 4). Many of the grazing scenarios with new fence and low leafy spurge canopy cover would not be recommended, although most scenarios with new fence and high leafy spurge canopy cover could be recommended for all but the least productive rangeland. In a 10-year period, none of the small flock scenarios would be recommended at rangeland carrying capacities of 0.494 AUMs ha^{-1} or less (Table 4).

Factors Influencing Returns from Control

Many factors may influence the economics of using sheep to control leafy spurge. One of the biggest factors influencing returns from leafy spurge control, when a sheep enterprise is added to an existing ranch, would be enterprise returns. When enterprise returns were positive, discounted net returns from leafy spurge control were positive in all of the treatment scenarios examined. In some cases, economic returns from leafy spurge control were substantial. When sheep enterprise returns were negative (because of assumed poor flock proficiency, Table 2), other factors determined the economics of control.

Large infestations were more economical to treat than small infestations, based on the fundamental assumptions used in this study. Fencing costs per hectare were modeled to be less with larger infestations, since overall pasture size was fixed across infestation sizes. In reality, per ha fencing costs for a 101.2-ha infestation could be the same as for a 20.2-ha infestation. Because some efficiencies in sheep production occur when moving from small flocks (e.g., 50 ewes) to larger flocks (e.g., 200 ewes), enterprise returns improved with flock size. Thus, lower per ewe fencing costs and more favorable enterprise

Table 4. Least-loss analysis[1] of the control of leafy spurge using sheep under seasonal grazing.

	20.2–ha Infestation Infestation Canopy Cover (%)						101.2–ha Infestation Infestation Canopy Cover (%)					
Carrying	5	15	30	5	15	30	5	15	30	5	15	30
Capacity	Modified Fence			New Fence			Modified Fence			New Fence		
AUMs ha^{-1}	poor flock proficiency with no debt											
0.5	no	no	no	no	no	no	no	yes	yes	no	no	yes
1.0	no	yes	yes	no	no	yes	yes	yes	yes	no	yes	yes
1.5	no	yes	yes	no	no	yes	yes	yes	yes	yes	yes	yes
2.0	yes	yes	yes	no	yes	yes	yes	yes	yes	yes	yes	yes
	poor flock proficiency with debt											
0.5	no	no	no	no	no	no	no	no	yes	no	no	no
1.0	no	no	yes	no	no	no	no	yes	yes	no	no	yes
1.5	no	yes	yes	no	no	yes	yes	yes	yes	no	yes	yes
2.0	no	yes	yes	no	no	yes	yes	yes	yes	yes	yes	yes

[1] In scenarios where discounted net returns from using sheep to control leafy spurge are negative, least-loss analysis indicates if using sheep grazing to control leafy spurge would result in less economic loss than if the leafy spurge infestation was left uncontrolled. A "yes" implies that the scenario will result in less economic loss than no treatment. A "no" implies that the scenario will result in more economic loss than no treatment.

returns were major reasons that returns from control were more favorable with larger infestations.

Returns from control improved as leafy spurge canopy cover and the resulting forage suppression increased. As grazing losses for cattle increase, potential returns from leafy spurge control also increase. This relationship directly influenced the amount of grazing recovery that could be expected from leafy spurge control. Returns from leafy spurge control improved proportionally to changes in grazing recovery. Since sheep grazing was only evaluated using relatively large infestations, the value of grazing retention (i.e., grazing output retained by preventing infestation spread) was a minor component of overall returns from treatment. Higher infestation densities and levels of canopy cover would affect net returns from leafy spurge control if grass recovery and forage available within the infestations differed from the levels/relationships used in this study.

Returns from control were directly proportional to rangeland productivity. Thus, holding all other factors constant, returns were greater on more productive rangeland. Similarly, holding all factors constant, returns change as AUM values change.

Enterprise debt affected discounted net returns from leafy spurge control. The level of debt used in this study had sufficient influence on returns from control (about \$30 to \$57 ha^{-1} over a 10-year period) to affect decisions regarding the economics of using sheep to control leafy spurge. The effects of added debt were most influential in the poor flock proficiency scenarios. When enterprise returns were negative, increased expense from additional enterprise debt was sufficient in some scenarios that sheep grazing of leafy spurge would be uneconomical.

The added expense for new fence had a much greater effect on discounted net returns for controlling small infestations (expense was divided among fewer ha). For example, with small infestations, discounted net returns from control improved about \$64 ha^{-1} when compared to scenarios with modified fence. Similarly, with large infestations, returns from control improved by only \$19 ha^{-1} when compared to scenarios with modified fence.

Alternative Scenarios

Additional treatment scenarios were examined, although not presented for sake of brevity. Twice-over rotational grazing systems were somewhat less economical than seasonal grazing strategies, due to reduced leafy spurge control and higher fencing costs (i.e., added cost for internal fences). However, over a 10-year period, the difference between discounted net returns from rotational and seasonal grazing strategies did not substantially influence the economics of using sheep to control leafy spurge.

Leasing sheep for leafy spurge control may be an alternative to adding a sheep enterprise to an existing ranch. Lease rates above \$1 head^{-1} month^{-1} did not provide positive net returns in many of the control scenarios examined. Lease rates of \$1 head^{-1} month^{-1} would likely result in positive net returns from control in many treatment scenarios and provide less economic loss than no treatment across a range of treatment scenarios.

Different time periods were also examined. Discounted net returns from treatment were not as favorable in a 5-year period, largely because sheep grazing requires several years to reduce infestation densities. Discounted net returns improved when treatment scenarios were increased from 10- to 15-year periods. Returns in the various periods would be sensitive to changes in the discount rate.

Conclusions

The basic premise for this study was that sheep would be used to control leafy spurge in rangeland by adding a sheep enterprise to an existing ranch. Sheep grazing as a leafy spurge control method was economical across many enterprise scenarios. In many of the scenarios with negative sheep enterprise returns, the benefits of leafy spurge control outweighed the negative enterprise returns.

In addition to economic criteria, other factors, such as labor and financial constraints, need to be considered before implementing a grazing control strategy. Even though returns may be positive for many control scenarios, they may not be sufficient to adequately compensate for unpaid inputs. If these constraints do not prohibit adding a sheep enterprise to an existing ranch, the economics of using sheep grazing to control leafy spurge appear favorable.

The economics of using sheep to control leafy spurge were sensitive to the grazing recovery rates assumed in this study. Long-term research over a wide range of treatment conditions is needed to refine the control responses assumed in this study. Additional refinement in those relationships would add confidence to the study results.

Several factors can influence costs and returns from using sheep grazing to control leafy spurge. As a result, a careful evaluation using site- and rancher-specific inputs would be recommended before implementing sheep grazing as a leafy spurge control method.

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Dietary structural types of polygastric herbivores at different environments and seasons

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Abstract

A classification of dietary structural types that represents different arrangements of forage classes is proposed. It may be especially useful for interpreting and comparing herbivore diets from different environments. As an example, a data set with the botanical composition of 55 pooled fecal samples determined by microhistological analysis was analyzed. These samples came from 4 species of range herbivores (cattle, sheep, goat, and guanaco -*Lama guanicoe*-), from 9 different environments of Northern Patagonia (Argentina) during 3 seasons. Based on plant characteristics related with the capacity of the animals to eat and digest each plant and with the occasional or permanent presence of them in the vegetation, the information was grouped into 5 forage classes: woody plants, perennial grasses, annual grasses, grasslikes, and forbs. A principal component analysis of the grouped data was conducted. The graphic representations evidenced the gradual changes in the structure of the data. Later, working over the subspace defined by the 3 first principal component axes, a hierarchical classification was performed that resulted in 9 dietary structural types. These types represented variation that resulted from the interaction of pasture differences, species of herbivore and season. This concept is an abstraction developed from the experience, to extend its utility beyond the particular cases.

Key Words: botanical diet composition, conceptualization, forage classes, microhistological analysis, multivariate analysis, similarity of diets.

Resumen

Se propone la clasificación de tipos estructurales de dietas, que representan diferentes ordenamientos de clases forrajeras previamente definidas. La misma puede ser especialmente útil para interpretar y comparar la dieta de herbívoros en diferentes ambientes. Como ejemplo se analizó un conjunto de datos correspondiente a la composición botánica, determinada mediante el análisis microhistológico, de 55 muestras compuestas de heces. Estas muestras provinieron de 4 herbívoros (bovino, ovino, caprino y guanaco –*Lama guanicoe*-), en condiciones extensivas de pastoreo en 9 ambientes diferentes del norte de Patagonia, en 3 estaciones. En base a características de las plantas relacionadas con la capacidad de los animales de comerlas y digerirlas y con la presencia ocasional o permanente de las mismas, la información fue agrupada en cinco clases forrajeras: plantas leñosas, gramíneas perennes, gramíneas anuales, hierbas y graminoideas. A partir de los datos agrupados se realizó un análisis de componentes principales. A través de sus representaciones gráficas se evidenciaron los cambios graduales en la estructura de los datos. Trabajando sobre el subespacio definido por los tres primeros ejes factoriales, se hizo una clasificación jerárquica, para formar los grupos que dieron origen a nueve tipos estructurales de dieta. Estos tipos representan variaciones resultantes de la interacción de diferencias entre pasturas, especie de herbívoro y estación. Este concepto es una abstracción desarrollada a partir de la experiencia, para que su utilidad trascienda los casos particulares.

The diets of livestock and wildlife in the shrub, shrub-grass steppes, and the mountain forests of Patagonia (Argentina) result from the complex interaction between available forage and animal species, their metabolic and reproductive status, the presence of predators and especially the location of water, as pointed out as a generalization by O'Reagain and Swartz (1995). Herbivores select diets from available forage in relation to their nutritional requirements (Hanley 1982).

Indices of diversity, diet overlap and/or selectivity have been used to describe and compare the botanical composition of range herbivore diets in Patagonia (e.g., Bonvissuto et al. 1982, 1986, Bonino et al. 1986) and by other authors in many other countries. However, Scarnecchia (1996) pointed out, as did other authors cited in his work, that these indices have little general use in the science of range management.

McInnis et al. (1990) applied hierarchical cluster analysis to the similarity indices to reveal patterns difficult to recognize in the matrix of similarity coefficients. Other multivariate methodologies such as principal component analysis and correspondence analysis have been used to analyze dietary information (Manacorda et al. 1996, Posse et al. 1996, Pelliza et al. 1997).

Conceptual models have been developed to explain foraging behaviors. Senft (1987) stated that generalized models might be useful to predict the response of the animal to changes in the composition of the plant communities or landscape mosaics.

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Hofmann (1989) classified ruminants into 3 feeding types: concentrate selectors, intermediate, and grass-roughage eaters. Provenza and Balph (1990) examined this classification and other models of diet-selection in ruminants, which are not mutually exclusive. They found that models based on morphophysiological characteristics and body size provide general predictions about foraging in unfamiliar environments and foraging in environments where the abundance and nutritional quality in dietary items vary temporally and spatially. Referring to mathematical models, Walker (1993) pointed out that the existence of several simulation models competing to explain foraging behavior suggests the difficulty in explaining diet selection by mathematical expressions.

To interpret changes in vegetation in rangelands, Friedel et al. (1988) reduced a large number of species to a small number of "functional groups," based on attributes selected according to their relevance for management. Similarly, defining forage classes according to the characteristics of the herbivores and the vegetation communities could enhance interpreting and comparing data from diets.

The objective of this study was to develop a new method for describing and interpreting diet information based on dietary structural types. This analysis is especially useful when studying diets from different environments. The usefulness of this procedure is demonstrated by analyzing diets of 4 polygastric herbivores grazing in different environments of Northern Patagonia.

Materials and Methods

Study area

The Río Negro Province, Argentina, is included in the vast region known as Patagonia. It has an area of 203.013 km^2 and extends 758 km from the Andes Mountains to the Atlantic Ocean and 485 km between 37° and 42° of south latitude (Fig.1). It has a moderately cold climate in the west and varies to warm-temperate toward the northeast (Soriano 1983). Mean annual precipitation, in part as snow, decreases from more than 2,000 mm in a forest dominated strip in the west to 150 mm in the central area, and increases again to 300 mm on the east of the Province. More than half of the Río Negro Province has a mean annual precipitation lower than 200 mm (Fig. 1). Strong, constant winds prevail from the west year-long (Muñoz and Garay 1985, Bustos 1996). Most of Río Negro Province rangelands are in the semiarid environments, with extensive grazing units.

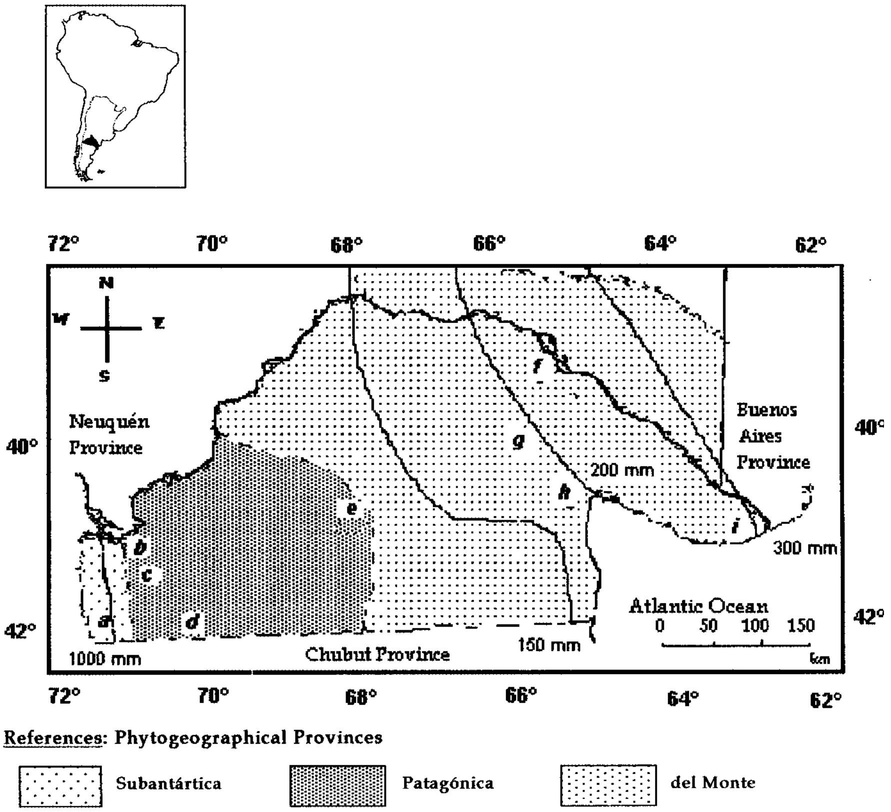

Fig.1. Location of Pastures *a* to *i* in the Río Negro Province, Argentina (South America) with the phytogeographical provinces (Cabrera, 1976) and isolines of precipitation. Map adapted from Ragonese & Piccinini (1969) and Muñoz & Garay (1985).

Cabrera (1976) described the phytogeographical regions and provinces of Argentina and Soriano (1956) subdivided one of the provinces in districts. The phytogeographical areas for Río Negro province are described in Table 1 and their locations presented in Figure 1. Diets of cattle, sheep, goat, and guanaco (*Lama guanicoe*) located in 9 pastures distributed across the Rio Negro Province were used in this study (Fig.1).

Analysis of diets

A minimum of 15 fecal samples from each of 4 herbivore species (cattle, sheep, goat, guanaco) were collected, when present, in each pasture during the summer, winter, and spring of 1991. Following 6 years of drought, the annual rainfall during the study was slightly greater than the mean (Unpublished data, Bustos). The feces were pooled to obtain 55 composite samples, each one of them corresponding to each combination of pasture, season, and animal species, which is referred to hereafter as a diet. Samples were analyzed microhistologically according to Holechek and Vavra (1981), determining percentage of frequency in accordance with Holechek and Gross (1982).

The plant species identified were classified as belonging to 1 of the following 5 "forage classes" based on morphological and anatomical characteristics, related to the capacity of the herbivores to eat and digest them, and their perennial or ephemeral availability:

1. Woody plants (WP): stems and roots with secondary structure, characterized by lignified cellular walls
2. Forbs (F): without secondary structure and with high digestibility
3. Perennial grasses (PG): without secondary structure with lignified cellular walls
4. Annual grasses (AG): without secondary structure with less lignified cellular walls than PG
5. Grasslike plants (G) (*Juncaceae* and *Cyperaceae* families): without secondary structure and digestibility similar to the PG.

Hanley (1982) showed that woody plants (WP) offer easily digestible forage with good nutritive quality in their buds, flowers, and fruits. Similarly, Somlo et al. (1985, 1997) reported that in our study area WP had good nutritive quality. Perennial grasses constituted an abundant and permanent forage, while the annual

Table 1. Characterization of the phytogeographical regions, provinces and districts in the study area.

Region	Province	District	Description	Pastures
AUSTRAL	Subantártica		Forests with tree species of austral distribution, mainly of the genus *Nothofagus* (Cabrera 1976). Grazing predominates in the forest of the deciduous "Ñire", *Nothofagus antarctica*, with grasses and forbs in the understorey. There are meadows with grasslike plants as: *Juncus* spp., *Carex* spp. and *Eleocharis* spp., grasses as *Poa pratensis* and forbs as *Trifolium repens* (Manacorda et al. 1996).	***a***
NEO TROPICAL	Patagónica	Occidental District	Characterized by tussock grasses (*Stipa* spp., *Poa ligularis*) and cushion-like shrubs as *Mulinum spinosum* and *Senecio* spp. (Soriano 1956). There are meadows characterized by *Juncaceae*, *Cyperaceae* and perennial grasses, such as *Juncus* spp., *Carex* spp. and *Festuca pallescens*, respectively (Boelcke 1957). Within those meadows, there are areas with the halophytic grass *Distichlis* spp. (Nicora 1978), towards the east (Marcolin et al. 1978).	***b***, ***c***, ***d***
		Central District	Plateaus and mountains of the center of the Río Negro Province with an altitude superior to 816 m. (Ragonese and Piccinini 1969). The dominant species are: *Chuquiraga avellanedae* and *Nassauvia glomerulosa* among shrubs and *Stipa* spp. among grasses. *Prosopis denudans* and other shrubs are sporadically present (Soriano 1956).	***e***
	del Monte		Xerophile, sandy and halophile steppes predominate, with short-shrubs, succulent and ephemeral species. The characteristic community is the "Jarillal" (pastures ***h*** and ***i***), an association of *Larrea* spp., with *Monttea aphylla*, *Bouganvillea spinosa* and other plants (Cabrera 1976). In the salinized depressions (pastures ***f*** and ***g***) a community characterized by halophytic shrubs of the genus *Atriplex* spp. dominates (Morello 1958).	***f***, ***g***, ***h***, ***i***

grasses (AG) have occasional presence. Grasslike plants are restricted to meadows.

Statistical analysis

To obtain dietary structural types, the data were grouped into the 5 forage classes and analyzed. They were arranged in a matrix $A=\{a_{ij}\}$, for i=1,...,55; j=1,...,5; being the element a_{ij} the percentage of the forage class "j" in the diet "i." Principal component analysis (PCA) was performed on this matrix to represent the data in a space of reduced dimensions with optimal properties (Lebart et al. 1995). The results of PCA allowed evaluating the similarity of diets, expressed through their proximity in the vectorial space. Diets with closer scores (coordinates of diets in the factorial axes) are more similar. These scores are a linear combination of the original dietary composition data that maximizes the variation in these resultant scores with the restriction that the different sets of principal component scores are not correlated to each other. This PCA also describes the correlation structure of the variables.

Next a hierarchical classification was carried out, according to the criterion of minimal variance, working over the subspace defined by the first 3 principal components. The semipartial R^2 was the statistic used to evaluate the change produced in the k-th step. This statistic expresses the magnitude of the increment in variability due to the union made in that particular step, relative to the total variance of the data. The objective of this analysis was to create the groups, characterizing them by the biological interpretation of the factorial axes employed. The groups were obtained by cutting the dendrogram with a continuous line, not necessarily straight, according to Benzécri (1992). The dendrogram was cut at a subjective level, which was established to get groups with a biological meaning in order to define the dietary structural types. Data analysis was conducted using SAS (1988).

Definition of dietary structural types

The dietary structural types represent different arrangements of the 5 forage classes. The terms a) characterized, b) accompanied, and c) associated were used to define the proportion of the diet that the forage classes represented. A forage class characterized a group of diets if it comprised the majority of those diets, whereas a forage class was considered accompanying if it was in a lower proportion. When the majority of the diets of a group had 2 forage classes in similar proportions, they were defined as associated.

Results

Table 2 shows the plant species or genus identified with values greater than 10%, grouped by forage class, pasture, season and herbivore. Figure 2a shows the first factorial plane of the PCA made on the dietary space (accounting for 47 and 28% of the total variation by axes 1 and 2, respectively), and Figure 2b presents the factorial plane of the variable space (i.e., forage class). Woody plants were separated from perennial grasses and grasslikes on the first PCA axis, with their estimated correlation coefficients r being: $r_{WP,PG}$ = –0.83 and $r_{WP,G}$ = -0.67. Figure 3 shows the dendrogram corresponding to the cluster analysis made with the diets described by the scores given by the first 3 axes of the PCA, and the resulting 9 groups that were identified. The botanical composition of these groups, at forage class level, was used to develop the 9 dietary structural types defined in Table 3.

Cluster analysis grouped 64% of the diets into structural types I, II, III, IV, and V based on the proportion of perennial grasses or woody plants in the diet (axis 1, Fig. 2b). This first component accounted for differences between the Monte and the other 2 phytogeographical provinces. The perennial grass-woody plant gradient was also seen in structural types VI, VII, VIII, and IX, which were separated along the second principal component axis based on the occurrence of forbs and annual grasses (axis 2, Fig 2b) and by perennial grasses and grasslikes (axis 3, which was used in the classification). The group defined as the structural type IX is more heteroge-

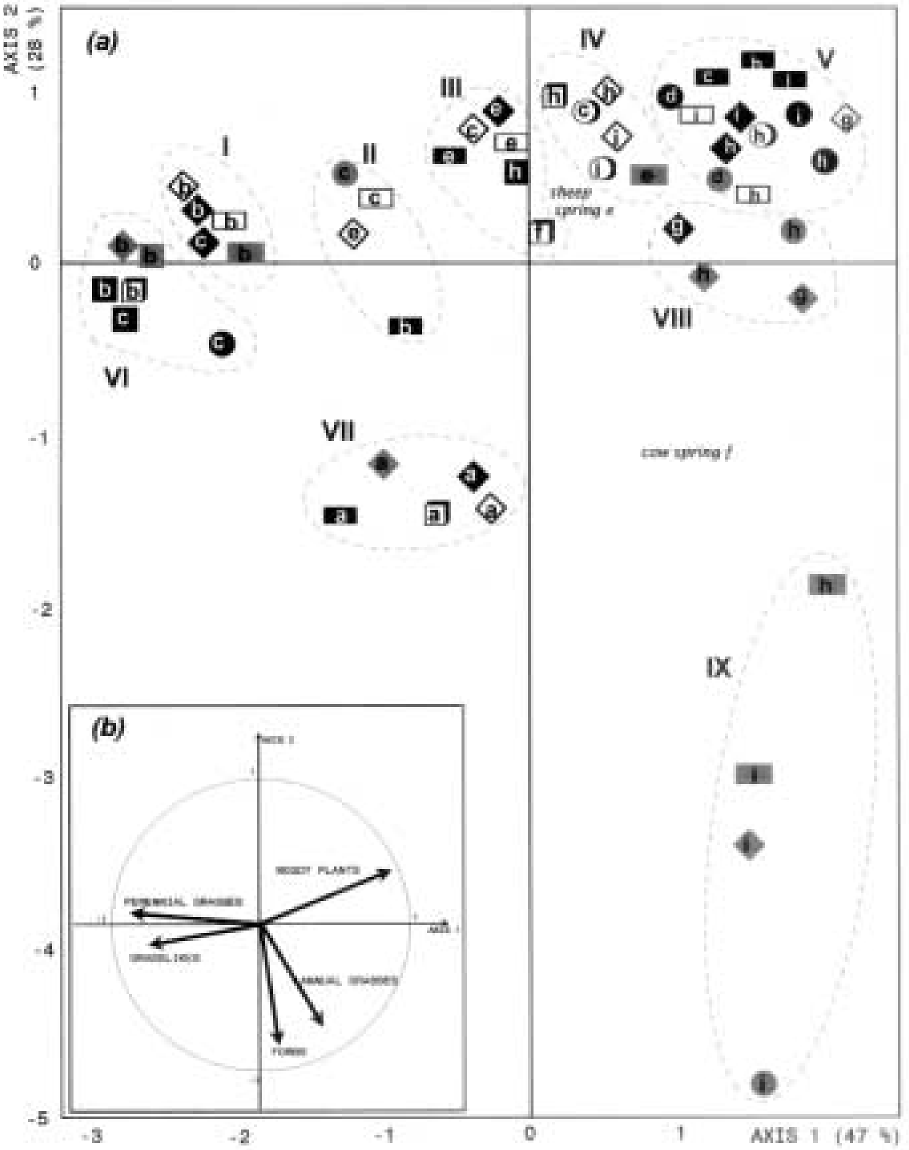

Fig 2. First factorial plane of the Principal Component Analysis of diet composition data, expressed in 5 forage classes, of 4 different herbivores from 9 pastures and 3 seasons. (a*)* Representation of the dietary space. Labels of the diets: *CATTLE*: ■ summer, ■ spring, ❑ winter; *SHEEP*: ◆ summer, ◆ spring, † winter; *GOAT*: l summer, l spring, m winter; *GUANACO*: n summer, n spring, o winter. The letter inside represents the pasture. The percentages of the total inertia explained by each axis are expressed between parenthesis. The diets that belong to each Dietary Structural Type (in roman numbers) are enclosed by a shut dotted line. (*b*) Representation of the variables (forage classes).

neous than the others, but it was taken as a single cluster because of the availability of the annual grasses, which characterized it, is more variable than the other forage classes. Two of the 55 diets analyzed did not correspond completely to the characterizations given to the structural types IV and VIII, so they were excluded. In the first case, the diet was the only one with a large amount of grasslikes (16%); and in the latter, forbs were present (12%) and there were fewer woody plants. These 2 diets appear in italics in Figure 2a and are indicated by an asterisk in Figure 3. In Figure 4, the contribution of each forage class in every diet is represented, showing the different diet compositions that characterize the defined dietary structural types.

The location of diets from pastures ***b*** and ***c*** on the first principal component axis (Fig. 2a) shows that most of the grazing in the Patagónica Province, Occidental District (Table 1), occurs in the meadows Bonvissuto et al. 1996. The diets of the 4 herbivores in pastures ***b*** and ***c*** contained a high proportion of perennial grasses with different proportions of grasslikes. In the Central District of the Patagónica Province and in the Monte, the steppes become predominant (Table 1), with different combinations of shrubs with perennial and/or annual grasses. Thus, in the dietary structural types of pastures ***e, f***, ***g***, ***h***, ***i***, woody plants were especially important, combined with different proportions of the other forage classes, apart from grasslikes. This tendency is more evident in sheep, goat, and guanaco diets than in cattle diets.

The communities of the Phytogeographical Subantárctica Province (Table 1) have a variety of perennial grasses, woody plants, grasslikes, and forbs available. Therefore, in all seasons, the diets of sheep and cattle, corresponding to pasture ***a***, were characterized by an association of all the forage classes considered, excluding the annual grasses.

It can also be noted (Fig. 2a) that there are dietary structural types defined almost exclusively by diets corresponding to one pasture: type VII by pasture ***a*** and types I and VI by pasture ***b***. Those pastures always containing grasslikes have greater forage availability than the pastures of the steppes.

Given the geographical location effect in the graphical diet distribution, the results also show a seasonal effect. It is especially evident in the dietary structural types V, mostly defined by summer diets, and in types VIII and IX, which are defined almost exclusively by spring diets (Fig. 2a.). In both cases, this remark is related with the seasonal foraging availability: in the first case, by woody plants that include fruits, and in the latter, by the presence of annual grasses (Tables 2 and 3).

Other authors (Bonino et al. 1986, McInnis et al. 1990, Manacorda et al. 1996) found a relationship between the results of dietary studies and animal species considered, although subordinated to the influence of the plant community. In this group of samples, 2 known tendencies were evident: a) Cattle tended to have diets characterized by grasslikes and perennial grasses, with minor influence of woody plants and b) the other herbivores, especially goat, tended to have dietary patterns with a strong component of woody plants (Figs. 2a, 2b, and 4).

Table 2. Plant species contributing 10% or more to the diets of 4 different herbivores in Northern Patagonia, Argentina. Diets are grouped by herbivore, pasture and season.

	Pastures **Seasons**	**a** **UWP**	**b** **UWP**	**c** **UWP**	**d** **UWP**	**e** **UWP**	**f** **UWP**	**g** **UWP**	**h** **UWP**	**i** **UWP**
Woody Plants	*Acantholippia seryphiodes*	. . .	. . .	. .	. . .	. . L	. . .	. . .	. . .	. . .
	Adesmia spp	. . .	. . .	. . .	. . G	. . .	. . .	. . .	. . .	. . .
	Atriplex spp	. . .	. . .	. . .	. . .	. . .	. .C	S S S	. . .	
	Berberis spp.	. C .	. . .	.G .	. . .	. . .	. . .	. . .	. . .	. . .
				L L .						
		. S .	.S .							
	Bredemeyera microphylla	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. G L .	. . .
	Capparis atamisquea	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. G .
		. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	S . .
	Cassia aphylla	. . .	. . .	. . .	. . .	. . .	C C	S S S	. . .	. . .
	Condalia microphylla	. . .	. . .	. . .	. . .	. . .	. . .	. . .	G G	. . .
									S . .	
	Cyclolepis genistioides	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . G	. . .
								S . S	. . S	
	Chuquiraga spp.	. . .	. . .	. . .	. . .	L. .	. . .	. . .	. . L L	. L .
						S . S			. S S	
									. C .	G . .
	Lycium spp	. . .	. . .	. . .	. G . .	. . L	. . .	. . .	. . .	. . .
	Maytenus boaria	S . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .
	Monttea aphylla	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. .G	. . .
	Mulinum spinosum	. . .	. . .	L G	. . .	. . .	. . .	. . .	. . .	. . .
	Nardophyllum spp.	. . .	. . .	L. .	. . .	. . .	. . .	. . .	. . .	. . .
	Nassauvia glomerulosa	. . .	. . .	. G	. . .	. . .	. . .	. . .	. . .	. . .
	Prosopidastrum globosum	. . .	. . .	. . .	. . .	. . .	. . .	. . .	S L	. . .
	Prosopis spp.	. . .	. . .	. . .	. . .	. . .	. . .	. . .	C C .	. . .
									G G .	G G .
									L L .	L L .
								S S .	S S .	S S .
	Retanilla patagonica	. . .	. . .	. . .	. . .	. L .	. . .	. . .	. . .	. . .
	Schinus spp.	. . .	. . .	G . .	. . .	. . .	. . .	. . .	GGG	. GG
									. S .	. LL
	Senecio spp.	. . .	L . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .
	Verbena spp. . . .	. . .	. . .	. .L	G . G .	. .L	. . .	. . .	. . .	. . .
Annual Grasses	*Schismus* spp.	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. .G	. . G
									L L .	L L .
								S S .	S S .	S S .
Grasses	*Distichlis* spp.	. . .	. . .	C . .	. . .	S	. . .	. . .	. . .	. . .
				G . .	. . .	. . .	. . .	. . .	. . .	. . .
	Festuca pallescens	. . .	C . C	C . .						
			L L L .	. L .						
			S S S	S S .						
	Poa spp. *(P.pratensis+*	C C .	C CC	C .	. . .	. . .	. . .	. . .	. . .	. . .
	P.lanuginosa+ P.ligularis)	L L L	G . .		. . L					
		S S S	S S S	S S .	. . S					
	Setaria spp. . . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . S
	Sporobolus rigens	. . .	. . .	. . .	. . .	. . .	. . .	S . .	. . .	. . .
	Stipa spp. *(S.tenuis + S.speciosa)*	. . .	. . .	G G	G . G	. . .	. . .	. . .	. G .	. G G
			L . .	. L .		L L L			L L .	. L L
			S S .			S S S			S S S	S S .
							. C C		C C .	
Forbs	*Blechnum* spp.	. S .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .
	Erodium cicutarium	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	G
	Sphaeralcea spp. . . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	G
	Trifolium repens	C . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .
	Verbascum thapsus	S. .								
Grasslikes	*Carex* spp.	. . .	C C C	C . .	. . .	. . .	. . .	. . .	. . .	. . .
	Eleocharis spp.	C . .	. . S	. . .	. . .	. S.	.. . .	. . .	. . .	. . .
	Juncus spp.	C CC	C . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .
			G . .							
			S . .							

Seasons are: U = sUmmer W = Winter P = sPring

Herbivores species are: C = Cattle G = Goat L = guanaco (*Lama guanicoe*) S = Sheep

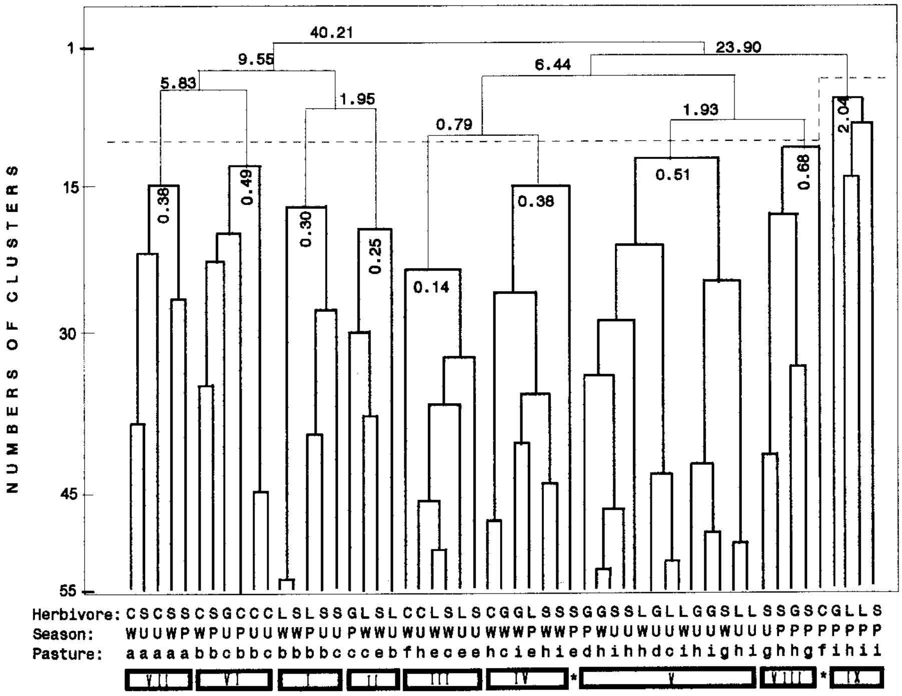

Fig. 3. Dendrogram of the cluster analysis based on the first three factorial axes of the PCA. The numbers are semipartial R square. Bold numbers represent the result from the last union that originate the clusters shown with bold lines. Soft numbers result from the unions above the last ones considered. The dotted line shows where the dendrogram was cut. C = Cattle, G = Goat, L = guanaco (*Lama guanicoe*), S = Sheep. P = sPring, U = sUmmer, W = Winter. Pastures = a to i. Dietary structural types = I to IX. Asterisks correspond to diets that were excluded from those patterns.

Discussion and Conclusions

Frequently, the lists of genus and/or plant species obtained through the survey on rangelands or through the analysis of range herbivore diets, are not enough to understand the complex animal-plant interaction. To get a more integral interpretation, plants generally are grouped into functional categories that are independent of taxonomic classification. Different functional groupings based on research objectives or characteristics of available forage have been proposed by Bonvissuto et al. (1996), Posse et al. (1996), and Friedel et al. (1988), among other authors. The forage classes proposed here are useful for the interpretation of the diet information from different environments.

This study differs from McInnis et al. (1990) in the objective and in methodological aspects. In this case, the objective is not only the classification of diets, but also the interpretation and the comparison of the foraging response of herbivores **in different environments.** About the transformation applied to the original dietary composition data prior to the classification of the diets using cluster analysis, McInnis et al. (1990) reduced the matrix of mean seasonal percentage botanical composition of different herbivores diet by creating a matrix of similarity indices. In our study the mean seasonal percentage composition of the 5 forage categories in the diets of 4 different herbivores was reduced to a matrix of first 3 principle component scores. But here PCA was not used merely as a transformation technique, it was mainly used to reduce the data dimension, allowing their distribution to be shown in graphics. Possible structures of the data could be seen, sometimes evidencing gradual changes. Instead, the classification methods, as cluster analysis, try to find discontinuities in the data, obtaining groups of similar individuals as a result. In Figure 2a, the groups that are clearly different can be separated from the others that, even when having more similarities within groups than between groups, show a slow and gradual change in the dietary composition. The biological meaning of the identified clusters in this study was based on the biological interpretation of each principal axis.

In an extensive work on most of Patagonia, Pelliza et al. (1997) employed a similar methodology (multiple correspondence analysis and cluster analysis), with the objective of systematizing the results of a dietary survey in the dominant production systems of the principal environments of Patagonia. Starting with dietary information from more than 300 fecal samples representing 10 monogastric and polygastric herbivores, in 3 seasons they defined 20 dietary types or patterns and presented them in cartographic form. The present work proposes to extract directly from the dietary information the conceptualization of dietary structural type. These types, in the sense proposed here, are a generalization that integrates the particular cases, helping in the interpretation of the variation found in the real situations. In Nature only the variation is real and the named "types" are statistical abstractions (Unpublished work, Valverde). The dietary structural types defined here do not differ conceptually from the dietary types or patterns of Pelliza et al. (1997). The different terminology was used to avoid confusions due to the meaning given to these terms in other works (McInnis et al. 1990, Owen-Smith 1993).

Table 3. Dietary structural types defined by cluster analysis of the scores obtained from the first 3 principal component axes of the PCA made on diet composition data expressed in 5 forage classes, of 4 different herbivores from 9 pastures and 3 seasons.

Dietary Structural Types	Description
I	Diets characterized by perennial grasses
II	Diets characterized by perennial grasses accompanied by woody plants.
III	Diets characterized by perennial grasses associated with woody plants.
IV	Diets characterized by woody plants accompanied by perennial grasses.
V	Diets characterized by woody plants.
VI	Diets characterized by grasslikes associated with perennial grasses.
VII	Diets characterized by perennial grasses associated with woody plants, accompanied by grasslikes and forbs.
VIII	Diets characterized by woody plants, accompanied by perennial grasses and annual grasses.
IX	Diets characterized by annual grasses associated with woody plants, accompanied by perennial grasses with a variable presence of forbs.

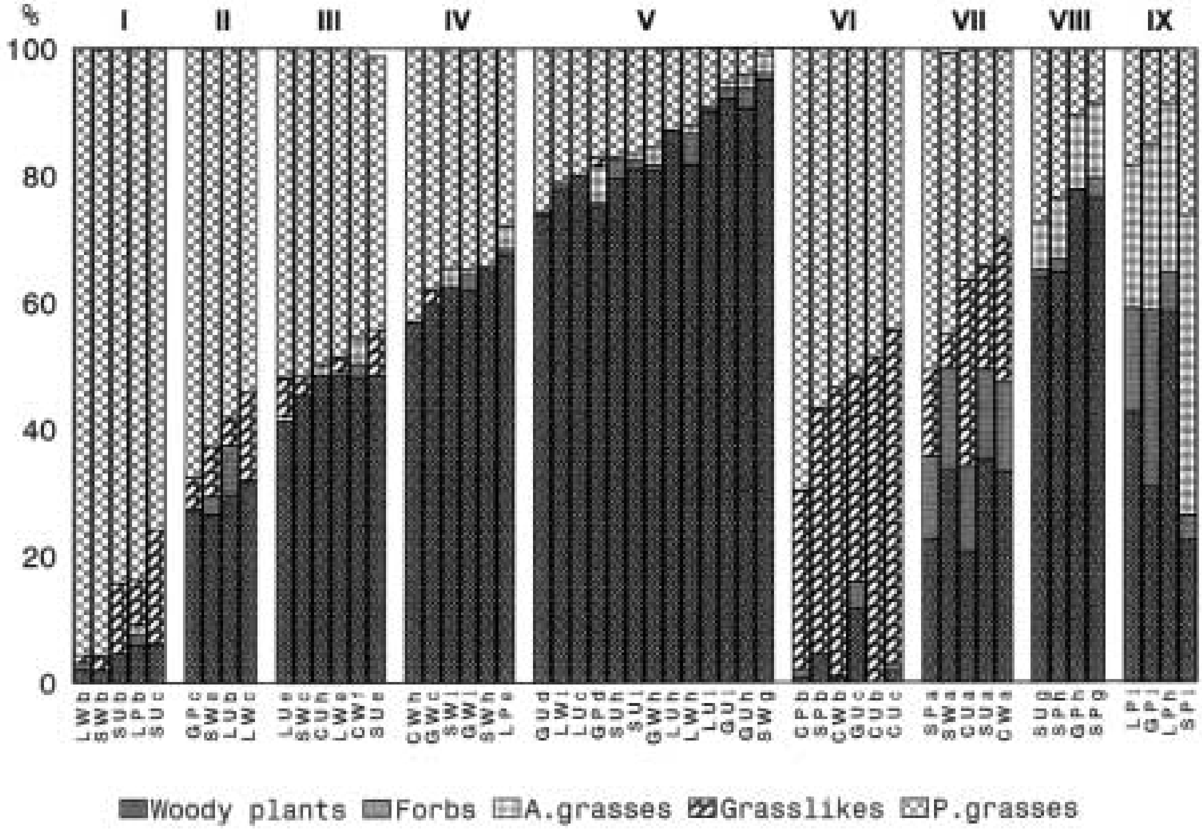

Fig. 4. Forage classes composition of diets grouped on the defined Dietary Structural Types (I to IX). C = Cattle, G = Goat, L = guanaco (*Lama guanicoe*), S = Sheep. P = sPring, U = sUmmer, W = Winter. Pastures = a to i.

With respect to the interpretation of plant-herbivore interaction, Senft (1987) suggested that there might be basic patterns of this interaction that are independent of vegetation type and perhaps of plant species, and that those patterns could differ with level of ecological organization. In this work, it was found that some of the dietary structural types were not independent of the structural and specific characteristics of the vegetation of each region, although they were conditioned to animal characteristics, as discussed by Hanley (1982). Thus, this approach helps in setting up the interaction between the herbivore morphophysiology and the vegetation type. There are cases, in which the same herbivore has similar diets in different environments, whereas in other cases, different herbivores at different environments have similar diets.

The concept of structural types defined in this study fulfills the characteristics cited by Scarnecchia (1996) for any conceptualization: it is an abstraction developed from the experience attempting to generalize the information so that its use transcends the particular cases. The types based on the contribution of forage classes in the diets may be integrated in future studies, to develop more complex conceptual models of dietary selection.

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Cattle use of foothills rangeland near dehydrated molasses supplement

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Abstract

Strategic supplement placement has been shown to be an effective tool to lure cattle to underutilized rangeland. The goal of this study was to determine where cattle grazed when supplement was placed in foothills rangeland. The study was conducted in 4 pastures in northern Montana that were dominated by cool-season grasses. For 2-week periods beginning in October 1998 and ending in January 1999, dehydrated molasses blocks (30% CP) were placed in locations within 3 pastures that were steeper and further from water. Forage utilization was measured at the time of supplement placement and again at removal. Increases in forage utilization during each period (14%) were similar ($P > 0.1$) at distances of 30 to 600 m from supplement, and increases were additive across periods. Forage utilization was evaluated in a fourth pasture during August and September 1999 at distances of 50 to 3,000 m from the supplement. Forage use declined ($P < 0.01$) at further distances from supplement, and forage use at distances less than 600 to 800 m from supplement was greater than the average of all measurements collected throughout the pasture. During the autumn and early winter at the 2 pastures located near Havre, Mont., 53% of the cows were observed within 600 m of supplement and 47% were observed at greater distances from supplement. Eighty-one of the 159 cows grazing the 2 pastures near Havre (245 and 330 ha) were fitted with Global Positioning System (GPS) tracking collars. The collared cows spent 37% of their time within 600 m of supplement. Uniformity of cattle grazing can be enhanced by the placement of dehydrated molasses supplement in rugged topography, and the area influenced can include distances up to 600 m from supplement.

Key Words: distribution, grazing, behavior, utilization

Uneven livestock grazing distribution is often associated with many resource concerns on rangelands. Increasing the uniformity of grazing and preventing concentrated heavy grazing in localized areas is one of the principles of rangeland management (Bell 1973). In addition to management practices such as developing water, salting, fencing and herding (Cook 1966, Bailey and Rittenhouse 1989), strategic placement of supplement has been used to modify livestock grazing distribution (Martin and Ward 1973, McDougald et al. 1989). Most commercially available supplements fed to cattle are palatable and potentially could be used to lure aimals to underutilized rangeland. Dehydrated molasses supplements are available in containers (blocks weighing up to 113 kg) that can be transported to rugged rangeland and then self fed. Most containers last up to 2 weeks before they are emptied and should be replaced to maintain intake. Bailey and Welling (1999) showed that cattle spent more time and grazed more forage in pasture areas where dehydrated molasses supplement was provided than in similar control areas where no supplement was provided. Although it was more effective in moderate terrain (10–20% slopes), strategic supplement placement noticeably changed livestock grazing patterns in steeper terrain (15–30% slopes) at greater distances from water. Ongoing work in

Resumen

La colocación estratégica del suplemento ha mostrado ser una herramienta efectiva para atraer el ganado hacia áreas subutilizadas del pastizal. La meta de este estudio fue determinar donde apacienta el ganado cuando el suplemento se coloca en los pastizales de pie de montaña. El estudio se condujo en cuatro potreros del norte de Montana dominados por zacates de estación fría. Por periodos de 2 semanas, iniciando en Octubre de 1998 y terminando en Enero de 1999, se colocaron bloques de melaza deshidratada (30% PC) en lugares dentro de los 3 potreros que eran áreas con pendiente pronunciada y lejos del agua. La utilización del forraje se midió al momento de colocar el suplemento y nuevamente al remover los bloques. Los incrementos en la utilización del forraje durante cada periodo fueron similares (14%) ($P>0.1$) en las distancias de 30 y 600 m del suplemento y el aumento fue aditivo a través de los periodos. La utilización del forraje se evaluó en un cuarto potrero durante Agosto y Septiembre de 1999 a distancias de 50 y 3,000 m del suplemento. El uso del forraje disminuyo ($P < 0.01$) conforme la distancia del suplemento fue mayor y el uso del forraje a distancias menores de 600 a 800 m del suplemento fue mayor que el promedio de todas las medidas colectadas a través del potrero. Durante el otoño e inicios de invierno en los 2 potreros localizados cerca de Havre, Mont., el 53% de las vacas se observaron dentro de una distancia de 600 m del suplemento y 47% restante se observó a distancias mayores. A 81 de las 159 vacas que apacentaban en los 2 potreros cerca de Havre (245 y 330 ha) se les colocó un collar de restero de un Sistema de Posicionamiento Global (GPS). Las vacas con collar gastaron el 37% de su tiempo dentro de 600 m del suplemento. En áreas de topografía escabrosa la uniformidad del apacentamiento del ganado se puede mejorar con la colocación de suplemento de melaza deshidratada y el área influenciada puede incluir distancia hasta de 600 m del suplemento.

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California (Mel George, personal communication) also suggests that dehydrated molasses supplement can modify cattle grazing patterns.

Although previous and ongoing research has demonstrated that strategic supplement placement can be effective, several aspects of this practice are not known. Protocols for its practical use are not in place and should be developed. Experimental procedures used in the past (Bailey and Welling 1999) would not be practical for range livestock producers. The effect of strategic supplement placement on livestock grazing distribution should be evaluated throughout the year. Bailey and Welling (1999) studied the effects of dehydrated molasses supplement on grazing distribution during the autumn and winter (October to January) when the forage was mature and dormant, but this practice also may be effective during late summer (August and September). To conduct economic evaluations of this practice, the area impacted by supplement placement must be estimated. Bailey and Welling (1999) found that forage use was similar at distances of 20 to 200 m from supplement. To determine the area impacted by a single placement, forage use must be evaluated at distances further from supplement.

Objectives of this study were to: 1) develop and evaluate a practical approach for strategic placement of dehydrated molasses supplements during late summer, autumn and early winter, 2) estimate the distance that cattle grazing distribution was affected by supplement placement. In this study, effect of supplement was initially evaluated at distances of 30 to 600 m from supplement, and distances of 30 to 3,000 m were examined later.

Methods

Study sites

The study was conducted at 3 locations in northern Montana: Thackeray Ranch, Dana Ranch, and IX Ranch. Forage measurements were collected at all locations, but animal behavior observations were collected only at the Thackeray Ranch, near Havre, Mont.

Thackeray Ranch. The Thackeray Ranch is located in the Bear’s Paw Mountains 30 km south of Havre, Mont. Two pastures were used at this study site, Rakes Draw and Anderson. The Rakes Draw pasture (48º 21'29"N 109º 34'31"W) is approximately 245 ha with elevations varying from 1,150 to 1,320 m. The Anderson pasture (48º 22'44"N 109º 37'21"W) is approximately 330 ha bisected with a perennial stream (Bull Hook Creek). Topographic relief varies from 1,055 to 1,222 m. Both pastures were dominated by Kentucky bluegrass (*Poa pratensis* L.), bluebunch wheatgrass (*Pseudoregnaria spicata* [Pursh] A Love), rough fescue (*Festuca scabrella* Torr.), and Idaho fescue (*Festuca idahoensis* Elmer). Soils were primarily shallow clays and gravelly loams.

Dana Ranch. The Dana Ranch is located 35 km south of Cascade, Mont. in rugged foothill rangeland near the Big Belt Mountains. Two study areas were established within a 4,900 ha pasture. Study areas were approximately 325 ha in size and located about 2.5 km from each other. One area was identified as Coyote (47º 01'38"N 111º 29'35"W) and the other was identified as Pine Coulee (47º 00'30"N 111º 30'00"W). The 2 study areas were evaluated simultaneously. Relief in the pasture varied from 1,220 to 1,680 m, but elevations in the study areas varied from 1,490 to 1,680 m. Study areas were dominated by timothy (*Phleum pratense* L.), rough fescue, and Kentucky bluegrass. Soils in the study area were primarily deep to shallow loams.

IX Ranch. The IX Ranch is located in the Bear’s Paws Mountains, approximately 30 km east of Big Sandy, Mont. (48º 04'55"N 109º 51'30"W). The study was conducted in a pasture (approximately 2,020 ha) containing gentle and rugged topography. Vegetation on gentler slopes (5 to 15% slopes) was dominated by Kentucky bluegrass with significant quantities of bluebunch wheatgrass, western wheatgrass (*Pascopyrum smithii* Rydb.(Love)), prairie junegrass (*Koeleria macrantha* (Ledeb.) Schult.) , and blue grama (*Bouteloua gracilis* (H. B. K.) Lag. ex Griffiths). On steeper slopes, vegetation was dominated by rough fescue and bluebunch wheatgrass. Elevation in the pasture varied from 1,100 to 1,460 m. Soils were primarily shallow to deep loams with some areas of clays.

Table 1. Nutrient concentration and ingredients of the dehydrated molasses supplement used in the study.

Nutrient	Level
	(%)
Crude protein	30.0
Not more than 12% equivalent crude protein from non-protein nitrogen	
Crude fat	4.0
Crude fiber	2.5

Ingredients: Molasses products, animal fat (preserved with ethoxquin), plant protein products, animal protein products, processed grain by-products, urea, monocalcium phosphate, dicalcium phosphate, calcium carbonate, magnesium oxide, sulfur, vitamin A acetate, D-activated animal sterol, vitamin E supplement, zinc sulfate, manganous oxide, ferrous sulfate, copper carbonate, calcium iodate, sodium selenite.

Supplement placement

Thackeray Ranch. Dehydrated molasses supplement (30% CP) was placed at a rate of 1 barrel (113 kg-block) per 20 cows (Table 1). In each pasture, 8 barrels were placed in pairs (2 barrels/site) about 30 m apart, similar to the Bailey and Welling (1999) study. Salt blocks (23 kg, >99 to 99.9% NaCl) were placed at 2 of the 4 supplement sites. The 4 supplement sites (site = 1 pair of barrels) were arranged in a rectangular pattern about 200 to 250 m between sites (Fig. 1). Supplement was not placed near water nor within extreme terrain (>40% slopes). In the Rakes Draw pasture, supplement was placed in areas classified as difficult using the criteria of Bailey and Welling (1999). Terrain classified as difficult was the usable area (<40% slopes) that contained the steeper slopes or was further from water than the moderate or easy terrain. Easy terrain was the gentle terrain near water. In the Anderson pasture, supplement was placed only in areas classified as difficult in the Bailey and Welling (1999) study.

Every 2 weeks, previously used supplement barrels were removed and full supplement barrels were placed in an adjacent area at least 250 m from the previous location (Fig. 1). Supplement was provided to cattle in the Rakes Draw pasture for three, 2-week periods (periods 1 to 3, 9 October 1998 to 26 November 1998) and in the Anderson pasture for four, 2-week periods (periods 4 to 7, 26 November 1998 to 19 January 1999).

The supplement placement pattern used in this study was based on previous experience (Bailey and Welling 1999). The purpose of placing new supplement in nearby underutilized areas was to facilitate cattle finding new supplement sites and to allow managers to progressively move supplement through underutilized sections of a pasture. Travel time to place supplement and remove empty barrels was reduced because new barrels were placed near empty barrels that needed to be picked up.

Dana Ranch. Ten dehydrated molasses supplement barrels (Table 1) were placed in each study area (i.e., Coyote and Pine Coulee) at the Dana Ranch (20 total). Supplement was placed in a rectangular pattern similar to that used at the Thackeray Ranch with the additional 2

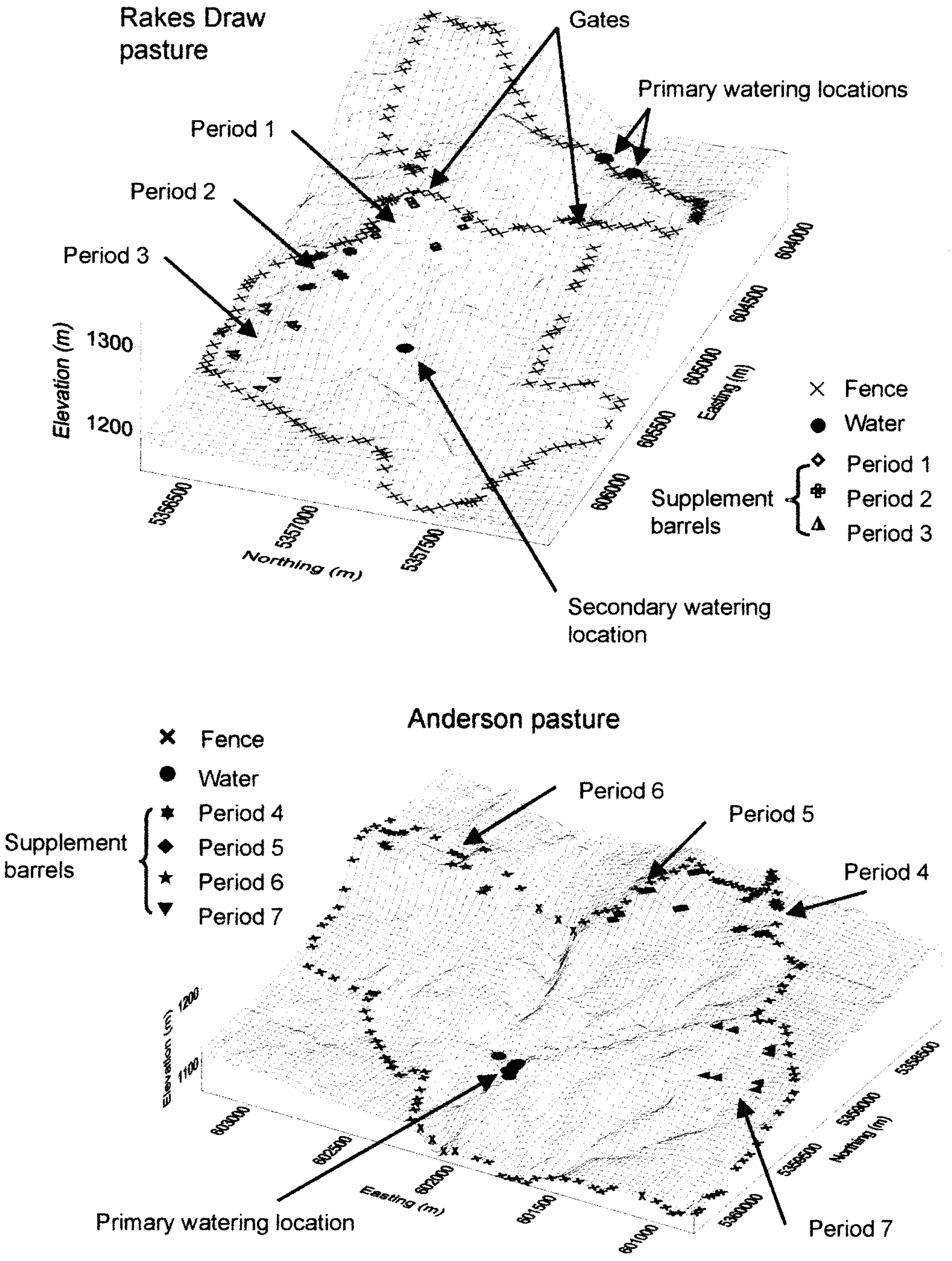

Fig. 1. Diagrams of the Anderson and Rakes Draw pastures. Fencelines are indicated by "x". Two open gates allowed cattle access to the 2 sections of the Rakes Draw pasture. Eight supplement barrels were placed during each 2-week period. In the Anderson pasture, cattle watered in Bull Hook Creek that bisects the pasture. Most cattle watered at the location marked primary watering location. In the Rakes Draw pasture cattle watered at the primary watering location. The secondary water location provided enough water for only 40 to 50 of the 159 cows in the pasture.

barrels placed in the middle of the rectangular supplement area. Salt blocks (described previously) were placed at 3 of the 5 sites (pair of barrels). New supplement barrels were placed and previously placed barrels were removed every 2 weeks. The study was conducted for three, 2-week periods in each study area beginning 4 November 1998 and ending 15 December 1998. Supplement was placed only in terrain classified as difficult (Bailey and Welling 1999).

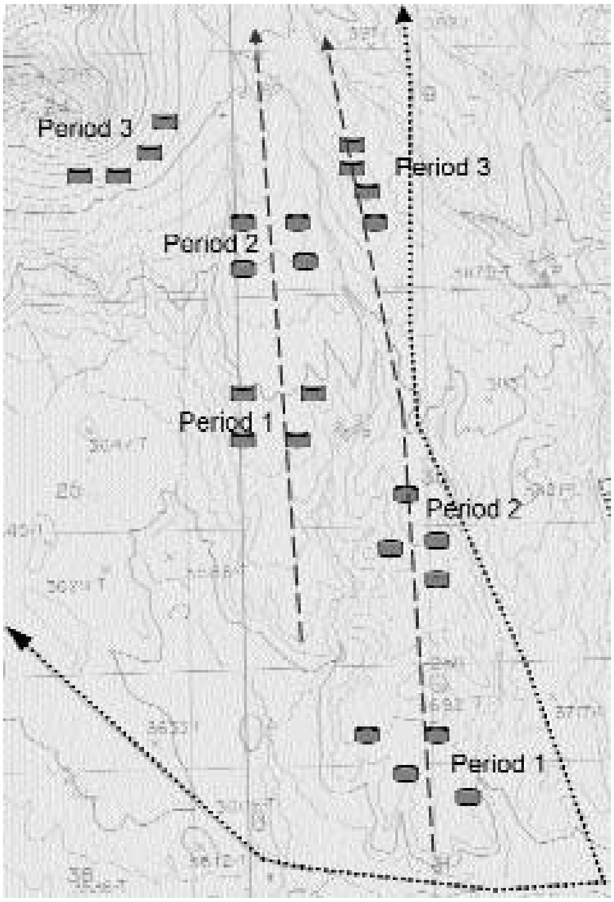

Fig. 2. Map of a portion of the pasture at the IX Ranch where the study was conducted. The map was adapted from a 7.5-minute topographic map. Contour intervals are 12 m. The pasture fence is indicated by a dotted line (….). The north-south lines where vegetative measurement transects were collected are indicated by dashed lines (----). Dark cylinders indicate the approximate locations of supplement barrel pairs. Barrels were placed in 2 general locations in each of 3 periods.

IX Ranch. The IX Ranch study was conducted after completing the studies at the Thackeray and Dana Ranches. The protocol was changed slightly to facilitate measurement of forage utilization at distances further from supplement and to fit the terrain and management goals of the ranch. At the beginning of each period (10 to 14 days), new dehydrated molasses supplement barrels (Table 1) were placed, and previously placed supplement barrels were removed. Period 1 began 12 August 1999 and ended 29 August 1999, period 2 began 30 August 1999 and ended 12 September 1999, and period 3 began 13 September 1999 and ended 23 September 1999. During each period, supplement (8 to 12 barrels) was placed in each of 2 general locations (Fig. 2). Eight to 12 barrels were placed in each location. Similar to the Thackeray and Dana Ranch studies, supplement barrels were placed in pairs in a rectangular pattern. Loose salt (99 to 99.9% NaCl) was placed in 2 separate locations roughly 200 m from water.

The study was designed so that supplement would be moved along benches in a south to north direction. The benches contained similar topography and vegetation (Fig. 2). The benches were considered easy to moderate terrain based on the criteria used by Bailey and Welling (1999), but they have historically received little grazing use (Steve Roth, personal communication). During period 3, supplement was placed on steeper terrain (> 20% slopes) near the west bench.

Cattle

The protocol for this study was approved by the Institutional Animal Care and Use Committee of Montana State University. Management was typical of northern Montana rangeland cattle operations. Two of the ranches (Dana and IX) were large commercial cow-calf operations (>1,500 AU) that utilized extensive rangeland pastures. Cattle were treated at least annually for external parasites and may or may not have been treated for internal parasites. Treatment for internal parasites did not affect performance of rangeland beef cows in northern Montana (Bailey et al. 1997). Vaccination programs were based on recommendations from local veterinarians.

Thackeray Ranch. A total of 159 cow-calf pairs of Hereford and Tarentaise breeding were provided dehydrated molasses supplement for 2 weeks before the study (14 September 1998 to 30 September 1998) to reacquaint them with the supplement. These cows had 1 year's previous experience with dehydrated molasses supplement in the Bailey and Welling (1999) study. Mean cow weight during the study was 590 kg. Cow age averaged 5 year and varied from 3 to 8 year. Calves were weaned on 1 October 1998 at the Thackeray Ranch, and the study began on 9 October 1998 in the Rakes Draw pasture. Cows were moved from the Rakes Draw to the Anderson pasture on 26 November 1998. Cows were moved from Anderson pasture and the study ended on 19 January 1999.

Dana Ranch. Approximately 1200 non-lactating cows with Angus and Angus x Hereford breeding were placed in the pasture on 4 November 1998. Although the study ended on 15 December 1998, cattle remained in the pasture until mid-March 1999. Cattle had been exposed to dehydrated molasses supplement for 4 consecutive years before this study, including the Bailey and Welling (1999) study in 1997.

IX Ranch. Cow-calf pairs (n = 824) with Hereford and Red Angus breeding grazed the study pasture from 12 August 1999 to 23 September 1999. Cattle had not been exposed to dehydrated molasses supplements prior to the study. To initially train the cattle, 12 barrels of dehydrated molasses supplement were placed near water (100 to 400 m) in separate pastures from 1 August 1999 to 12 August 1999.

Forage measurements

Thackeray and Dana Ranches. Forage use was measured before placement and after supplement removal at 2 randomly selected locations within the rectangular barrel pattern. Measurements also were obtained at distances of 200, 300, 400, 500 and 600 m from supplement (Fig. 3). The 200-, 400-, and 600-m measurements were repeated in 2 directions away from the rec-

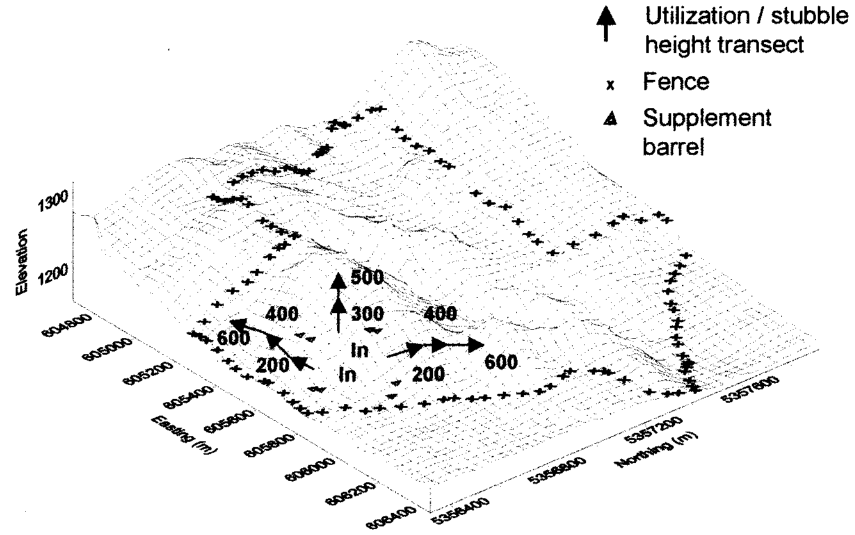

Fig. 3. Example of forage utilization and stubble height measurements in period 3 (third barrel placement) in the Rakes Draw pasture. Utilization/stubble height transects began at distances of 200, 300, 400, 500, and 600 m from supplement as indicated by the end of the arrow. In addition, 2 transects (identified as "In") were completed inside the rectangular barrel pattern.

tangular supplement placement pattern along the contour. The measurements 300 and 500 m from supplement were collected along a line perpendicular to the 200-, 400-, and 600-m measurements. Forage measurements at each interval consisted of measuring the stubble height of 20 grass plants along a 40-m transect (2 m between plants). The beginning and end of each transect was marked with plastic surveyor flags to help ensure that measurements before and after supplement placement were collected in the same location. The slope at each transect was recorded using an inclinometer. Observers were trained to measure the intervals between transects and measure the 2-m intervals between stubble height readings using steps so that the measurements could be collected in a reasonable amount of time. Stubble heights were converted to forage utilization levels using height-weight curves (Cook and Stubbendieck 1986). Ungrazed heights were measured before grazing when supplement was first placed in the pastures. Height-weight curves were developed for major species (Kentucky bluegrass, rough fescue, and timothy) and published relationships (US Forest Service 1980) were used for other grasses.

In the Anderson pasture, deep snowdrifts prevented retrieval of supplement at the end of period 6. Additional supplement was placed in a new location (opposite side of the pasture) during period 7 (Fig. 1). Forage measurements for the supplement placed during period 6 were collected at the beginning of period 6 and the end of period 7.

Standing crop was measured before grazing by clipping to ground level randomly placed 0.09 m^2 plots. Clipped forage was separated into current year's growth of grass and forbs and the previous year's standing vegetation (standing dead). Forage was dried for 48 hours at 50° C and weighed. Clipped grass samples were ground to pass a 1-mm screen and analyzed for nitrogen content using a micro-kjeldahl process (AOAC 1990).

IX Ranch. Forage measurements were identical to those used for the Thackeray and Dana Ranches except for the following differences. Forage use was measured every 200 m along 2 south to north lines that roughly bisected each of the benches where the supplement was placed (Fig. 2). This allowed forage use to be evaluated at distances of 30 to over 3,000 m from supplement. Intervals were estimated by pacing or by an odometer and were not marked. At each interval, stubble height of 15 plants was measured along a 30 m transect (1 plant every 2 m).

At the end of the final period, additional forage utilization measurements were collected along 2 lines running east and west across the pasture, perpendicular to the north-south lines (Fig. 2). These 2 lines were south of the steeper terrain found on Ryan Butte (Fig. 2). Forage use measurements were also collected in a line west of the supplement placed on the southern slope of Ryan Butte and included steeper slopes (> 20%). In addition, forage utilization was observed at 14 randomly-selected locations throughout the entire pasture. All of these additional forage utilization measurements were collected using the protocol described above.

Grazing behavior—Thackeray Ranch

Horseback observations. The location of cows within the study pastures was recorded 2 times per week by observers on horseback, usually once in the morning and once in the afternoon. Pastures were divided into map units (1 to 6 ha), based on slope, aspect, elevation, and distance to water. The number of cows in each map unit was recorded during each observation. Average distance from supplement and water were calculated by measuring the distance from the map unit to supplement and water locations on scaled maps. In addition, the number of cows at supplement barrels (< 30 m) was recorded.

GPS collars. Cattle were fitted with Lotek GPS 2000 collars (Lotek Engineering, Newmarket, Ontario) that record the location of cattle within 5 to 12 m (Moen et al. 1997). Seven to 12 collars were available to track cattle. At the beginning of the study, 4 randomly selected cows were fitted with collars that were powered with disposable batteries capable of recording and storing 3,000 locations. These 4 cows were tracked at 10-minute intervals for 10 days (7 days during period 1 and 3 days in period 2). At the end of period 1, cattle were tracked with collars powered by rechargeable batteries capable of recording and storing 500 to 1,000 locations during mild to moderate temperatures. At cold temperatures (consistently <–12°C) collars with rechargeable batteries generally recorded and stored 150 to 300 locations. Because of the variation in collar performance, locations were sampled with several sampling schedules. Initial performance of the rechargeable batteries allowed sampling intervals to be changed to every 5 minutes during the day and every 10 minutes at night. Later as performance declined, the sampling interval was changed back to every 10 minutes. During the last 2 periods in late December and January, the schedule was changed to every 15 minutes during the day and every 30 minutes at night to extend battery life during cold weather.

A total of 81 randomly-selected cows were tracked during the study. Collars

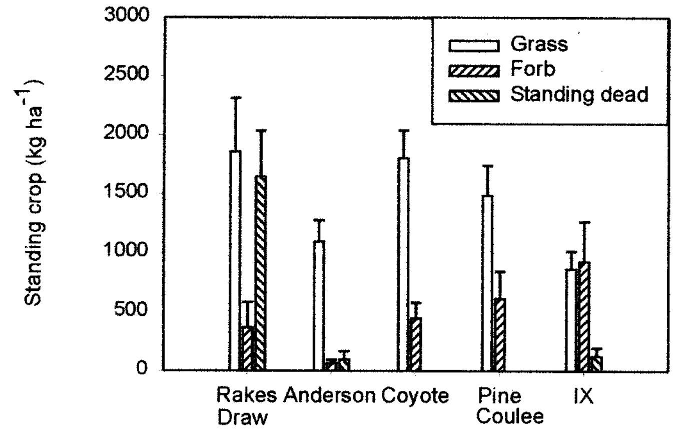

Fig. 4. Standing crop of current year's growth of grasses and forbs and previous years' vegetation (standing dead) at the Thackeray Ranch (Rakes Draw and Anderson pastures), Dana Ranch (Coyote and Pine Coulee sites) and IX Ranch. Standing dead vegetation could not be distinguished at the Dana Ranch and forage was pooled into grass and forbs.

were placed on sets of cows 9 different times. For each set of cows (7 to 12 animals), individual cow locations usually were recorded for 4 or 5 days. Then collars were removed, and the data were downloaded to a computer. Batteries were recharged, and collars were prepared and placed on another set of cows. These cycles from placement on 1 set of cows to placement on the next set took 7 to 9 days.

The location of supplement barrels were recorded with an 8-channel, L-Band GPS receiver with ± 1 m positional accuracy (Omnistar, Houston, Tex.). Locations of fence boundaries, gates, water and terrain features were also mapped with this GPS receiver.

Statistical analyses

Forage measurements—Thackeray and Dana Ranches. Changes in forage use and stubble height from the beginning to the end of a period (before supplement placement and after removal) were regressed on distance to supplement and slope (SAS 1985). Distance to water was not included in these analyses because it was highly correlated with distance to supplement. Changes in forage use also were regressed on distance to supplement alone. The 4 study sites (Anderson and Rakes Draw pastures and Coyote and Pine Coulee areas) were analyzed separately and included data from all periods.

Forage measurements—IX Ranch. Similar statistical procedures were used for the IX Ranch data except that distance to water was added to the multiple regression model. Changes in forage use and stubble height were regressed on distance to supplement, distance to water and slope. Data from each period were analyzed separately to determine if the relationships were consistent from the beginning to the end of grazing in the pasture.

In addition to evaluating changes in forage use from the beginning to end of a period, all use observations collected at the end of period 3 were examined in a separate analysis to determine the overall effect of supplement placement. Distance to supplement, distance to water and slope were used as independent variables. Separate simple regression models also were used to individually evaluate effects of distance to supplement, distance to water and slope on forage utilization. Distance to supplement in the final use analyses refers to distance to nearest supplement during any of the 3 periods.

Grazing behavior—Thackeray Ranch. Distances that cattle were observed from supplement (horseback and GPS data) were analyzed using chi-square procedures (Lehner 1979). The observed frequencies of cattle located at 200-m increments from supplement were compared to expected values using a goodness of fit test. Expected values were determined by multiplying the proportion of the pasture that each incremental distance comprised by the total number of cows observed at all distances from supplement. The size (ha) of each incremental distance from supplement was estimated using a planimeter within the geographical information system (ArcViewTM, ESRL, Redlands, Calif. Each cow location recorded by an observer was considered an observation. For the horseback observations, each pasture was analyzed separately. For GPS collar data, each cow during a period was considered an observa-

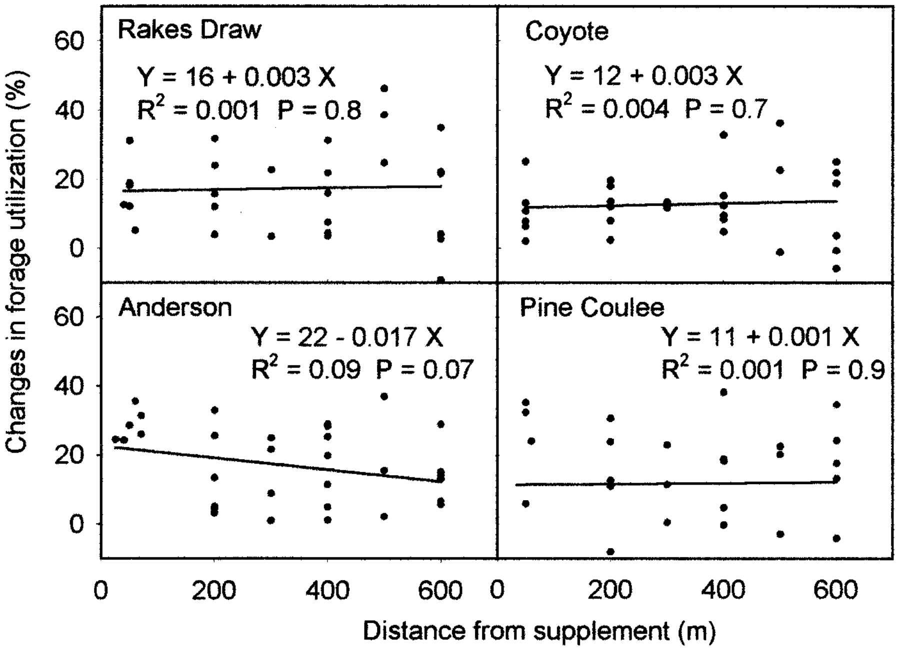

Fig. 5. Scatter plot of changes in forage utilization versus distance from supplement in the Rakes Draw and Anderson pastures at the Thackeray Ranch and Coyote and Pine Coulee study areas at the Dana Ranch. Changes in forage utilization were not related (P > 0.05) to distance to supplement.

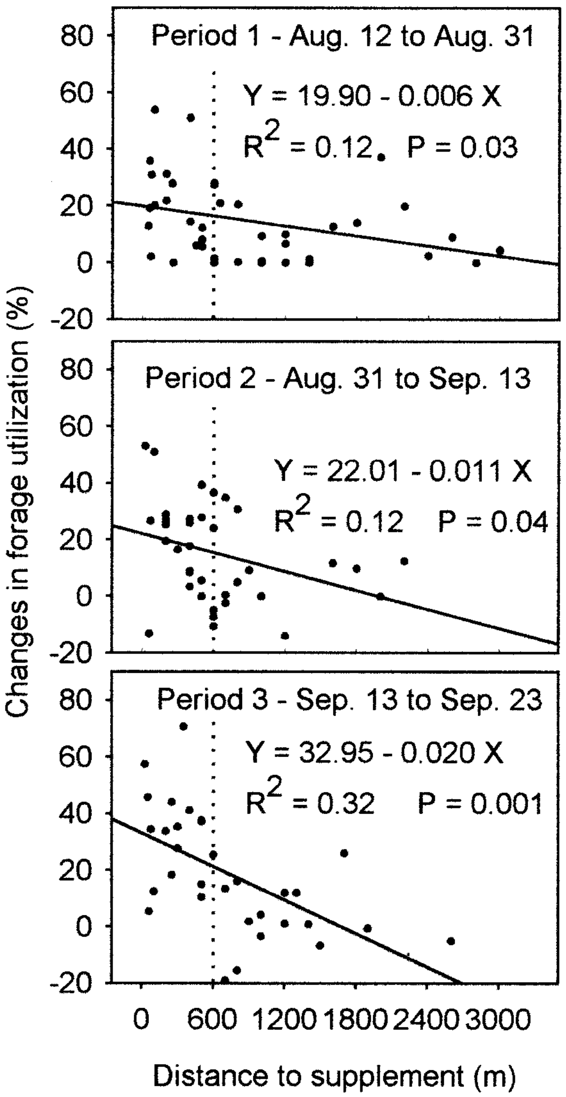

Fig. 6. Scatter plot of changes in forage utilization and distance to supplement during periods 1, 2, and 3 at the IX Ranch. Changes in forage utilization were related (P < 0.05) to distance to supplement during all periods.

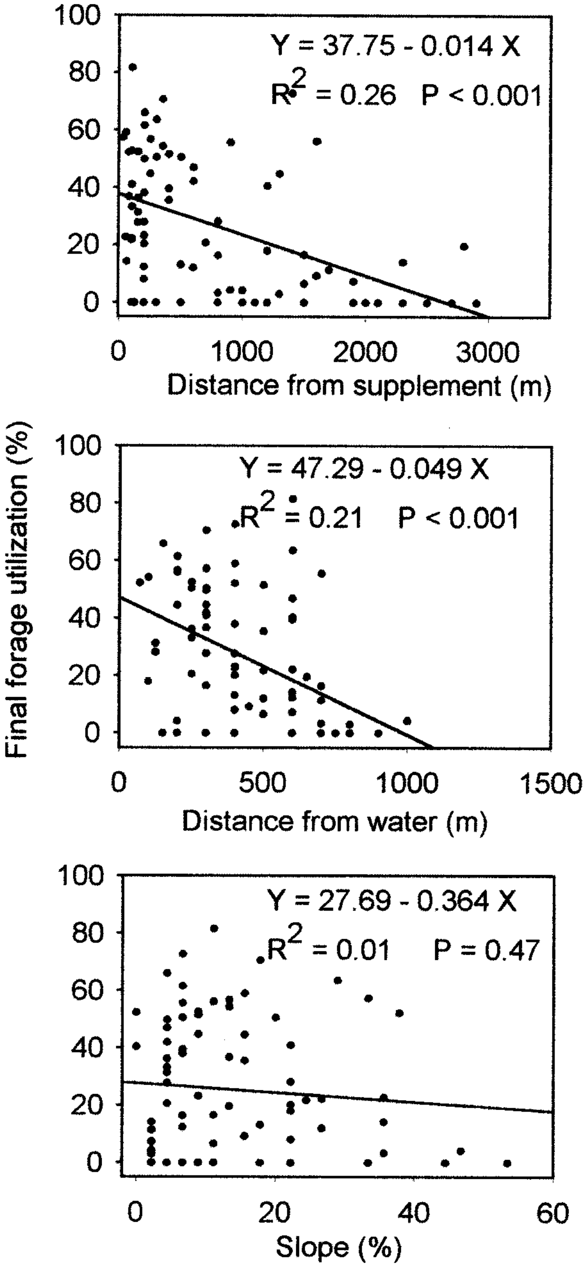

Fig. 7. Scatter plot of final utilization values and distance to supplement, distance to water and slope at the IX Ranch.

tion, and data for a cow during a period were averaged. Some cows (n = 24) were observed in 2 periods, and the data from each period was considered a separate observation. The rationale for considering them separate observations was that the supplement was placed in different locations during each period (Fig. 1).

Results

Vegetation measurements

Initial forage conditions. At the Thackeray Ranch, mean total standing crop (current year's growth of grass and forbs) in the Rakes Draw pasture was 2,230 kg ha^{-1} (Fig. 4). This pasture had not been grazed since July 1997 and contained a large quantity of previous years' vegetation (standing dead). The Anderson pasture had been grazed for 10 days in May 1998 and the total standing crop was about 1170 kg ha^{-1}. Little standing dead vegetation was observed in the Anderson pasture. Mean standing crop at the Dana Ranch was 2,180 kg ha^{-1}. We were unable to distinguish standing dead at the Dana Ranch, and any standing dead vegetation was pooled into the grass and forb categories. At the IX Ranch, mean standing crop was 1,790 kg ha^{-1} with a large forb component and little standing dead vegetation.

Forage generally was dormant during autumn 1998 at the Thackeray and Dana Ranches and the nutritive value as measured by crude protein (CP) was consistently low. Crude protein concentration of grass at the Dana Ranch was 4.5% in the Coyote study area and 5.7% in the Pine Coulee study area at the beginning of the study (4 November 1998). At the end of the study (17 December 1998), forage CP concentration in the 2 study areas aver-

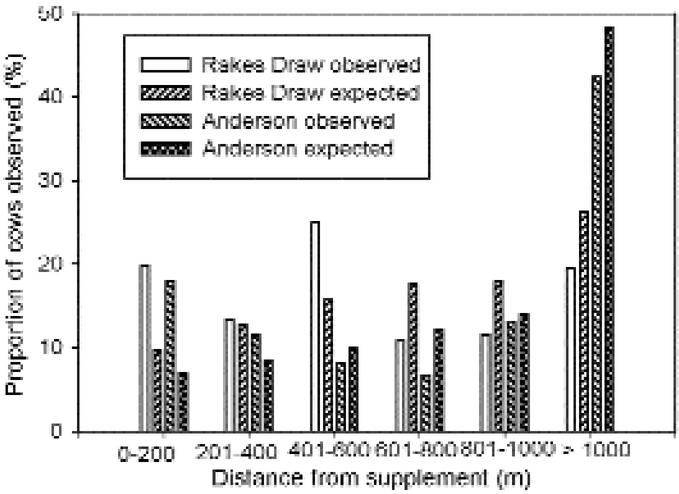

Fig. 8. Mean number of cattle at varying distances from supplement observed by horseback observers. Expected values reflect the proportion of the pasture that the incremental distance from supplement represents and the number of cattle observed. A total of 159 cattle grazed in both pastures. Grazing patterns differed from expected values ($P < 0.05$).

aged 4.1%. In the Rakes Draw pasture during October 1998, mean CP concentration of the current year's grass growth was 6.5% and 4.4% for the bottoms and slopes, respectively. In the Anderson pasture during November 1998, mean CP concentration of the current year's grass was 5.4%.

Forage utilization—Thackeray and Dana Ranches. In all study areas, changes in forage utilization and stubble height were similar ($P > 0.05$) at all distances from 30 to 600 m (Fig. 5). Slope of terrain where vegetation was measured did not influence ($P > 0.1$) change in forage use or stubble height. The mean increase in forage utilization was 14 percentage points during a period, but individual forage-utilization measurements varied by more than 20 percentage points at every distance measured in every study area (Fig. 5). Stubble heights decreased by an average of 20 cm within a period.

Forage utilization—IX Ranch. Using the multiple regression model, changes in forage utilization and stubble height were related ($P < 0.01$) to distance from supplement (30 to 3,000 m) during periods 2 and 3, but in period 1 there was no relationship ($P > 0.1$). Changes in forage utilization and stubble height were not related ($P > 0.1$) to distance to water and slope during any period. If distance to water and slope were removed from the model, changes in forage utilization decreased ($P < 0.01$) as distance from supplement increased in all 3 periods (Fig. 6).

Final forage utilization (end of period 3) decreased with distance to supplement ($P < 0.001$), distance to water ($P = 0.02$) and slope ($P = 0.09$) in the multiple regression analysis. Individual regressions of changes in forage utilization on distance to supplement, distance to water and slope (simple linear regression, Fig. 7), were similar to the multiple regression analyses except that the relationship between forage utilization and slope was no longer important ($P = 0.47$).

Cattle observations—horseback

Observations near barrels. In the Rakes Draw pasture, the mean number of cows observed at the 8 supplement barrels was 12, or 1.5 cows per barrel. In the Anderson pasture, the mean number of cows observed at barrels was 6, or 0.75 cows per barrel. The number of cows observed at all 8 barrels ranged from 0 to 24 total animals or 0 to 3 cows per barrel in Rakes Draw. The range of cows at all 8 barrels in the Anderson pasture was 0 to 20 cows, or 0 to 2.5 cows per barrel. The number of cows observed at the barrels was similar ($P > 0.1$) in the morning and afternoon.

Entire pasture observations. During the study, an average of 86% of the herd was observed. Cattle were not distributed uniformly ($P < 0.001$) across pastures (Fig. 8). In both the Rakes Draw and Anderson pastures, 18% of cows were within 200 m of supplement, and these areas made up 10% and 7% of the pasture acreage, respectively. In the Rakes Draw pasture, 58% of the cows were observed within 600 m of supplement (38% of the pasture). In the Anderson pasture, 38% of the cows were observed within 600 m of supplement (26% of the pasture).

GPS collar observations

Collared cows spent about 17% of their time within 200 yards of supplement in the Rakes Draws pasture and about 16% of their time in the Anderson pasture (Fig. 9). Cattle use of the areas between 0 to 200, 201 to 400, 401 to 600, and greater than 600 m from supplement was not different from what would be expected by chance ($P > 0.05$). Collared cows spent 40% and 33% of their time within 600 m of supplement in the Rakes Draw and Anderson pastures, respectively (Fig. 9).

Discussion

Forage utilization

Utilization levels. During the autumn and winter at the Thackeray and Dana Ranches, areas within 600 m of dehydrated molasses received grazing use by cattle even though the supplement sites were located on some of the steepest terrain and furthest areas from water. The mean increase in forage utilization in this study (14 percentage points) was similar to the 11 percentage point increase observed by Bailey and Welling (1999) in the same or similar pastures.

Forage utilization measurements show that cattle continued to forage in previously grazed areas as long as the areas remained within 600 m of supplement. In this study supplement was usually moved to an adjacent area 250 to 400 m from the first location (Fig. 1). Since change in forage utilization was consistent at all distances from supplement, forage utilization increased 20 to 30 percentage points during a month (2 periods) when supplement was nearby. So long as forage utilization is less than acceptable levels (40 to 55%), placing supplement adjacent to undergrazed sites will likely encourage cattle to graze nearby.

Slope and distance to water. In contrast to other studies (Valentine 1947, Mueggler 1965, Cook 1966), slope and distance to water did not consistently affect forage utilization. Utilization measurements were not collected in areas where slopes exceeded 40%. At the IX Ranch where distance to water was used as a variable, the pasture was well watered, and cattle had to travel less than 800 m to reach water in most of the pasture.

Area affected by supplement

For economic analyses of supplement placement on cattle grazing distribution, the extent of effects of supplement placement must be estimated. The relationships

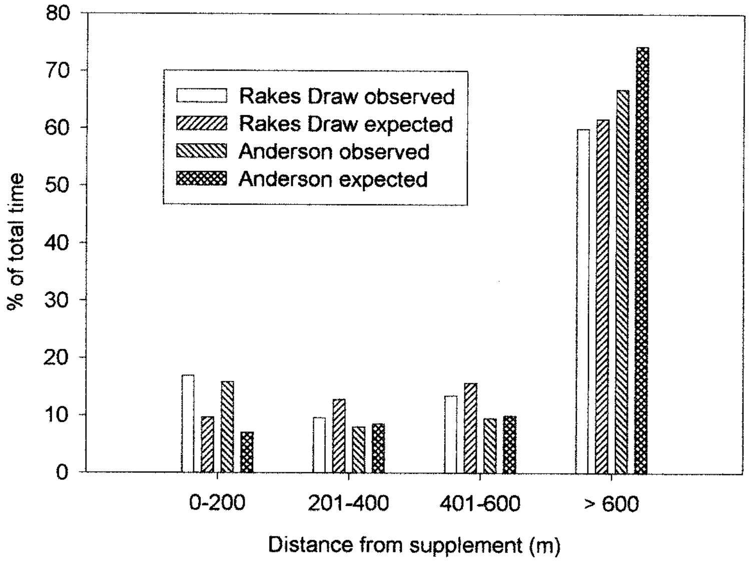

Fig. 9. Average use of terrain at varying distances from supplement by GPS collared cows in the Rakes Draw and Anderson pastures. Values are averages of individual collared cows (n = 81). Expected values reflect the proportion of the pasture that the incremental distance from supplement represents. Grazing patterns did not differ (P > 0.05) from expected values.

between changes in forage use and distance from supplement at all 3 locations (ranches) were used to estimate the distance to which 8 to 12 barrels (907 to 1,361 kg) of supplement might affect cattle grazing patterns. Bailey and Welling (1999) found forage use was relatively consistent for distances from 20 to 200 m from supplement. In contrast to our initial expectations, overall forage use at the Thackeray and Dana Ranches was relatively consistent for distances up to 600 m. We expected a decline in forage use at 300 to 600 m from supplement. An additional study was conducted at the IX Ranch to estimate the furthest distance beyond which supplement would not affect cattle grazing patterns.

Unlike the results observed at Thackeray and Dana Ranches, forage use decreased linearly with increasing distance from supplement at the IX Ranch. Forage measurements were collected at distances greater than 2,000 m from supplement at the IX Ranch but at the other ranches measurements were not collected at distances greater than 600 m from supplement. When observations greater than 600 m from supplement were excluded from the analyses of IX Ranch data, the relationship between change in forage utilization and distance to supplement was not important (P > 0.1) for any period.

At the IX Ranch during period 1, the predicted change in forage utilization equaled the average measured change in forage utilization at 815 m from supplement. At distances greater than 815 m from supplement, the predicted change in forage use was less than the average observed. Thus, grazing distribution was not affected at distances of greater than 815 m from supplement during period 1.

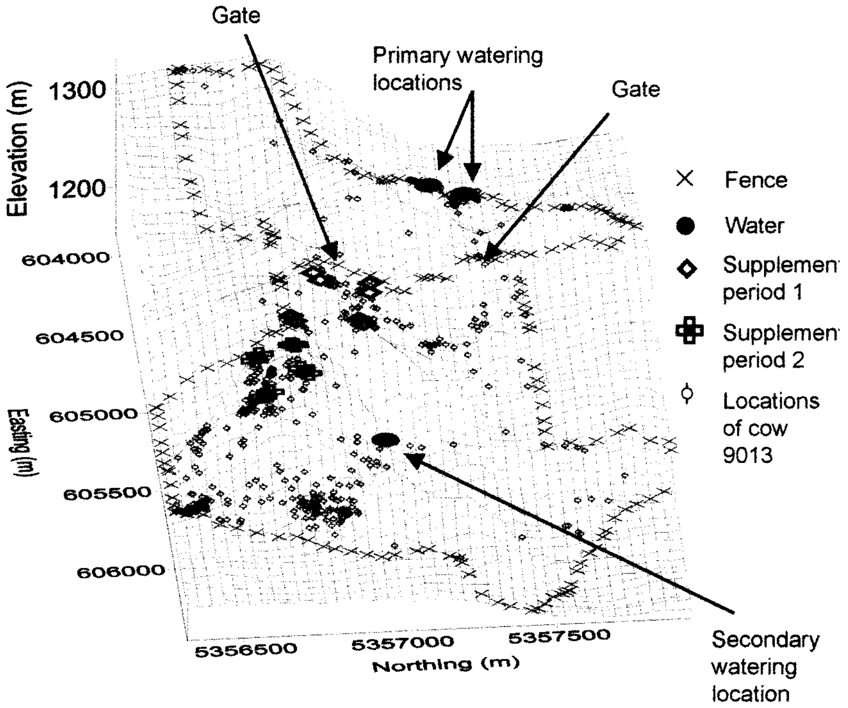

Fig. 10. Locations of cow 9013 the last 4 days of period 1 and the first 2 days of period 2 in the Rakes Draw pasture. Locations were recorded at 10 minute intervals using GPS collars.

For period 2, the predicted change in forage utilization equaled the average measured change in forage utilization at 638 m from supplement. For period 3, predicted change in forage use equaled the average observed change in forage use at 725 m from supplement. During all 3 periods at the IX Ranch, cattle were not lured to areas further than 600 to 800 m from supplement. The consistency of the response to supplement from 30 to 600 m at the Thackeray and Dana Ranches and the estimated end of influence after 600 m at the IX Ranch suggests that the area that cattle were lured to graze by a single placement of supplement included areas up to 600 m, but the effect of supplement on grazing patterns rapidly declined at distances greater than 600 m and ended before 800 m from supplement.

Effective seasons of use

Previous work with dehydrated molasses supplement to modify grazing distribution was conducted during the autumn and winter (Bailey and Welling 1999). Results from this study using nonlactating cows during the autumn and winter resulted in similar grazing patterns observed in the earlier study. At the IX Ranch, the decline in forage use at distances further from supplement demonstrated that dehydrated molasses supplement can effect grazing patterns of cow-calf pairs during August and September. Many concerns with livestock grazing in riparian and other areas occur during late summer (DelCurto et al. 1999).

Cattle location

Observations of cattle location corresponded well with vegetative measurements. Horseback observations showed that 18% of the cows were observed within 200 m of supplement and that cattle used areas further than 600 m from supplement less than expected by chance. Less than 20% of the cows were observed within 200 m of the primary water source. Data from GPS collars also showed that cattle distributed themselves relatively evenly from 0 to 600 m from supplement (e.g., Fig. 10). In the Bailey and Welling (1999) study about 30% of the cattle were observed in the areas (subunits) with supplement and only 3% were observed in control areas. Control areas were separated from areas with supplement in the Bailey and Welling (1999) study. In the Rakes Draw pasture, cattle utilized almost all of the difficult terrain near supplement, about 25% of the total area. Historically, this area of the pasture had received little grazing use by cattle.

At the IX Ranch, cattle historically used the western half of the pasture. Over 80% of the cattle were gathered from the western half of the pasture, and less than 20% were found on the eastern half (Steve Roth, personal communication). At the end of this study, the majority of the cattle (over 55%) were gathered on the eastern half of the pasture. This anecdotal observation is consistent with the vegetative measurements that show that cattle grazed more near supplement placed in the eastern half of the pasture.

Conclusions and Implications

When dehydrated molasses supplement was placed in rugged foothills rangeland, cattle grazed nearby areas relatively evenly for distances of 0 to 600 m from supplement. If evaluated at distances greater than 600 m, forage use declined linearly with increasing distances from supplement. Placement of 8 to 12 barrels (113 kg/barrel) of dehydrated molasses supplement affects cattle grazing patterns for distances up to 600 m, but the influence rapidly declines beyond 600 m. Supplement should not be expected to lure cattle to areas beyond 600 to 700 m from placement.

Placing dehydrated molasses supplement in undergrazed rangeland was an effective tool to modify cattle grazing distribution during late summer, autumn, and winter. Supplement should be placed in undergrazed rangeland within a limited area (5 to 15 ha in this study). When the supplement is consumed, new supplement should be placed in an adjoining undergrazed area. All cattle used to evaluate dehydrated molasses supplement in this study had been exposed to the supplement before the study began. Supplement may not be effective if cattle are not exposed to the supplement before it is placed in undergrazed rangeland.

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Complementary grazing of native pasture and Old World bluestem

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Abstract

Native pasture and Old World bluestems (*Bothriochloa* spp.) have contrasting herbage production characteristics that suggest potential for incorporation into a complementary forage system. We compared 2 yearling beef production systems consisting of either native pasture (Native) or Old World bluestem combined with native pasture (Old World bluestem-Native) over 5 years. Crossbred steers (initial weight 257 kg) grazed only native pasture in the Native system, but alternated between Old World bluestem and native pastures in the Old World bluestem-Native system. Production system had no effect on the frequency of any plant species in the native pastures ($P > 0.16$) even though stocking rate in the growing season was increased 31% in the Old World bluestem-Native system. Peak standing crop of Old World bluestem averaged 4640 kg ha^{-1} but did not differ between the cultivars 'WW-Iron Master' and 'WW-Spar' ($P = 0.16$). Individual steer gain was higher in the Native system during the Winter ($P < 0.01$) and Early Native ($P = 0.03$) management periods, but was greater in the Old World bluestem-Native system when steers were grazing Old World bluestem in June and July ($P < 0.001$). Over the entire season, steers in the Native system gained 13.5 kg head^{-1} more than steers in the Old World bluestem-Native system. Total livestock production was greater in the Old World bluestem-Native system (77 versus 47 kg ha^{-1}, $P < 0.01$). Relative economic returns between the 2 systems were dependent on the marginal value of livestock gain and the relative costs of production for the 2 types of pasture. With average costs for native pasture of \$17 ha^{-1} and for Old World bluestem pasture of \$62.10 ha^{-1}, the Native system was often more profitable, even though livestock production per ha was much higher with the Old World bluestem-Native system. Lower costs for native pasture and high values of livestock gain favored the Native system.

Key Words: mixed prairie, complementary forages, Old World bluestem, *Bothriochloa*, livestock performance

Resumen

Las praderas nativas y los zacates "Old World bluestems" (*Bothriochloa* spp.) tienen características de producción de forraje contratantes que sugieren un potencial para incorporarlos en sistemas complementarios de producción de forraje. Durante 5 años comparamos dos sistemas anuales de producción de carne consistentes de pradera nativa (Nativa) o "Old World bluestem" combinado con pradera nativa ("Old World bluestem"- Nativa). Novillos cruzados (peso inicial de 257 kg) apacentaron solo pradera nativa en el sistema Nativa y en el sistema "Old World bluestem'-Nativa alternaron entre "Old World bluestem" y pradera nativa. El sistema de producción no tuvo efecto en la frecuencia de ninguna de las especies de la pradera nativa ($P > 0.16$) a pesar de que en el sistema "Old World bluestem"- Nativa la carga animal se incremento en 31% durante la estación de crecimiento. El pico de máxima producción de forraje en pie del "Old World bluestem" promedio 4,640 kg ha^{-1}, pero no difirió entre los cultivares 'WW-Iron Master' y 'WW-Spar' ($P = 0.16$). La ganancia individual por novillo fue mayor en el sistema Nativa ($P < 0.01$) durante el invierno y durante los periodos de manejo tempranos($P = 0.03$), pero fue mayor en el sistema "Old World bluestem"- Nativa cuando los novillos apacentaron en "Old World bluestem"en Junio y Julio ($P < 0.001$). A lo largo de la estación completa, los novillos en el sistema Nativa ganaron 13.5 kg cabeza^{-1} mas que los novillos del sistema "Old World bluestem"-Nativa. La producción total fue mayor en el sistema "Old World bluestem"- Native (77 versus 47 kg ha^{-1}, $P < 0.01$). Los retornos económicos relativos entre los dos sistemas fueron dependientes del valor marginal de la ganancia del ganado y los costos relativos de producción para los dos tipos de sistema. Con costos promedio de \$17 ha^{-1} en la pradera nativa y de \$62.10 ha^{-1} en la pradera de "Old World bluestem", el sistema Nativa fue mas rentable, a pesar de que la producción del ganado por ha fue mucho mas alta en el sistema "Old World bluestem"- Nativa. Los bajos costos de la pradera nativa y el alto valor de la ganancia del ganado favorecieron al sistema Nativa.

Complementary forage systems combine different types of forages in an effort to overcome deficiencies in seasonal production and nutrient content that are inherent in any single forage. Major advantages of complementary forage systems include more efficient use of each individual forage, improved range condition, and higher overall stocking rates. The complementary forage system is one of the few grazing management methods that can substantially increase livestock production from forage-livestock systems in the Great Plains (Launchbaugh et al. 1978, Sims and Bailey 1995).

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Old World bluestems (*Bothriochloa* spp.) and native pasture have potential as components of a complementary forage system. Old World bluestems are highly productive warm-season grasses that respond well to nitrogen fertilization (Berg 1990). However, 70% of their growth occurs during the month of June and nutritive value declines rapidly (White and Dewald 1996). Old World bluestem starts rapid growth about 4 weeks later than native pasture. Native mixed prairies are dominated by warm-season grasses but also have a moderate component of cool-season grasses including annual bromegrasses (*Bromus* spp.) and, on sandy soils, Texas bluegrass (*Poa arachnifera* Torr.) Integration of Old World bluestem and native pasture could allow the capture of the short-term, high productive potential of Old World bluestem and the earlier spring growth of native prairie into a more feasible production system for stocker cattle.

Our objective was to compare steer production systems based wholly on native pasture or a combination of native and Old World bluestem pastures. Specific interests centered on the impact on the native pastures and on livestock production, the performance of 2 cultivars of Old World bluestem, and the relative net returns from the 2 systems.

Materials and Methods

This study was conducted from 1993 through 1997 at the USDA-ARS Southern Plains Range Research Station in northwest Oklahoma (36° 35'N, 99° 35'W, elev. 630 m). The regional climate is continental. Average annual precipitation is 560 mm with 72% falling during the April–September growing season. Average monthly temperatures are 2.3°C in January and 28°C in July. Minimum and maximum recorded temperatures are –27°C and 45°C.

Two major types of pastures were included in this study. The first type consisted of native sand sagebrush (*Artemisia filifolia* Torr.)-mixed prairie growing on deep sandy soils on gently undulating, stabilized dunes (Berg 1994). Pratt soils (sandy, mixed thermic Psammentic Haplustalfs) were on the lower slopes and more level areas, and Tivoli soils (mixed, thermic Typic Ustipsamments) occurred on the upper slopes. A mixture of tall, mid, and short warm-season grasses dominated the vegetation. Applications of 2,4-D (2,4-dichlorophenoxyacetic acid) in the 1970's and 1980's had reduced canopy cover of sand sagebrush to less than 5% on the study pastures. All study pastures were contiguous.

The second pasture type was a monoculture of the introduced grass Old World bluestem (*Bothriochloa ischaemum* L.). Two different cultivars of Old World bluestem, 'WW-Spar' and 'WW-Iron Master,' were studied. The WW-Spar pastures were seeded in 1980 and the WW-Iron Master pastures were seeded in 1983. Both cultivars were seeded on Pratt fine sandy loams. Prior to seeding to Old World bluestem, these fields supported monocultures of various forage grasses or short-term (3 year) production of winter wheat since 1940. Old World bluestem pastures were located within 1 km of the rangeland pastures.

The Old World bluestem pastures were burned each spring in early to mid April to remove dead standing forage. We did not burn these pastures in the spring of 1996 because of low precipitation and high fire danger throughout the spring. Nitrogen was applied at a rate of 67 kg N ha^{-1} as ammonium nitrate in the third or fourth week of April each spring. Broadleaf weeds, primarily horseweed [*Conyza canadensis* (L.) Cronq.], were controlled with 0.56 kg ha^{-1} 2,4-D on 13 June 1995 and with 0.84 kg ha^{-1} 2,4-D on 13 June 1997. No cultural practices were applied to the rangeland pastures.

Experimental treatments consisted of 2 basic production systems. The first system contained only native pasture (Native). The second system combined Old World bluestem and native pasture (Old World bluestem-Native). Within the Old World bluestem-Native system, there were 2 subsystems differing only in the variety of Old World bluestem they contained. One sub-system contained WW-Spar and the second contained WW-Iron Master. There were 2 replications of each of the 3 systems or subsystems for a total of 6 experimental units. The experimental units for the Native treatment were approximately 20 ha in size. Each experimental unit for the Old World bluestem-Native treatments consisted of a 20-ha rangeland pasture matched with a 2.6-ha Old World bluestem pasture.

The grazing season was divided into 4 periods. Average dates for these periods were: a) Winter, 21 December to 15 March (84 days); b) Early Native, 15 March to 9 June (86 days); c) Old World Bluestem, 9 June to 30 July (51 days); and d) Late Native, 30 July to 31 August (32 days). The total grazing season averaged 253 days. In the Native system, steers grazed native pasture for the entire grazing season. In the Old World bluestem-Native system, steers grazed Old World bluestem during the Winter and Old World Bluestem periods and native pasture in the Early Native and Late Native periods.

Stocking rates for the native pastures were based on a moderate stocking rate of 3.9 ha steer^{-1} for 320 days or about 53 steer-days ha^{-1} (Sims and Gillen 1999). Our stocking rate was also 53 steer-days ha^{-1} with a land allowance of 3.2 ha steer^{-1} and a grazing season of 253 days. This stocking rate should maintain plant vigor over years. Information on forage and livestock production on Old World bluestem over a range of stocking rates is not available. However, the stocking rate chosen for this study has been tested for this environment and determined to be sustainable over years (Berg and Sims 1995).

Six yearling beef steers were allocated to each experimental unit for the Native system and 12 steers were allocated to each Old World bluestem-Native unit. Steers were typical crossbred yearlings (*Bos taurus* x *B. indicus*, maximum 1/8 *B. indicus*) originating in north-central or south Texas. Steers were randomly allocated to treatment groups such that average initial weights were equal among experimental units. Weight classes within the original steer herd were proportionately represented in the treatment groups. Initial weights averaged 257 kg (SD = 12 kg). Steers were weighed on each management date after being held for 18 hours without feed or water. Steers were implanted with Synovex-S[1] (Ft. Dodge Animal Health, Overland Park, Kan.) at the start of grazing and again in early May. We fed a 38% crude protein cube to the steers at a rate of 1.7 kg head^{-1} day^{-1} from the start of grazing until about mid April. Actual practice was to feed 3.9 kg head^{-1} of supplement 3 times per week. Steers were treated for internal parasites with Ivomec[1] (Merial Limited, Iselin, N.J.) in early May. They had unlimited access to block salt. All procedures for animal care and management were in accordance with accepted guidelines (Consortium 1988).

In the winter of 1994, all steers on the Old World bluestem-Native units were grouped together as a single herd and grazed Old World bluestem pastures that were not in the study for 55 days (49% of the Winter period). In 1996, severe

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[1] Names are necessary to report factually on available data, however, the USDA neither guarantees nor warrants the standard of the product, and the use of the name by USDA implies no approval of the product to the exclusion of others that may also be suitable.

drought in the early growing season delayed grazing on the Old World bluestem until June 21. Abundant precipitation in July and August resulted in high production of Old World bluestem and the steers were left on the Old World bluestem units until the end of the grazing season, August 28. This eliminated the late summer grazing period on rangeland for the Old World bluestem-Native steers. Because of these inconsistencies in grazing management, steer gains for 1994 and 1996 were excluded and only gains from 1993, 1995, and 1997 were used in the analyses.

Frequency sampling was conducted in the native pastures to determine the effects of production system on plant species composition. Four transects consisting of 50 quadrats (0.1 m^{-2}) were located in each pasture for a total of 200 quadrats per pasture. The distances between transects and quadrats were calculated to allow uniform spacing across the pastures and quadrats were located by pacing. The first sample was taken in October 1993, at the end of the first year of treatment. Presence or absence in the quadrats was recorded for all plant species. A second sample was taken in late September 1996, after 4 years of treatment. Presence or absence of 25 plant species was recorded. The species list for the second sample was based on the 25 most common plant species from the first sample.

Peak standing crop of Old World bluestem was determined at the end of the summer grazing period for Old World bluestem. One plot measuring 1.3 x 4.9 m was harvested with a sickle bar mower at a height of 7 cm within each of 5 exclosures per experimental unit. The exclosures were moved each year. Forage samples were dried at 60°C. Only data from the years 1993 and 1995 to 1997 were included in the analyses because data from 1994 were lost.

Frequency of plant species within the rangeland units was analyzed with a completely randomized analysis of variance with repeated measures (Milliken and Johnson 1984). Production system was the whole plot independent variable and year was the repeated independent variable. The variance due to production system was further partitioned into orthogonal contrasts of Native versus Old World bluestem-Native and WW-Spar versus WW-Iron Master (within Old World bluestem-Native). A probability level of P = 0.10 was used to declare significant treatment effects.

Peak standing crop of Old World bluestem was analyzed with a completely randomized analysis of variance with repeated measures. Variety of Old World bluestem was the whole plot independent variable and year was the repeated independent variable.

Steer gains were analyzed as a completely randomized analysis of variance with repeated measures. Production system was the independent variable and year was the repeated variable. Gain per head was analyzed separately for each management period and for the entire season. Gain per ha was analyzed for each forage type within production system and over all production systems.

The main focus of the economic analysis was to determine the factors that favor one production system over the other in terms of net returns (NR).

$$NR = GI - LiP - LiVC - LaC, \tag{1}$$

where,

GI = gross income
LiP = livestock purchase costs
LiVC = livestock variable costs of production
LaC = land costs.

These terms can be rewritten as

GI = Head x Sale Weight x Sale Price
LiP = Head x Purchase Weight x Purchase Price
LiVC = Head x Variable costs head^{-1}
LaC = Head x $[(\text{Cost}_{Np} \times \text{ha}_{Np}\ \text{head}^{-1}) + (\text{Cost}_{OWBp} \times \text{ha}_{OWBp}\ \text{head}^{-1})]$,

where,

subscript N_p = native pasture
subscript OWB_p = Old World bluestem pasture.

If net returns are equal for the 2 production systems,

$$GI_N - LiP_N - LiVC_N - LaC_N = GI_{ON} - LiP_{ON} - LiVC_{ON} - LaC_{ON}, \tag{2}$$

where,

subscript N = Native production system
subscript ON = Old World bluestem-Native system.

We assumed that livestock purchase and variable costs would be similar between the systems. This assumption is warranted because the type of animal, period of ownership, and livestock management (other than grazing management) are essentially identical between systems. This reduces equation (2) to

$$GI_N - LaC_N = GI_{ON} - LaC_{ON} \tag{3}$$

Making substitutions for GI and LaC for each production system results in:

$$(\text{Head}_N \times \text{Sale Weight}_N \times \text{Sale Price}_N) - [\text{Head}_N \times (\text{Cost}_{Np} \times 3.2\ \text{ha})] = (\text{Head}_{ON} \times \text{Sale Weight}_{ON} \times \text{Sale Price}_{ON}) - \{\text{Head}_{ON} \times [(\text{Cost}_{Np} \times 1.6\ \text{ha}) + (\text{Cost}_{OWBp} \times 0.2\ \text{ha})]\}. \tag{4}$$

Equation 4 can be further simplified by assuming the 2 production systems will produce the same number of steers. This will require different total land areas. The equation can then be rearranged and reduced to:

$$(\text{Sale Weight}_N \times \text{Sale Price}_N) - (\text{Sale Weight}_{ON} \times \text{Sale Price}_{ON}) = (1.6 \times \text{Cost}_{Np}) - (0.2 \times \text{Cost}_{OWBp}). \tag{5}$$

The left hand side of this equation is the difference in total sale price between a steer from the Native system and a steer from the Old World bluestem-Native system. This quantity can also be expressed as a function of the difference in weights between the 2 types of steers and the marginal value of gain:

$$(\text{Sale Weight}_N \times \text{Sale Price}_N) - (\text{Sale Weight}_{ON} \times \text{Sale Price}_{ON}) = (\text{Sale weight}_N - \text{Sale Weight}_{ON}) \times \text{Value of Gain} \tag{6}$$

The value of gain is inversely related to the difference between the price per kg of lighter versus heavier animals. As the difference between the unit price of lighter and heavier animals becomes smaller, the value of gain approaches the actual sale price. As the difference in unit price increases, the value of gain decreases. The marginal value of gain is always lower than the sale price as long as lighter-weight steers are worth more per kg than heavier-weight steers. This is the most common price structure in the U.S. beef cattle market. Substituting this alternative expression into equation 5 results in:

$$(\text{Sale weight}_N - \text{Sale Weight}_{ON}) \times \text{Value of Gain} = (1.6 \times \text{Cost}_{Np}) - 0.2 \times \text{Cost}_{OWBp}). \tag{7}$$

Sale weights of the steers from each system are biological responses dependent on the treatments themselves. The economic advantage of one production system over the other is also dependent on 3 external factors: the value of gain, the cost of native pasture, and the cost of Old World bluestem pasture. The value of gain for the type of steers used in this study averaged $\$1.20\ \text{kg}^{-1}$ at the Oklahoma City Stockyards from 1985 to 1995. The minimum value of gain was $\$0.60\ \text{kg}^{-1}$ and the maximum was $\$1.50\ \text{kg}^{-1}$. We used these values of gain and systematically varied the cost of rangeland from \$12 to $\$26\ \text{ha}^{-1}$. At each combination of these 2 factors, we then solved for the cost of Old World bluestem that would equalize returns between the 2 production systems.

Results and Discussion

Weather

Precipitation during the study period was close to or higher than the long-term average with 2 exceptions (Fig. 1). The June to July period in 1994 was well below average. While precipitation totals for 1996 were above average, the distribution was highly skewed. Only 36 mm were received during the October 1995 to April 1996 period. This is a record low and is only 17% of the average of 213 mm for this period. Later that year, 488 mm (2.6 times the average amount) were received in the months of July, August, and September.

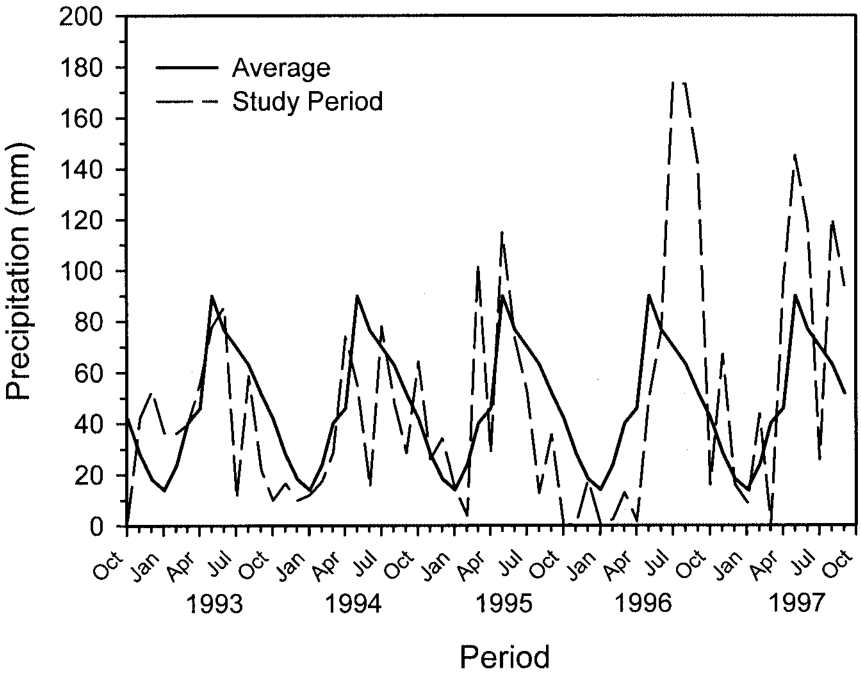

Fig. 1. Precipitation at the Southern Plains Experimental Range, Harper County, Okla., during the study period. Average precipitation calculated over the period 1940 to 1998.

Species Composition of Native Pastures

Production system had no impact on the frequency of any plant species in the rangeland pastures (P = 0.16 to 0.98, Table 1). There were no interactions between production system and year (P = 0.12 to 0.90). Growing season stocking rates were higher on the native pastures in the Old World bluestem-Native system compared to the Native system, 50.5 versus 38.5 AUD ha^{-1}, but this increase did not affect plant populations. This may be attributable to the rest period of 51 days in the Old World bluestem-Native system while the steers grazed Old World bluestem in June and July.

Species that did not change in frequency over years included sand bluestem, switchgrass, little bluestem, sand lovegrass, sand paspalum, and purple threeawn. All of these are warm-season grasses and all except purple threeawn would be considered palatable decreasers. Populations of dominant warm-season grasses on the central and southern Great Plains have generally not been affected or have increased slightly with intensive early stocking (Owensby et al. 1988, Olson et al. 1993, Gillen and Sims 1999). Perennial threeawn increased moderately as stocking rates were reduced in west central Oklahoma but its reaction to grazing has been mixed in other studies (Gillen et al. 2000).

Sideoats grama, sand dropseed, fall witchgrass, sand sedge, windmillgrass, blue grama, sandbur, and sand sagebrush all increased over years, regardless of treatment (Table 1). All are warm-season species except sand sedge. Sandbur is a warm-season annual grass that may have responded to abundant precipitation in July and August of 1996.

Species decreasing over years included Texas bluegrass, Scribner's dicanthelium, western ragweed, annual buckwheat, camphorweed, and plantago. Texas bluegrass and Scribner's dicanthelium are both cool-season grasses and their decrease may be a reflection of the severe winter-spring drought just prior to the second sample period. This drought was probably also responsible for the decreases in forb species. Three of these species, annual buckwheat, camphorweed, and plantago, are annuals and susceptible to adverse spring growing conditions. Camphorweed and plantago were essentially absent in the second sample (Table 1).

Old World Bluestem Standing Crop

Standing crop of Old World bluestem was similar (P = 0.16) for WW-Iron Master (4,790 ± 1,350 kg ha^{-1}) and WW-Spar (4,480 ± 1,190 kg ha^{-1}) when averaged over years. There was no interaction between variety and year (P = 0.80) indicating a consistent response over years. WW-Iron Master produces about 50% more forage than WW-Spar when growing on calcareous, iron-deficient soils (Berg et al. 1986).

The average peak standing crop over years and cultivars was 4,640 kg ha^{-1}. Old World bluestem standing crop was affected by year (P < 0.01) ranging from a low of 3,200 ± 548 kg ha^{-1} in 1997 to a high of 6,270 ± 620 kg ha^{-1} in 1996 when averaged over cultivars. Gillen et al. (1999) measured peak standing crops of 4580 kg ha^{-1} for WW-Iron Master growing on an Enterprise fine sandy loam (coarse-silty, mixed, thermic Typic Ustochrept). Berg (1990, 1993) reported annual production of 2,840 kg ha^{-1} for WW-Spar growing on a Woodward sandy loam (coarse-silty, mixed, thermic Typic Ustocrept) in this same region and 2,945 kg ha^{-1} from WW-Iron Master growing on a Carey loam (fine silty, mixed, thermic, Typic Argiustoll). Precipitation in the May to August period was 5–30% above average for all of these studies and nitrogen fertilizer rates were comparable. The maximum production potential for these grasses may be higher than previously thought.

Steer Gain

Winter gains were greater for steers on native pastures compared with those on Old World bluestem (Table 2). This resulted in average daily gains of 0.34 kg head^{-1} day^{-1} for steers on the Native system and 0.19 kg head^{-1} day^{-1} for steers on Old World bluestem. Stocking density was 16 times higher in the Old World bluestem pastures. Forage standing crop was not measured but was probably no more than 3 to 4 times higher in the Old World bluestem pastures. This resulted in a higher grazing pressure in the Old World

Table 1. Plant frequency (%) in rangeland pastures as affected by production system and year and P-values from analyses-of-variance.

Species	Production System	Plant Frequency 1993	Plant Frequency 1996	P-values Treatment	P-values Year	P-values Trt xYear
		- - - - - - (%) - - - - - -				
Sand bluestem	Native	21.7	28.8	0.79	0.30	0.60
(*Andropogon hallii* Hack.)	OWB-Native	25.4	28.0			
Switchgrass	Native	16.0	18.8	0.56	0.34	0.60
(*Panicum virgatum* L.)	OWB-Native	11.8	14.1			
Little bluestem	Native	11.7	12.5	0.98	0.33	0.83
[*Schizachyrium scoparium* (Michx.) Nash]	OWB-Native	11.0	13.5			
Sand lovegrass	Native	6.1	11.3	0.38	0.50	0.50
[*Eragrostis trichodes* (Nutt.) Wood]	OWB-Native	4.7	4.5			
Sand paspalum	Native	10.5	13.5	0.24	0.16	0.38
(*Paspalum setaceum* Michx.)	OWB-Native	17.0	20.9			
Sideoats grama	Native	6.7	7.5	0.68	0.06	0.37
[*Bouteloua curtipendula* (Michx.) Torr.]	OWB-Native	2.9	7.3			
Sand dropseed	Native	40.3	47.0	0.90	0.09	0.42
[*Sporobolus cryptandrus* (Torr.) Gray]	OWB-Native	38.3	47.8			
Purple threeawn	Native	1.8	5.5	0.29	0.74	0.36
(*Aristida purpurea* Nutt.)	OWB-Native	1.6	0.5			
Fall witchgrass	Native	8.9	19.5	0.90	0.04	0.42
[*Digitaria cognata* (J.A. Schultes) Pilger]	OWB-Native	9.5	18.4			
Texas bluegrass	Native	63.5	37.8	0.28	0.02	0.43
(*Poa arachnifera* Torr.)	OWB-Native	51.9	29.3			
Sand sedge	Native	6.9	28.5	0.98	0.01	0.52
(*Cyperus schweinitzii* Torr.)	OWB-Native	6.7	28.9			
Scribner's dicanthelium	Native	7.4	5.0	0.74	0.06	0.13
[*Dicanthelium oligosanthes* (J.A. Schultes) Gould]	OWB-Native	6.7	4.4			
Windmillgrass	Native	11.0	19.0	0.30	0.01	0.61
(*Chloris verticillata* Nutt.)	OWB-Native	4.4	16.0			
Blue grama	Native	54.9	69.0	0.96	0.01	0.17
[*Bouteloua gracilis* (Willd. *ex* Kunth) Lag. *ex* Griffiths]	OWB-Native	50.3	70.1			
Sandbur	Native	7.2	21.5	0.16	0.01	0.33
(*Cenchrus carolinianus* Walt.)	OWB-Native	16.7	38.5			
Western ragweed	Native	72.5	4.3	0.26	0.01	0.69
(*Ambrosia psilostachya* DC.)	OWB-Native	64.6	1.9			
Annual buckwheat	Native	7.9	1.8	0.72	0.07	0.51
(*Eriogonum annuum* Nutt.)	OWB-Native	9.9	1.9			
Camphorweed	Native	5.6	0.3	0.81	0.06	0.90
[*Heterotheca subaxillaris* (Lam.) Britt. & Rusby]	OWB-Native	17.2	0.0			
Plantago	Native	14.8	0.0	0.25	0.04	0.41
(*Plantago patagonica* Jacq.)	OWB-Native	17.9	0.0			
Sand sagebrush	Native	1.0	1.8	0.49	0.01	0.12
(*Artemisia filifolia* Torr.)	OWB-Native	1.5	2.8			

bluestem pastures that reduced the opportunity for selective grazing. Selectivity was also favored in the native pastures by the greater variety of plant species present. Marston et al. (1993) found crude protein content of steer diets was higher in native pastures compared to Old World bluestem during this period but in vitro organic matter digestibility was higher in Old World bluestem pastures. Winter gains did not differ between the 2 cultivars of Old World bluestem (Table 2).

Steers in both production systems grazed native pasture in the Early Native management period. Steers in the Native system again gained more weight than steers in the Old World bluestem-Native system (Table 2). This resulted in respective average daily gains of 0.85 and 0.70 kg head^{-1} day^{-1} from the 2 systems. Although steers in both systems were grazing the same pasture type, the stocking density for steers in the Native system was one-half the stocking density of steers in the Old World bluestem-Native system. Steer gains are often less sensitive to stocking density during the spring period because forage quality is uniformly high (Owensby et al. 1988, Olson et al. 1993). However, earlier studies of intensive early stocking at this same location also reported reduced steer growth when stocking densities were increased in the early portion of the growing season (Gillen and Sims 1999).

The steers grazed different forage types during the Old World bluestem management period. Gains for Native steers were less than for Old World bluestem-Native steers (Table 2). Average daily gains for steers grazing native pasture, WW-Iron Master, and WW-Spar, were 0.89, 1.09, and 0.94 kg head^{-1} day^{-1}. Forage quality was likely higher in the Old World bluestem pastures during this period. The dominant warm-season native grasses had been growing rapidly for about 4 weeks when this management period began while the Old World bluestems were just beginning rapid vegetative growth. In addition, the Old World bluestems were fertilized with nitrogen, which has been shown to increase forage crude protein content (Berg and Sims 1995). Diets of steers grazing nitrogen-fertilized Old World bluestem were higher in crude protein and in vitro organic matter digestibility than diets of steers grazing native pasture during June and August in west-central Oklahoma (Gunter et al. 1992).

Steers grazing WW-Iron Master gained more than steers grazing WW-Spar during the Old World bluestem management period (Table 2). On 7 sample dates over 3 years, Sims et al. (1983) reported that WW-Iron Master was always higher than or equal to WW-Spar in crude protein content with an overall mean of 8.0% for WW-Iron Master and 7.6% for WW-Spar.

Table 2. Individual steer gain for different management periods. Average dates: a) Winter, 21 Dec. to 15 Mar.; b) Early Native, 15 Mar. to 9 Jun.; c) Old World Bluestem, 9 Jun. to 30 Jul.; and d) Late Native, 30 Jul. to 31 Aug. All steers grazed native pastures during the Early and Late Native periods. Steers in the Old World bluestem-Native systems grazed Old World bluestem during the Winter and Old World bluestem periods. Numbers in parentheses represent 1 standard deviation.

	Management period				
Production system	Winter	Early native	Old World bluestem	Late native	Total
	kg steer^{-1}				
Native	28 (10)	74 (19)	45 (5)	14 (10)	161 (22)
'WW- Iron Master' - Native	17 (7)	62 (24)	56 (5)	18 (10)	152 (19)
'WW- Spar' - Native	15 (9)	59 (23)	48 (6)	22 (8)	144 (23)
P-Values for contrasts					
Native vs. Old World bluestem Systems	<0.01	0.03	<0.01	0.25	0.05
Old World bluestem cultivars	0.38	0.34	<0.01	0.15	0.14

WW-Iron Master also had greater or equal in vitro dry matter digestibility on 6 of 7 dates with an overall mean of 62.6% for WW-Iron Master and 61.4% for WW-Spar (Sims et al. 1983). This advantage in nutrient concentration may explain the higher steer gains on WW-Iron Master.

For the final management period, Late Native, all steers were again on native pasture. There was no difference in steer gains for Native or Old World bluestem-Native steers (Table 2) or between steers that had grazed on the different cultivars of Old World bluestem (Table 2). Average daily gains were 0.45 and 0.62 kg head^{-1} day^{-1} for the Native and Old World bluestem-Native systems, respectively. There were no interactions for steer gain ($P > 0.08$) between production system and year for any management period.

Total gains over all management periods averaged 13.5 kg head^{-1} greater for the Native system (Table 2) over the Old World bluestem-Native system and did not differ between sub-systems of Old World bluestem-Native. This difference was attributable to the Winter period when gains were 12 kg head^{-1} higher for the Native system. Growing season gains (combined over the last 3 management periods) were not different between production systems ($P = 0.70$). Winter gain was only 13% of total gain but was important in subsequent economic analyses.

Livestock production per ha from the native portion of each system was not different ($P = 0.89$, Fig. 2). To increase gain per ha on native pasture, stocking rate must usually be increased because gain per head is near maximum under moderate stocking rates. With the ratio of native:Old World bluestem used in this study, stocking rate for the native pasture in the Old World bluestem-Native system actually decreased 5% below moderate stocking rates so there was little potential to increase gain per ha. With an overall mean of 47 kg ha^{-1}, the gains from native pasture are similar to the 42 kg ha^{-1} reported from earlier stocking rate studies at this location (Sims and Gillen 1999).

Production per ha was not different between cultivars of Old World bluestem within the Old World bluestem-Native systems ($P = 0.17$, Fig. 2) or for the total system area ($P = 0.69$). Gain per ha was about 6.5 times higher on Old World bluestem than native pasture. At 306 kg ha^{-1}, gains from Old World bluestem were not greatly different than the 270 kg ha^{-1} reported from earlier work at this same location (Berg and Sims 1995, Gillen et al. 1999). The value of using Old World bluestem in a relatively short, intensive grazing period can be seen when these gains are compared to the 200 kg ha^{-1} gains produced by continuous grazing of Old World bluestem from December to September (Sims et al. 1983). The increase was largely attributable to the concentration of steer grazing during the portion of the grazing season when quality of Old World bluestem was highest.

Total livestock production per ha increased by 64% with the Old World bluestem-Native system compared to the Native system ($P < 0.01$, Fig. 2). The increase in production was strictly due to the addition of the Old World bluestem since production per ha from the native portion of each system was not different.

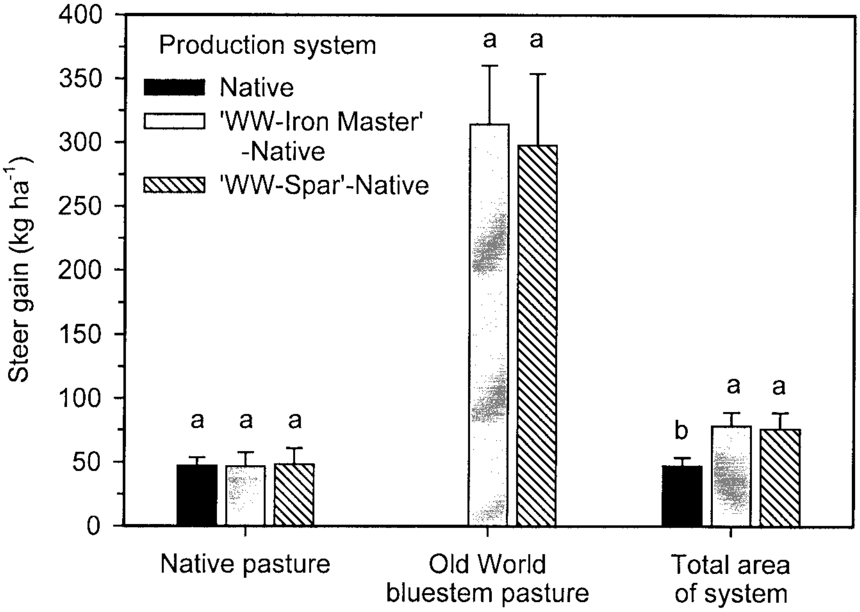

Fig. 2. Livestock production from the different forage types and the total land area in the 2 production systems. Within forage type, production systems with different letters are significantly different ($P < 0.05$). Bars denote 1 standard deviation.

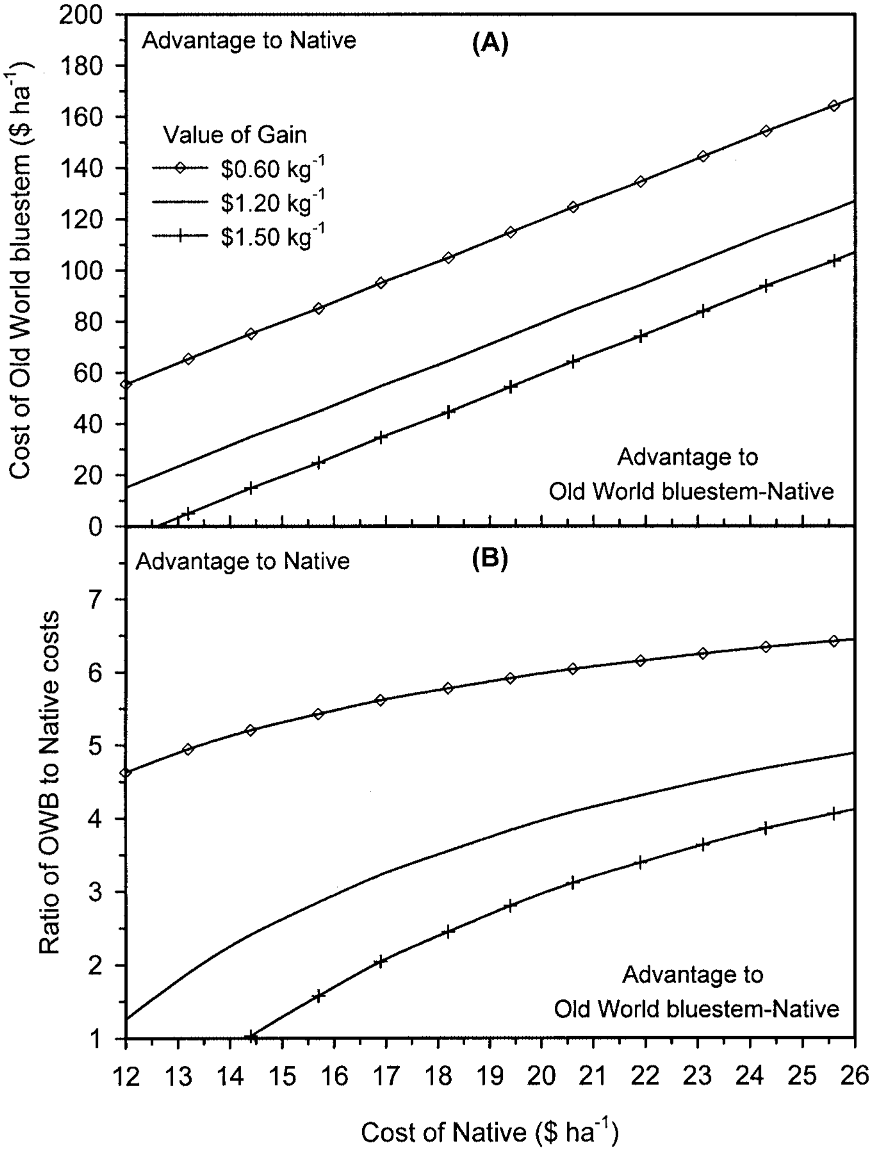

Fig. 3. Relative economic returns between the Native and Old World bluestem-Native production systems. A) The effects of value of gain and land costs. B) The effects of value of gain and ratio of land costs. The lines represent equal returns between the 2 systems. The Native system has greater net returns in the upper left portion of the figures and the Old World bluestem-Native system has greater economic returns in the lower right portion of the figures.

Total system stocking rate was 53 AUD ha^{-1} in the Native system compared to 90 AUD h^{-1} in the Old World bluestem-Native system, an increase of 69% for the complementary system.

Economic Comparisons

The relative economic response between systems was dependent on the management costs for the 2 forage types. To frame the following discussion, regional rental rates for native pasture averaged $16.70 ha^{-1} with a range of $2.50 to $37.0 ha^{-1} (Doye et al. 1999). Regional rental rates for Old World bluestem pasture averaged $27.70 ha^{-1} with a range of $2.50 to $111.20 ha^{-1}. In addition to rent, costs associated with the management practices used for the Old World bluestem pastures in this study (Kletke and Doye 1998) include nitrogen fertilization (average $28.00 ha^{-1}, range $19.10 to $40.20 ha^{-1}) and weed control every second year (average $6.50 ha^{-1}, range $5.00 to $11.90 ha^{-1}). This resulted in an average total cost for Old World bluestem of $62.10 ha^{-1} with a range of $26.60 to $163.20 ha^{-1}. Rent averaged only 44% of the total cost of Old World bluestem. Ratios of land costs (Old World bluestem:native) based on the extremes were 0.75 to 66.5. The average ratio was 3.7.

The cost of Old World bluestem that maintained equal returns between production systems was linearly and positively related to the cost of native pasture (Fig. 3A). As the cost of native pasture increased, the cost of Old World bluestem could also increase and still maintain equal returns. For each $1 ha^{-1} increase in the cost of native pasture, Old World bluestem could increase $8 ha^{-1} because 1 ha of Old World bluestem substituted for 8 ha of native pasture in the Old World bluestem-Native system. At a value of gain of $1.20 kg^{-1} and a cost of native pasture of $17 ha^{-1}, returns were greater for the Old World bluestem-Native system only if the cost of Old World bluestem was less than 3.3 times the cost of native pasture (Fig. 3B). As the cost of native pasture increased, the competitive advantage increased for Old World bluestem. At a native pasture cost of $26 ha^{-1}, Old World bluestem could cost 4.9 times as much as native pasture.

As the value of gain increased, the economic penalty for lower steer gains in the Old World bluestem-Native production system also increased. This means a producer could not afford to pay as much for land costs for Old World bluestem in the Old World bluestem-Native system (Fig. 3A). Conversely, as the value of gain declined, the cost of Old World bluestem could increase. Higher values of gain (narrow price differentials) favor the Native system while lower values of gain (wide price differentials) favor the Old World bluestem-Native system. If native pasture costs $17 ha^{-1} and value of gain is $1.50 kg^{-1}, returns are only greater for the Old World bluestem-Native system if the cost of Old World bluestem is less than $36 ha^{-1} or 2.1 times greater than the cost of native pasture (Fig. 3B). However, if the value of gain is $0.60 kg^{-1}, the cost of Old World bluestem can increase to $96 ha^{-1} or 5.6 times the cost of native pasture. For each $0.01 kg^{-1} decrease in value of gain, the allowable cost of Old World bluestem increases $0.67 ha^{-1}. The ratio of allowable land costs was less sensitive to value of gain as the cost of native pasture increased (Fig 3B).

The lower season-long gain of 13.5 kg head^{-1} in the Old World bluestem-Native system was a key factor in the analysis. At a value of gain of $1.20 kg^{-1}, the ratio of land costs that equalizes net returns ranges from 1.3 to 5.2. If steer gains had been similar between systems, the allowable ratio of land costs increases to 8 and is not dependent on value of gain. The Winter management period accounted for much of the difference in steer gains. One approach to improving gains for the Old World bluestem-Native system would be to put half the steers on native pasture during the Winter period. In this study, native pasture in the Old World bluestem-Native system was not utilized in the Winter period. Since the stocking density of steers on native pasture would be equal between the 2 production systems, gains should at least be equalized on half of the steers. With the resulting lower stocking density on Old World bluestem, gains might also improve for the steers still grazing Old World bluestem.

This economic analysis was based on relative returns between the 2 production systems. Actual profitability for either system depends on many other factors such as purchase and sales prices, marketing arrangements, death loss, feed costs, and many others. However, these factors would generally affect both systems. Given average values for livestock gain of \$1.20 kg^{-1}, and average costs for native pasture of \$17 ha^{-1}, the Old World bluestem-Native system was economically competitive as long as the ratio of land costs was 3.3. Since the average ratio of land costs was 3.7, the Native system was often more profitable, even though the livestock production per ha was much higher with the Old World bluestem-Native system. Conditions further favoring the Native system included low costs for native pasture and a high marginal value of livestock gain. When value of gain is low, the Old World bluestem-Native system would likely be more profitable at almost any cost level for native pasture.

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Upland erosion under a simulated most damaging storm

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Abstract

A 2 year study was conducted to determine the effects of surface cover and roughness on sediment yield from plots subjected to a simulated most damaging storm. This storm, based on long term sediment records from 3 Wyoming streams, produced approximately 18 mm of precipitation in 15 min with an intensity of 97 mm hour^{-1}. The rainfall simulator covered 2 plots; each 0.6 by 2 m. Plots were on 9% slopes with highly erosive soils (silt and fine sand texture) on native rangeland in 3 areas of Wyoming. Cover and surface roughness were measured with a point frame.

Sediment production typically peaked approximately 120 sec after runoff started and reached steady state within 6 min. Plots with no cover (tilled) seldom produced runoff due to high infiltration and the short duration rainfall. Sediment yield was moderately correlated with total cover for total cover less than 30%, and sediment yield decreased to 0.1 tonnes ha^{-1} (assumed allowable soil loss) or less for greater than 30% cover. There was a weak correlation between surface roughness and sediment yield, and surface roughness was slightly correlated with total cover. These results suggested that maintaining at least 30% total cover could control sediment yields from short duration-intense storms. Experimental results also indicated considerably higher sediment yields than those predicted by the Revised Universal Soil Loss Equation or a modified version of that equation.

Key Words: sediment yield, surface cover, surface roughness, eolian sediment, RUSLE, non-point source pollution, water quality

Resumen

Se condujo un estudio de 2 años para determinar los efectos de la cobertura superficial y la rugosidad en la producción de sedimento de parcelas sujetas simulación de la tormenta mas dañina. Esta tormenta, basada en registros de largo plazo de la producción de sedimento de 3 corrientes de Wyoming produjo aproximadamente 18 mm de precipitación en 15 minutos con una intensidad de 97 mm hora^{-1}. El simulador de lluvia cubrió 2 parcelas, cada una de 0.6 x 2 m. Las parcelas se localizaron en tres áreas de Wyoming en pastizales nativos con pendientes del 9% y suelos altamente erosivos (textura de limo y arena fina). La cobertura y rugosidad de la superficie se midieron con un marco de puntos. La producción de sedimento típicamente estuvo en su mas alto punto a los 120 segundos después de que inicio el escurrimiento y alcanzo el estado de equilibrio dentro de 6 minutos. Las parcelas sin cobertura (con labranza) raramente produjeron escurrimiento debido a la alta infiltración y a la corta duración de la lluvia. La producción de sedimento se correlaciono moderadamente con la cobertura total en coberturas menores al 30% y la producción de sedimento disminuyo a 0.1 ton ha^{-1} (perdida de suelo que se asume permitida) o menos en coberturas mayores al 30%. Hubo un a correlación débil entre la rugosidad de la superficie y la producción de sedimento y la rugosidad de la superficie se correlaciono ligeramente con la cobertura total. Estos resultados sugieren que manteniendo al menos 30% de cobertura total se podría controlar la producción de sedimento de tormentas de corta duración-alta intensidad. Los resultados experimentales también indicaron producciones de sedimento considerablemente mas altas que las predichas por la Ecuación Universal de Perdida de Suelo Revisada o una versión modificada de esa ecuación.

Sediment contaminates more kilometers of Wyoming's rivers and streams than any other non-point source (Hogan 1988), a situation typical in many western states (Heady and Child 1994). Runoff and sediment transported with runoff from rangelands also transports biological and chemical pollutants into rivers and streams while removing vital plant nutrients. Thus, erosion decreases range productivity (Binkley and Brown 1993), and pollutants accumulate in water supplies, which reduces water quality (Hogan 1988).

Vegetation cover, plant life form (grasses, forbs, shrubs), ground cover, soils, and topography influence runoff and erosion (Simanton et al. l991, Benkobi et al. 1994). The type and amount of vegetation also affects the spatial and temporal variation of runoff and erosion (Weltz and Wood 1986, Blackburn and Wood 1990). Eolian sediment deposition, which is influenced by the same factors (Skidmore 1994), may be an important source of sediment from rangelands during precipitation events. Wind speeds of 40 km hour^{-1} (less than twice the average daily wind speed on many rangelands) cause erosion at approximately the same rate as many precipitation events, but windstorms occur more frequently (Skidmore 1994).

Rangeland runoff and erosion are controlled by a complex combination of soil, plant, microtopographic, and hydrologic interactions (Seyfried 1991, Weltz and Blackburn 1995). For example, the spatial arrangement of vegetation and plant life form affects litter and roughness of the soil surface (Blackburn et al. 1992) thereby affecting runoff and sediment filtration (Weltz

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et al. 1992) and soil properties (Naeth et al. 1991). Coppice dunes, which may be partially formed by deposition of eolian sediment, are associated with surface roughness and aggregate stability, and by influencing infiltration, influence runoff and erosion (Blackburn et al. 1990). Eolian sediment typically has the same texture (silt and fine sand) as soils which are highly susceptible to rainfall erosion. While there is ample evidence in the literature of the impact of precipitation events on runoff and erosion, there is little information to show the impact of vegetation and soil surface characteristics on sediment yield caused by a "most damaging storm".

The objective of this research was to evaluate the effects of cover and surface roughness on the sediment yield caused by a simulated most damaging storm. Sediment yield was defined as the amount of soil detached from an area which passed a downslope point (Ponce 1989), and the most damaging storm was defined as the rainfall event which caused the greatest average annual sediment load for 3 Wyoming streams (Huffsmith 1988). It was hypothesized that sediment yields produced by a most damaging storm would be greater and more sensitive to cover than those predicted by the Revised Universal Soil Loss Equation (Renard et al. 1994) or a modified version of that equation (Benkobi et al. 1994).

Methods

Study Site

Three upland range sites were selected for this research; Fifteen Mile drainage west of Worland, Wyo. (108°20'W, 44°11'N), provided the least cover, Ten Mile Creek north of Worland, Wyo. (108°8'W, 44°21'N), provided intermediate cover, and areas along Beaver and Jack Creeks south of Rawlins, Wyo. (107°7'W, 41°27'N), provided the greatest cover. Soil types were different at the 3 sites; however, surface soils at all sites had similar texture. Vegetative and cover differences were evaluated in terms of height, total cover, canopy cover, litter, rock, and biomass.

Fifteen Mile Drainage receives a mean annual precipitation of 203 mm and has an average annual temperature of 7°C. Soils belong to the Greybull-Persayo association. The drainage is sparsely vegetated with saltbush (*Atriplex* spp.), pricklypear cactus (*Opuntia* spp.), blue grama (*Bouteloua gracilis* (H.B.K.) Lag.), and various shrubs. Steeply sloped badlands cover much of the area. Primary historical uses are grazing, recreation, and oil and gas production. The drainage contributes approximately 0.8% of the mean annual flow of the Bighorn River, but also contributes 75% of the annual sediment load (Cooper 1979).

Ten Mile Creek has the same average rainfall and temperature as Fifteen Mile, but has greater canopy cover. Soil in the area is an Uffens-Rairdent complex. Vegetation consists of wheatgrasses (*Agropyron* spp.), needle-and-thread (*Stipia comata* Trin.&Rupr.), and big sagebrush (*Artemisia tridenta* Nutt.) with limited blue grama and pricklypear cactus. Primary historical use is for grazing, but there was no evidence of grazing before the simulations were run.

Beaver and Jack Creeks are in the Stratton Sagebrush Hydrology Study Area. Soils belong to the Youga series, mixed Argic Cryboroll. Beaver Creek receives an annual precipitation of 381 mm, has an annual average temperature of 5°C, and was being grazed at the time of the simulations. Jack Creek receives an average annual precipitation of 516 mm, has an average annual temperature of 5°C, and has not been grazed since 1960. Vegetation consists of big sagebrush and grasses such as fescues (*Festuca* spp.), blue grasses (*Poa* spp.), and needle grasses (*Stipa* spp.). Litter cover, which was often several cm thick, influenced cover and surface roughness at this site.

Rainfall Simulator

The rainfall simulator was a 0.2 scale model of the "Swanson type" simulator (Laflen et al. 1991) which covered 2 plots, each 0.6 by 2 m. Pearce et al. (1998) found that sediment yields from plots of this size were more sensitive to cover and surface roughness than from larger (3 by 10 m) Swanson plots. Simulator nozzles (Veejet 9570, Spraying Systems Inc.[1]), and operating parameters were selected based on laboratory calibration and nozzle manufacturer's data. Using these results, the nozzles were located on a radius of 1.6 m and height of 2.9 m. This configuration, with an operating pressure of 42 kPa, produced a relatively uniform spray pattern over the plot areas. The median drop size (2 mm) was within values discussed by Lal and Elliot (1994) for high intensity storms. Measured drop maximum velocity averaged 7.4 m sec^{-1} compared to 6.5 m sec^{-1} for natural raindrops falling in still air (de Ploey and Gabriels 1980).

The most damaging storm was defined as the storm that produced the greatest average annual stream sediment load. Using records for 3 Wyoming watersheds, Huffsmith (1988) showed that most damaging storms produced 16 to 19 mm of rainfall with return periods of approximately 2 years. Branson et al. (1981) concluded that many rangeland storms produced less than 17 mm of rainfall, had durations of less than 60 min, and reached peak intensity in less than 10 min. Using a relationship presented by Linsley et al. (1982), the minimum duration for such storms is approximately 7 min. Assuming 15 min duration and using an analysis presented by Haan et al. (1994), the intensity should be approximately 100 mm hour^{-1}. In preliminary tests, it was observed that plot runoff and sediment yield stabilized within 6 min or less with a simulator rainfall intensity of 97 mm hour^{-1}. Therefore, the simulator operating parameters represented a reasonable compromise of the most damaging storm.

Cover and Surface Roughness

Surface cover was the controlled variable in this research, and plots were selected at the 3 study sites over the range of 0 to 100% cover. Cover and surface roughness were measured using the point frame method (Bonham 1989). The point frame covered an entire plot and contained 100 equally spaced pins (20 rows and 5 columns). Pin height was measured relative to the frame top using a digital micrometer, and surface roughness was calculated as the standard deviation of the pin elevations (Renard et al. 1994). Cover type was calculated based on the cover (plant canopy, litter, rock, etc.) touched on the first hit of 50 pins.

Field Experimental Procedure

Specific plots were selected on 9% slopes and by visual observation of cover. A frame, which outlined both simulator plots and located the center of the simulator, was then placed on the ground parallel to the slope and sheet metal plot boundaries were driven approximately 3 cm into the soil. After collecting surface soil samples adjacent to the plots and surface roughness and cover data, covered collection pans were placed at the lower end of each plot, the plots were covered with plastic, and the simulator was started. The plastic was removed (time = 0) and the times at which runoff started were recorded. Runoff samples were collected for 10 sec at times of 30, 60, 90, 120, 150, 180 sec, and at each 60 sec thereafter following the start of runoff.

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[1] Use of trade names is for information purposes only and does not constitute endorsement by the authors or their employers.

Eighteen simulations were run at Fifteen Mile with canopy cover ranging from 6 to 43% and surface roughness ranging from 1.5 to 15.7 mm; 12 simulations were run at Ten Mile with canopy cover ranging from 5 to 62% and surface roughness ranging from 5.3 to 17.6 mm; and 8 simulations were run at Beaver and Jack Creeks with canopy cover ranging from 29 to 73% and surface roughness ranging from 8 to 35 mm. Simulations were also run on tilled plots (no cover) at Ten Mile and Beaver and Jack Creeks. Plots were not tilled at Fifteen Mile because of the presence of an erosion pavement. Tilled plots seldom produced runoff and were therefore excluded from the analysis. Seven plots identified as outliers were also excluded from the analysis (Belsley 1991).

Laboratory Analyses

The volume of runoff and mass of sediment collected in each sample (10 sec runoff) were determined by drying and weighing. Sieve and hydrometer analyses (ASTM D-442-63) were used to determine the texture of the surface soil on each simulation site. Although soil texture differed somewhat between the 3 sites, the soils had very little clay (maximum of < 7% finer than 0.002 mm) and approximately 30% silt and fine sand (0.002 to 0.1 mm). These soils are highly erosive (Goldman et al. 1986). The overall average soil texture was 4% clay, 17% silt and 79% sand.

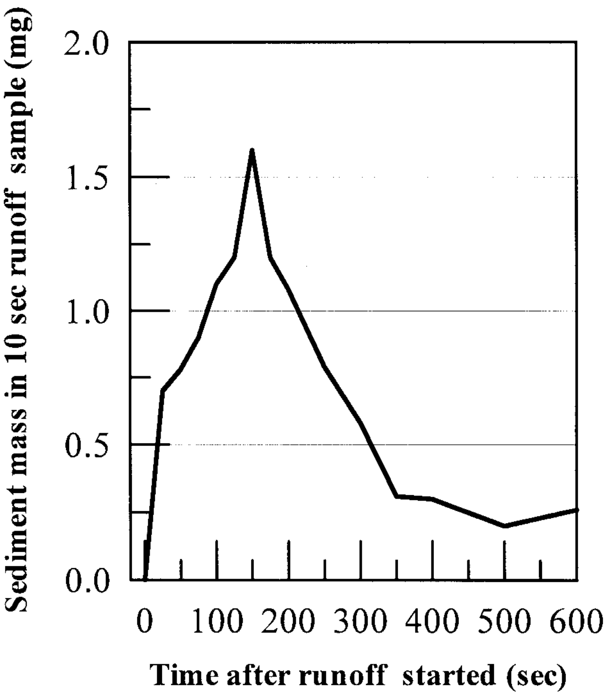

Fig. 1. Sediment mass in 10 sec runoff samples for a simulation with 26% total cover. The general shape of this curve is typical of most simulations, although the peak value decreased as total cover increased.

Results and Discussion

Sediment Yield

Sediment mass in 10 sec runoff samples was plotted as a function of time after runoff started. A typical simulation is shown in Figure 1. In all simulations, peak sediment mass was observed 120 to 180 sec after runoff started and sediment mass decreased to a relatively steady value within approximately 6 min. For plots with total cover < 30%, the steady value was generally less than 15% of the peak value. Highly erodible surface soil was flushed off the plot and then rainfall erosion occurred at a relatively constant rate. Schreiber and Renard (1978) and Wilcox and Wood (1988) reported similar initial flushing. Possible explanations for this response include disturbance caused by installing plot boundaries, desiccation of the soil surface during dry periods, surface sealing during the intense storm, and accumulated deposition of eolian sediment. Soil disturbance caused by installing plot boundaries was minimal because the plot boundaries were driven rather than dug in. Surface soils were susceptible to desiccation and surface sealing because there was considerable fine sand and silt; however, tilled plots did not exhibit surface sealing.

Eolian sediment deposition would depend on wind characteristics, topographic features, and vegetation height, diversity, and morphological characteristics. In addition to accumulation on the ground surface, eolian sediment would be deposited on plant leaves and stems and would be washed off at the beginning of rainfall events. The accumulation of eolian sediment would also depend on the frequency of rainfall events of magnitude sufficient to transport sediment off the site. Devine et al. (1998) reported that spring time sediment yields observed in New Mexico might have resulted from wind deposition of fine sediment. Higher wind blown dust levels during winter and spring were also reported by Pease et al. (1998). The texture of eolian sediment, silt and fine sand (Skidmore 1994), is typical of the texture of the surface soils in this research.

Although this discussion is subjective, it offers an explanation for high stream sediment loads produced by short duration-high intensity storms which occur at approximately 2 year intervals. The time interval between these storms is sufficient for accumulation of eolian sediment in areas adjacent to streams under climatic conditions typical of many western rangelands.

Cover

With 7 data points deleted as outliers, regression analysis indicated that total cover explained 74% of the variability in sediment yield for total cover ≤ 30% (Fig. 2). However, regression analysis was not significant for total cover > 30% (r^2 = 0.01) (Fig. 3). A possible explanation of these results is that micro-channel networks, which controlled sediment transport off the plots, were better developed on plots with total cover ≤ 30%, and networks improved as total cover decreased from 30%. However, for plots with total cover > 30%, micro-channel networks were less developed and more random. Thus, sediment transport off plots with total cover > 30% was decreased and sediment yields were more random. Given the short duration of the simulated storm used in this study and the relatively small sediment yields, it is unlikely that micro-channel networks were altered significantly by the rainfall simulations.

On plots at Beaver and Jack Creeks with total cover > 70%, litter cover explained 56% of the variability in sediment yield. Few if any raindrops reached the soil surface of these plots because of the high litter cover, and only 1 plot which had total cover > 30% had a sediment yield greater than 0.1 tonnes ha^{-1}, the assumed allowable soil loss (Fig. 3). This value was selected as 5% of the soil loss tolerance (2

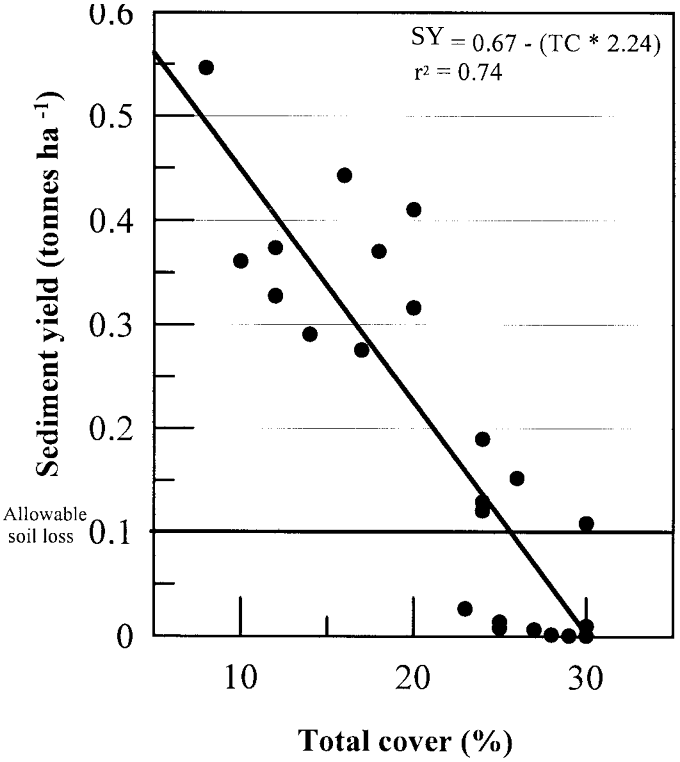

Fig. 2. Sediment yields (SY) for total cover (TC) less than or equal to 30%. The regression line is statistically significant ($p < 0.01$). Allowable soil loss was assumed to be 5% of the soil loss tolerance.

tonnes ha^{-1}) for this soil (Morgan 1987). Sediment yields decreased for plots with total cover > 30%, and were very low for total cover > 70%, with the exception of 4 plots with total cover = 100%. Runoff from these plots transported litter, which affected the sediment determination.

Surface Roughness

Surface roughness reflects the undulations of the soil surface and the surface cover, and is related to the effectiveness of the surface to influence sediment yield (Renard et al.1994). Regression analysis indicated that total cover accounted for only 19% of the variability in surface roughness, and surface roughness was weakly correlated to sediment yield (r^2 = 0.06). In this study, cover was the decision variable rather than surface roughness; thus surface roughness was less significant.

A possible explanation for the variability of sediment yield with surface roughness may be that plots with similar surface roughness had more or less developed micro-channel networks to transport sediment. Surface roughness did not reflect the degree of micro-channel development, and thus some plots with similar surface roughness produced much greater sediment yields than did others. An attempt to use point frame pin elevations to predict plot micro-topography and identify micro-channel networks was unsuccessful. Note that the pin spacing was approximately 5 cm.

Revised Universal Soil Loss Equation Analysis

Using cover, soil, storm characteristics, and surface roughness, sediment yields were estimated using the Revised Universal Soil Loss Equation and a modified version of that equation (Benkobi et al. 1994). Results are shown in Figure 4, and compared with sediment yields determined from the simulations. Sixteen plots with sediment yields > 0.1 tonnes ha^{-1} and plots with no measured sediment loss were not included in this figure. The Revised Universal Soil Loss Equation and modified version predicted very low sediment yields compared to simulation sediment yields although the modified version predicted slightly greater values than did the Revised Universal Soil Loss Equation. For total cover > 70%, the comparison improved; however, sediment yields were generally very low. Neglecting the flushing of fines would reduce sediment yield values by approximately 60%; however,

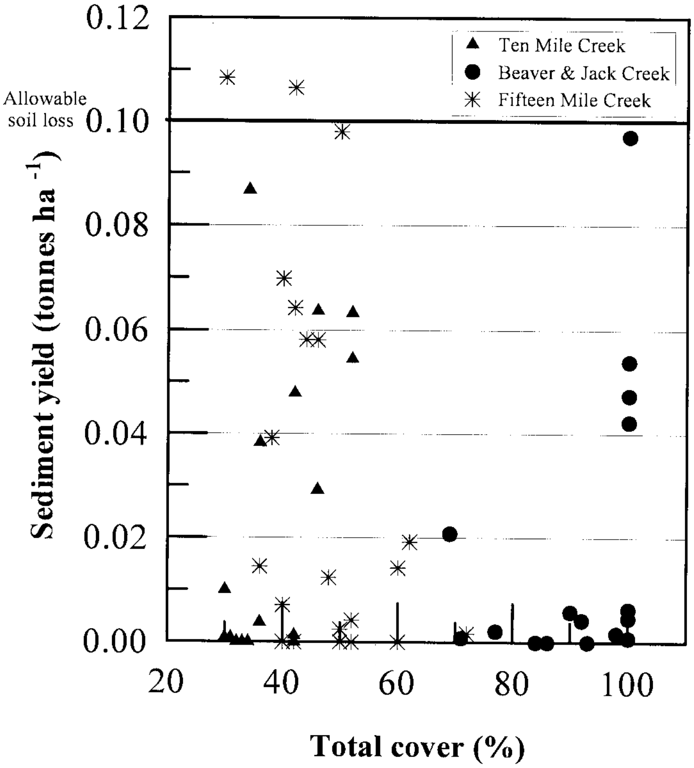

Fig. 3. Sediment yields for total cover greater than 30%. The relationship is not statistically significant. Allowable soil loss was assumed to be 5% of the soil loss tolerance.

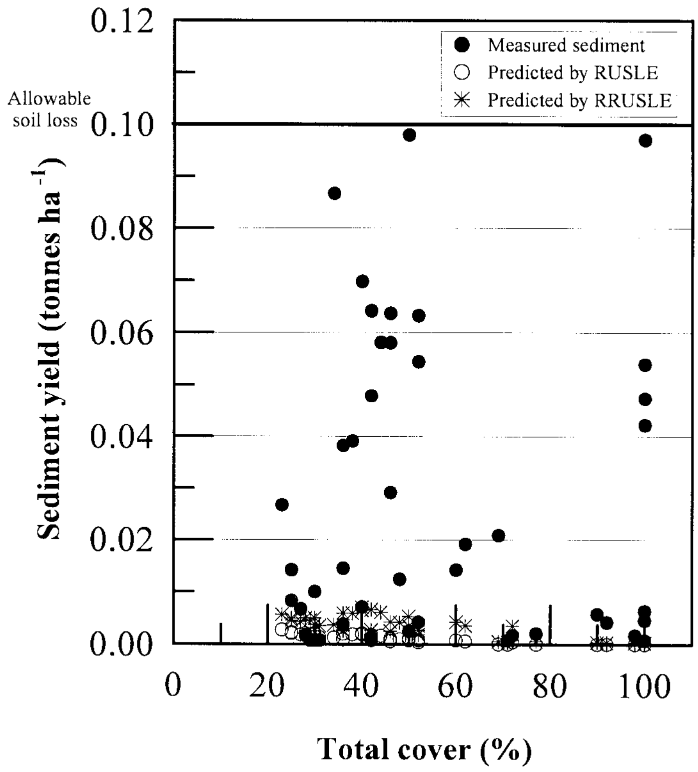

Fig. 4. Sediment yields predicted using the Revised Universal Soil Loss Equation (RUSLE) and a modified version of that equation (RRUSLE) (Benkobi et al. 1994), as a function of total cover for a most damaging storm. Sediment yields from the simulations are included for comparison; however, 16 simulations with sediment yields greater than 0.1 tonnes ha^{-1} and 7 plots identified as outliers are not included. Allowable soil loss was assumed to be 5% of the soil loss tolerance.

measured values would still be considerably greater than predicted values.

Blackburn et al. (1992) concluded that erosion and runoff models were inadequate for rangelands because model parameters did not adequately account for rangeland variability. In this study, parameters were evaluated in detail yet the Revised Universal Soil Loss Equation and modified version of that equation predicted very low sediment yields compared to measured values. The degree of micro-channel development on the plots and the resulting sediment transport capability may have been a factor in this comparison and in Blackburn's study. Micro-channel networks are not considered in current rangeland erosion and runoff models.

Summary and Conclusions

Rainfall simulations were used to evaluate soil erosion from 3 undisturbed upland Wyoming range sites. A 0.2 scale (2 plots, each 0.6 x 2 m) "Swanson type" simulator, was used to simulate a most damaging storm which was defined as the storm that produced the maximum average annual sediment load in 3 Wyoming streams. Sediment yields were evaluated in terms of cover and roughness on 9% slopes having highly erosive surface soils.

Sediment mass eroded from the plots was characterized by a high initial rate as loose sediment was flushed from the surface and a lower approximately steady level typical of longer duration-less intense storms. It is plausible that the source of most of the sediment flushed from the plots was accumulated eolian sediment deposition.

Assuming an allowable soil loss of 0.1 tonnes ha^{-1} (5% of the allowable soil loss tolerance for the soil), 30% total cover provided adequate erosion protection for the most damaging storm. Sediment yields decreased moderately for greater than 30% total cover and were very low for greater than 70% total cover. The influence of cover on the relative development of micro-channel networks and thus on sediment transport off the plots, may explain these results.

Sediment yields from simulation plots were much higher than those predicted by the Revised Universal Soil Loss Equation or a modified version of that equation. However, the comparison improved for total cover values greater than 70%. The silt and fine sand soil texture of the surface soil and the flushing of fines were partially responsible for differences between sediment yield values measured on simulation plots and predicted values. The relative degree of micro-channel development on the plots may also have contributed to these differences.

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Restoring tallgrass prairie species mixtures on leafy spurge-infested rangeland

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Abstract

Leafy spurge (*Euphorbia esula* L.) reduces northern Great Plains rangeland carrying capacity. Treatment strategies were evaluated that suppressed leafy spurge and facilitated establishment of mixtures of native grasses and legumes on range sites near Mason City and Tilden, Nebr. Glyphosate at 1,600 g a.i. (active ingredient) ha^{-1} was applied with or without imazapic at 140 or 210 g a.i. ha^{-1} in October 1995. In April 1996, standing crop was burned or mowed. Mixtures of native grasses [big bluestem (*Andropogon gerardii* Vitman), indiangrass (*Sorghastrum nutans* (L.) Nash), switchgrass (*Panicum virgatum* L.), little bluestem (*Schizachyrium scoparium* (Michx.) Nash), and sideoats grama (*Bouteloua curtiplendula* (Michx.) Torr.)] were then planted with or without native legumes [leadplant (*Amorpha canescens* (Nutt.) Pursh), Illinois bundleflower (*Desmanthus illinoensis* (Michx.) MacM.), and purple prairieclover (*Petalostemum purpureum* (Vent.) Rybd.)] at 440 pls m^{-2} into a non-tilled seedbed. Imazapic was applied at 70 g a.i. ha^{-1} in June 1996 to half the plots that had been treated with imazapic in October 1995. Frequency, dry matter yield, and leafy spurge density were measured 14 to 16 months after planting. Leafy spurge density and yield were least, and frequencies and yields of the planted grasses usually were greatest where imazapic had been applied with glyphosate in October 1995. Purple prairieclover was the only planted legume to persist 14 months after planting, and yields were greatest where imazapic was applied with glyphosate. Imazapic applied in June 1996 usually did not improve planted species yields or leafy spurge control. Total vegetation yields were greater where imazapic was applied with glyphosate at both sites and where native species were seeded at Mason City. Vegetation suppression with fall-applied herbicides and removal of standing crop enabled successful establishment of desirable species, increased forage yields, and suppressed leafy spurge.

Key Words: Prescribed fire, grassland restoration, imazapic, glyphosate, warm-season grasses, cool-season grasses, legumes, invasive plants

Resumen

El “Leafy spurge (*Euphorbia esula* L.) reduce la capacidad de carga de los pastizales del norte de las Grandes Planicies. Se evaluaron estrategias de tratamiento que suprimen el “Leafy spurge” y facilitaron el establecimiento de mezclas de zacates nativos y leguminosas en sitios de pastizal cercanos a Mason City, Nebr. En Octubre de 1995 se aplico Glifosato en dosis de 1600 g i.a. (i.a. = ingrediente activo) con y sin Imazapic en dosis de 140 o 210 g i.a. ha^{-1}. En Abril de 1996 el forraje en pie fue segado o quemado y después se plantaron mezclas de zacates nativos [“Big bluestem” (*Andropogon gerardii* Vitman), “Indiangrass” (*Sorghastrum nutans* (L.) Nash), “Switchgrass” (*Panicum virgatum* L.), “Little bluestem” (*Schizachyrium scoparium* (Michx.) Nash), and “Sideoats grama” (*Bouteloua curtiplendula* (Michx.) Torr.)] con y sin leguminosas nativas [“Leadplant” (*Amorpha canescens* (Nutt.) Pursh), “Illinois bundleflower” (*Desmanthus illinoensis* (Michx.) MacM.), and “Purple prairieclover” (*Petalostemum purpureum* (Vent.) Rybd.)] a una densidad de 440 SPV m^{-2} en camas de siembra sin labranza. En Junio de 1996 a la mitad de las parcelas que en Octubre de 1995 habían sido tratadas con Imazapic se les aplico Imazapic a una dosis de 70 g i.a ha^{-1}. Después de 14 a 16 meses de la siembra se midió la frecuencia, densidad y rendimiento de materia seca de “Leafy spruge”. La densidad y rendimiento de "Leafy spurge" fueron menores y las frecuencias y rendimientos de los zacates plantados usualmente fueron mayores en las áreas donde se aplico Imazapic con Glifosato en Octubre de 1995. La única leguminosa que persistió después de 14 meses de la siembre fue el “Purple prairieclover” y los rendimientos fueron mayores donde se aplico Imazapic con Glifosato. El Imazapic aplicado en Junio de 1996 usualmente no mejoro los rendimientos de las especies plantadas o el control de "Leafy spurge”. Los rendimientos totales de la vegetación fueron mayores donde se aplico Imazapic con Glifosato, esto fue similar en ambos sitios y donde las especies nativas se sembraron en Manso City. La supresión de vegetación con herbicidas aplicados en otoño y la remoción de la vegetación en pie permitio el establecimiento exitoso de especies deseables, incrementó los rendimientos de forraje y suprimió el “Leafy spurge”.

Leafy spurge (*Euphorbia esula* L.) is an invasive noxious weed that alters the function and structure of North American rangeland ecosystems. Leafy spurge was introduced from Eurasia into the northern Great Plains and prairie provinces of Canada in the

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late 1800s (Watson 1985) and now infests more than 1 million ha in North America (Dunn 1979). This invasive plant displaces native species (Belcher and Wilson 1989) and reduces livestock carrying capacity (Lym and Kirby 1987). Leafy spurge invasiveness is attributed to its ability to reproduce from seed, adventitious shoot buds on the crown and roots (Raju 1985), and the lack of natural enemies in North America (Harris et al. 1985). High seed yields and viability and rapid seedling development enable new infestations to establish quickly (Selleck et al. 1962). Past management practices appear to have hastened leafy spurge establishment and spread in the Great Plains (Masters et al. 1996).

Chemical and biological controls have been the primary means to manage leafy spurge. Long-term control of leafy spurge is possible with picloram (4-amino-3,5,6-trichloro-2-pyridinecarboxylic acid) applied at 2.2 kg a.i. (active ingredient) ha^{-1} or greater rates (Lym and Messersmith 1985). The high cost of this treatment and concerns about surface water and groundwater contamination precludes picloram use on large infestations. Application of 2,4-D [(2,4-dichlorophenoxy)acetic acid] + picloram at 1.1 + 0.28 kg a.i. ha^{-1} or 2,4-D alone at 2.2 kg a.i. ha^{-1} provides short-term control of leafy spurge and reduces seed production. Imazapic {2-[4,5-dihydro-4-methyl-4-(1-methyl-ethyl)-5-oxo-1H-imidazol-2-yl]-5-methyl-pyridine carboxylic acid}, applied in the fall for 2 consecutive years at 140 g a.i. ha^{-1} controlled more than 90% of the leafy spurge 11 to 12 months after the second application (Masters et al. 1998). The efficacy of imazapic results from high absorption, preferential translocation to roots and adventitious shoot buds, and slow rate of metabolism of this herbicide by leafy spurge (Thompson et al. 1998). Biological control agents used against leafy spurge include goats (Lym et al. 1997), sheep (Landgraf et al. 1984), and insects (Hansen et al. 1997). Flea beetles reduced leafy spurge densities at some sites in North Dakota, but these reductions did not have a positive effect on grass yields (Kirby and Carlson 1998). Establishment of flea beetle populations has been highly variable in the northern Great Plains and factors responsible for this uneven success have not been identified (Lym 1998).

Historically, rangeland weed management research has emphasized development of chemical and biological control tactics. There is growing recognition that rangeland weed research should shift from the search for a single control technology to development of integrated strategies composed of multiple technologies used in sequences and combinations that optimize weed control and rangeland improvement (Scifres 1987). A goal of rangeland weed management should be to improve degraded rangeland communities so they are less susceptible to invasion by weeds (Masters et al. 1996, Sheley et al. 1996, Masters and Nissen 1998). Invasive plants appear to be a symptom of management problems that must be corrected before sustained progress can be made toward controlling weeds and improving rangeland productivity. Removing a weed species with chemical or biological controls may only provide an open niche for another undesirable species unless desirable species are present to occupy the vacated niche. In many instances, rangeland vegetation has deteriorated to the point that desirable species are either not present or in such low abundance that plant community recovery may not occur without revegetation with desirable species.

Approaches that include herbicide application and establishing monoculture stands of introduced or native perennial grasses have been used successfully to suppress leafy spurge and improve forage production on rangeland. In Wyoming, seedbed preparation consisted of multiple applications of glyphosate [N-(phosphonomethyl)glycine] in spring and summer followed by tillage before planting introduced cool-season grasses (Ferrell et al. 1998). Introduced cool-season grasses were planted in a tilled seedbed following application of glyphosate and 2,4-D in North Dakota (Lym and Tober 1997). The planted grasses that were most effective in suppressing leafy spurge were 'Bozoisky' Russian wildrye [*Psathyrostachys juncea* (Fisch.) Nevski] and 'Luna' pubescent wheatgrass [*Elytrigia intermedia* (Host) Beauv.] in Wyoming, and 'Rebound' smooth bromegrass (*Bromus inermis* L.) and 'Reliant' intermediate wheatgrass [*Thinopyrum intermedium* (Host) Barkw. & D.R. Dewey] in North Dakota. In Nebraska, monoculture stands of native warm-season grasses, big bluestem (*Andropogon gerardii* Vitman), indiangrass [*Sorghastrum nutans* (L.) Nash], and switchgrass (*Panicum virgatum* L.), established on leafy spurge-infested rangeland increased herbage yields by more than 40% and reduced leafy spurge density and yield (Masters and Nissen 1998). The sites were treated with imazapyr {2-[4,5-dihydro-4-methyl-4-(1-methylethyl)-5-oxo-1H-imidazol-2-yl]-3-pyridinecarboxylic acid} and sulfometuron {2-[[[[(4,6-dimethyl-2-pyrimidinyl)amino]carbonyl]amino]sulfonyl]ben zoic acid} in the fall and burned the following spring before tallgrasses were planted into the herbicide-suppressed sod without tillage. These studies demonstrate that leafy spurge-infested rangeland can be improved in the short-term by planting monoculture stands of desirable forage grasses; however, the rate of leafy spurge recovery and management required to maintain monoculture grass stands, while suppressing leafy spurge, has not been determined.

The focus of our rangeland improvement research effort was to develop integrated management strategies that suppress leafy spurge and associated vegetation, and facilitate planting and establishment of multiple native warm-season grass and legume species. Conceptually, multispecies assemblages should more fully use resources on degraded rangeland and more completely preempt resource use by less desirable species, including leafy spurge.

The purpose of this study was to determine if application of herbicides followed by mowing or burning the herbaceous standing crop could enhance establishment of planted mixtures of native species and reduce leafy spurge productivity. Glyphosate and imazapic were the herbicides selected to suppress leafy spurge and existing resident vegetation. Glyphosate controls cool-season grasses that are actively growing at the time of application, but provides no residual weed control. Imazapic provides residual control of leafy spurge, annual grasses, and broadleaf plants that would interfere with establishment of planted species. Imazapic is tolerated by a number of warm-season grasses (Rivas-Pantoja et al. 1997, Beran et al. 2000), forbs (Beran et al. 1999a) and legumes (Beran et al. 1999b). Herbaceous standing crop was removed to reduce the quantity of the plant residue that would otherwise interfere with no-till of planting desirable native species into the herbicide-suppressed sod.

Materials and Methods

Experiments were established on leafy spurge-infested rangeland near Mason City (41° 17' N, 99° 17' W) and Tilden City (42° 00' N, 97° 53' W), Nebr. The distance between the sites is about 150 km, and Mason City and Tilden are located in south-central and northeastern Nebraska, respectively. These sites occur in the mixed-grass prairie region of the central Great Plains. Soil at Mason City was a Uly silt loam (mixed, mesic, Typic Haplustoll) and at Tilden was a Thurman fine sand (mixed, mesic, Udorthentic Haplustoll). The flora at both sites was dominated by leafy spurge, Kentucky bluegrass (*Poa pratensis* L.), and smooth bromegrass. Warm-season grasses at Mason City included buffalograss [*Buchloe dactyloides* (Nutt.) Engelm.], tall dropseed [*Sporobolus asper* (Michx.) Kunth], and red threeawn (*Aristida longiseta* Stued.). At Tilden, warm-season grasses included sand bluestem (*Andropogon halli* Hack.), big bluestem, sand dropseed [*Sporobolus cryptandrus* (Torr.) A. Gray], and blue grama [*Bouteloua gracilis* (H.B.K.) Lag. *ex* Steud.]. Both sites had a management history of moderate to heavy continuous grazing by cattle during spring and summer. Sites were not grazed or hayed during the study.

Experiments at both sites were designed as a randomized complete block arranged as a split-split plot with 4 replications per treatment combination. Standing crop management schemes were the main plot (10- by 48-m at Mason City and 16- by 30-m at Tilden), herbicides were the subplot (8- by 5-m in size), and native plant mixtures were the sub-subplot (8- by 1.6-m in size) treatments. At Mason City, the standing crop on 4 main plots was mowed to a 10 cm stubble height followed by removal with a dump rake on 3 April 1996 and was removed from the remaining 4 main plots by burning on 4 April 1996. At Tilden, the Kentucky bluegrass thatch that remained after mowing and raking the standing crop on 4 of the 8 main plots on 8 April 1996 was too heavy to allow penetration of the grass drill double disk openers during planting. This thatch layer was reduced on 9 April 1996 with a self-propelled dethatcher followed by raking. Standing crop was removed from the remaining main plots by burning on 17 April 1996. Main plots at both sites were burned according to Masters et al. (1990).

Herbicide treatments were applied to separate subplots in October 1995 and June 1996. Glyphosate at 1600 g a.i. ha^{-1} was applied alone or in combination with imazapic at 140 or 210 g a.i. ha^{-1} on 3 October 1995 at Mason City and 11 October 1995 at Tilden. Imazapic was applied at 70 g a.i. ha^{-1} on 19 June 1996 at Mason City and 17 June 1996 at Tilden to half the number of plots that had been treated with imazapic in October 1995. This treatment was used to determine if additional suppression of leafy spurge and less desirable warm-season grasses (red threeawn, sand dropseed, buffalograss, and blue grama) by imazapic applied in June 1996 would further enhance establishment of the planted species. Leafy spurge and cool-season grasses were growing, and warm-season grasses were dormant when herbicides were applied in October. Leafy spurge and cool-season grasses were flowering, while warm-season grasses were vegetative when herbicide was applied in June. Herbicides were applied in a total delivery volume of 187 liters ha^{-1} at 3 km hour^{-1} and at 250 kPa with a tractor-mounted, compressed-air-pressurized sprayer. Methylated seed oil and 28% urea ammonium fertilizer, each at 1.25% (v/v), were included in spray solutions to optimize foliar uptake of herbicides.

At each site, there were 3 different planting treatments per sub-subplot. Two seed mixtures, grass mixture only or grass and legume mixture, were planted in separate sub-subplots, and no species were planted in the third sub-subplot. Equal numbers of pure live seed of each species were included in each mixture to achieve a seeding rate of 440 pls m^{-2}. The grass species in the grass or grass and legume mixtures were big bluestem, indiangrass, switchgrass, little bluestem [*Schizachyrium scoparium* (Michx.) Nash], and sideoats grama [*Bouteloua curtipendula* (Michx.) Torr.]. Legumes in the grass and legume mixture were leadplant [*Amorpha canescens* (Nutt.) Pursh], Illinois bundleflower [*Desmanthus illinoensis* (Michx.) MacM.], and purple prairieclover (*Petalostemum purpurea* Vent.). Seed mixtures were planted directly into the sod with no tillage on 11 April 1996 at Mason City and 26 April 1996 at Tilden using a 7-row plot drill with an 18-cm spacing between rows at a 1.3-cm depth. Native

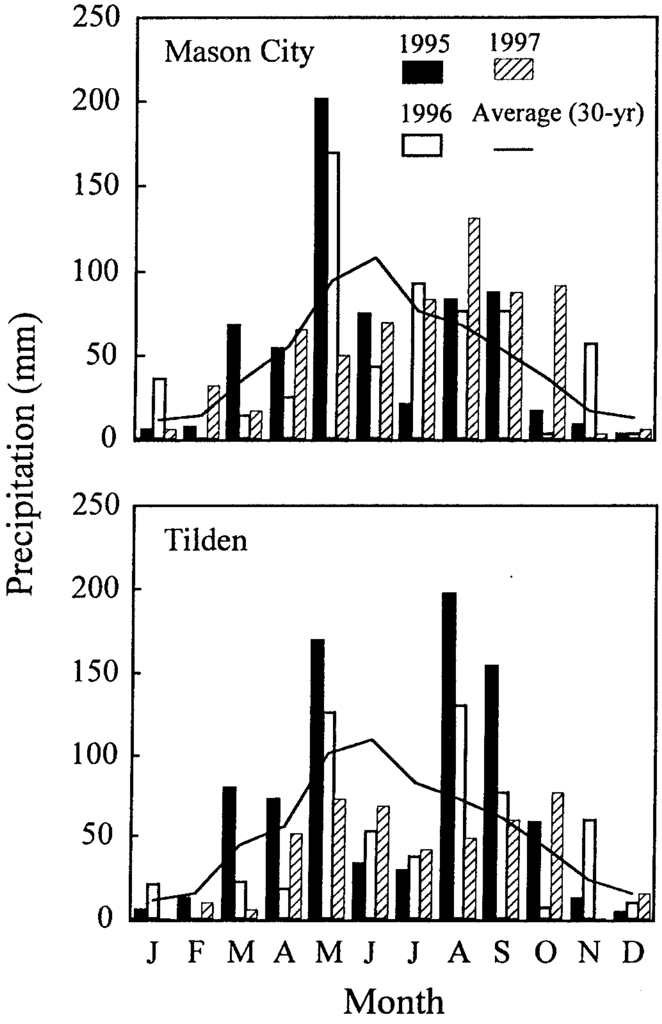

Fig. 1. Monthly precipitation for 1995 through 1997 and 30 year averages at Mason City and Tilden, Nebr.

plant mixtures were planted without tillage to reduce soil erosion, soil water loss, and cost of seedbed preparation.

Frequency and herbage dry matter yield were measured between 14 and 16 months after planting. Measurements were taken the year after planting because establishment of perennial plants from seed is best determined after plants have survived a period of dormancy during the winter (Cook and Stubbendieck 1986). Both sites were burned in mid-spring 1997 to reduce interference of standing dead herbage with vegetation sampling.

Frequency was measured because it integrates pattern and abundance (Goldsmith and Harrison 1976), 2 important attributes when determining planted species establishment. Frequencies were determined in mid-June 1997 using a 90- by 90-cm (0.81 m^2) metal frame partitioned into a grid of twenty-five, 18- by 18-cm, cells. The frame was placed over the center 5 rows at 2 locations within each subplot. Presence or absence of a seeded grass or legume in each cell within the frame was recorded. Frequency within each frame was calculated by dividing the number of cells that contained at least 1 seeded species by 25 and then multiplying by 100 to convert the calculated proportion to a percentage. For this study, a threshold frequency above which establishment of the planted grasses was considered successful was determined. Launchbaugh and Owensby (1970) reported that >10 plants m^{-2} were needed for successful grass establishment in the central Great Plains. We estimated that a planted grass frequency of 32% (≥ 1 grass plant in 8 of the 25 cells within the grid used to determine frequency) was about equivalent to 10 plants m^{-2}. This is a conservative estimate, since it is based on the presence of only 1 seeded grass plant in each of 8 cells within the frequency grid.

Dry matter yield of selected components of the vegetation and leafy spurge shoot density were determined in early August 1997. Dry matter yields were determined by harvesting vegetation within two, 0.25-m^2 quadrats within each sub-subplot. Vegetation within each quadrat was clipped to a 2-cm stubble height, separated, oven-dried at 60° C to a constant weight, and weighed. Vegetation was separated into the following categories: big bluestem; switchgrass; indiangrass; little bluestem; sideoats grama; purple prairieclover; leadplant; Illinois bundleflower; leafy spurge; warm-season grasses (not including planted grasses); cool-season grasses; and forbs (not including planted legumes or leafy spurge). Leafy spurge density was determined by recording the number of live shoots emerging from the soil surface within quadrats placed in each sub-subplot during harvest.

Data from each site were analyzed separately using the general linear model procedure (SAS 1996). Frequency, density, and yield data were tested by analysis of variance using a split-split plot model. Response variables were analyzed within site because several variables had significant ($P \le 0.05$) site interactions and heterogeneous error variances as indicated by Hartley's F-max test (Hartley 1950). Planted species and leafy spurge yield data were log transformed (Lentner and Bishop 1993). Data from significant ($P \le 0.05$) highest order interactions are presented with means separated using Fisher's- protected LSD (alpha = 0.05) (Ott 1977).

Results and Discussion

Annual precipitation at National Oceanographic and Atmospheric Administration stations within 15 km of the study sites during 1995, 1996, and 1997 ranged from 2 to 10% above the 30-year average near Mason City and from 30% below average to 29% above average near Tilden (Fig. 1). April through August encompasses the time that the perennial native grasses and legumes were planted and period of peak production of the various vegetation components. Cumulative precipitation from April through August 1996 near Mason City was 408 mm and near Tilden was 368 mm. Cumulative precipitation was 401 and 286 mm at Mason City and Tilden during this period in 1997.

Leafy spurge density and yield in August 1997 were usually reduced where imazapic was applied with glyphosate (Table 1). At Mason City, leafy spurge density averaged 147 shoots m^{-2} where no herbicide was applied and 62 shoots m^{-2} where imazapic at 210 g ha^{-1} was applied with glyphosate. At Tilden, leafy spurge densities averaged ≥ 97 shoots m^{-2} where no herbicide or glyphosate was applied. In contrast, leafy spurge densities were reduced to ≤ 14 shoots m^{-2} where imazapic was applied with glyphosate. At both sites, leafy spurge yields were reduced more than 65% where imazapic was applied with glyphosate compared with yields where no herbicide was applied. Imazapic reapplied in June 1996 did not provide additional reduction in leafy spurge density or yield compared with imazapic applied in October 1995. The amount of imazapic applied in June may have been insufficient to provide additional leafy spurge control.

At Mason City, native grass frequency was influenced by herbicide and standing crop treatments (Table 2). Native grass frequencies where no herbicide or only glyphosate was applied were 11% or less compared with frequencies that exceeded 34% where imazapic was applied with glyphosate. Native grass establishment was successful (≥ 32%) only where imazapic was applied with glyphosate. Frequencies were greater where the residue was mowed and raked before planting. Residue that remained after mowing and raking could have ameliorated the seedbed environment, dampening

Table 1. Leafy spurge density and yield at rangeland sites near Mason City and Tilden, Nebr. in August 1997 that were treated with herbicides, burned or mowed, and seeded with grass or grass and legume mixtures.[1, 2]

	Rate		Mason City		Tilden	
Herbicide	Fall	Spring	Density	Yield[3]	Density	Yield[3]
	(g a.i. ha^{-1})		(no. m^{-2})	(kg ha^{-1})	(no. m^{-2})	(kg ha^{-1})
Non-Treated	0	0	147	340 a	117	240 a
Glyphosate	1600	0	125	250 b	97	150 a
Imazapic + glyphosate	140 1600	0 0	82	120 c	14	60 b
Imazapic + glyphosate	140 1600	70 0	59	100 c	4	10 c
Imazapic + glyphosate	210 1600	0 0	62	120 c	8	10 c
Imazapic + glyphosate	210 1600	70 0	34	50 c	1	0 d
LSD $_{(0.05)}$			65	—	22	—

[1] Herbicides were applied in October 1995 (Fall) and June 1996 (Spring). Burn and mow treatments were applied and grass and grass and legume mixtures were planted in April 1996.

[2] Measured attributes are averaged across burn and mow treatments and planting treatments.

[3] Means followed by the same letter within a column are not significantly different ($P \le 0.05$). Non-transformed means are presented, but mean separation test is based on analysis of log transformed data.

Table 2. Frequency of planted native grasses (NG) and purple prairieclover (PPC) in June 1997 at rangeland sites near Mason City and Tilden, Nebr. that were treated with herbicides, burned (B) or mowed (M), and seeded with grass (G) or grass and legume mixtures (GL).[1]

			Mason City			Tilden				
	Rate		NG[2]			NG				
						B		M		
Herbicide	Fall	Spring	B	M	PPC[3]	G	GL	G	GL	PPC[3]
	(g a.i. ha^{-1})		(%)							
Non-Treated	0	0	0	1	0	0	1	0	0	0
Glyphosate	1600	0	0	11	4	33	51	33	33	4
Imazapic + glyphosate	140 1600	0 0	34	69	26	79	29	58	61	11
Imazapic + glyphosate	140 1600	70 0	45	73	20	57	63	68	45	11
Imazapic + glyphosate	210 1600	0 0	48	63	18	65	63	49	53	12
Imazapic + glyphosate	210 1600	70 0	53	68	19	69	50	61	59	15
LSD $_{(0.05)}$			12		8	16				8

[1] Herbicides were applied in October 1995 (Fall) and June 1996 (Spring). Burn and mow treatments were applied and grass and grass and legume mixtures were planted in April 1996.

[2] Native grass frequencies are averaged across grass and grass and legume mixture treatments.

[3] Purple prairieclover frequencies are averaged across burn and mow treatments.

variations in temperature extremes and soil water loss, compared with areas where the residue was consumed by fire.

At Tilden, native grass frequency was influenced by the interaction of herbicide, residue, and planting treatments (Table 2). Native grass frequencies where no herbicide was applied were 1% or less compared with frequencies that usually exceeded 32% where glyphosate was applied with or without imazapic. In a few instances, grass frequencies were lower where the grass and legume mixture had been planted compared with where only the grass mixture was planted. This could have been because more grass seeds were planted in the grass mixture compared with the grass and legume mixture. The total seeding rate was 440 pls m^{-2} per mixture, which was 88 pls m^{-2} for each of the 5 species planted in the grass mixture and 55 pls m^{-2} for each of the 8 species (5 grasses and 3 legumes) in the grass and legume mixture.

Imazapic applied with glyphosate improved combined yields of the planted species in the grass mixture or grass and legume mixture at both study sites (Tables 3 and 4). Combined yields ranged from 3.0 to 4.6 Mg ha^{-1} at Mason City and 1.9 to 3.0 Mg ha^{-1} at Tilden where imazapic was applied with glyphosate. In contrast, yields were 0.3 Mg ha^{-1} at Mason City and 1.2 Mg ha^{-1} at Tilden where only glyphosate was applied, and 0.3 Mg ha^{-1} or less at both sites where no herbicide was applied. Big bluestem and indiangrass were the dominant grasses in the planted stands. They comprised more than 60% of the combined yields where imazapic was applied with glyphosate at both sites. Big bluestem, indiangrass, and little bluestem yields at Mason City were greater where imazapic was applied than where no herbicide or only glyphosate was applied (Table 3). Sideoats grama and switchgrass yields were very low, regardless of herbicide treatment. Sideoats grama yields may have been low because this mid-grass is not as productive and may not have been as competitive as the planted tallgrasses. Low yields of switchgrass may reflect its susceptibility to imazapic as reported by Masters et al. (1996). At Tilden, indiangrass yields were greatest where imazapic was applied with glyphosate, whereas there was no difference in big bluestem yields where glyphosate was applied with or without imazapic (Table 4). When assessing yields of the various species within the planted mixtures it is important to note that these data reflect species composition early in the development of these plant stands. The distribution and composition of species will likely change as the stands mature under prevailing climate and management regimes.

Purple prairieclover was the only legume to persist 14 months after planting at both study sites. Frequency of purple prairieclover was ≥ 18% and 11% where

Table 3. Yield of big bluestem (BB), indiangrass (IN), little bluestem (LB), sideoats grama (SG), switchgrass (SW), and purple prairieclover (PPC) and combined yield of grass (G) and grass and legume (GL) mixtures in August 1997 at a rangeland site near Mason City, Nebr. that was treated with herbicides, burned (B) or mowed (M), and seeded with grass or grass and legume mixtures.[1, 2]

	Rate		Planted species[3]					
Herbicide	Fall	Spring	BB	IN	LB	SG + SW	PPC	Combined yield[4]
	(g a.i. ha^{-1})		(Mg ha^{-1})					
Non-Treated	0	0	0 a	0 a	0 a	0 a	0 a	0 a
Glyphosate	1600	0	0.1 b	0.1 b	0 a	0 a	0 a	0.3 b
Imazapic + glyphosate	140 1600	0 0	0.8 c	1.6 c	0.3 b	0.1 a	0.6 b	3.0 c
Imazapic + glyphosate	140 1600	70 0	0.9 c	2.1 c	0.3 b	0 a	0.2 b	3.5 c
Imazapic + glyphosate	210 1600	0 0	0.8 c	1.8 c	0.5 b	0 a	0.3 b	3.3 c
Imazapic + glyphosate	210 1600	70 0	1.1 c	2.9 c	0.3 b	0 a	0.4 b	4.6 c

[1] Herbicides were applied in October 1995 (Fall) and June 1996 (Spring). Burn or mow treatments were applied and grass or grass and legume mixtures were planted in April 1996.

[2] Means followed by the same letter within a column are not significantly different ($P \leq 0.05$). Non-transformed means are presented, but mean separation test is based on analysis of transformed data.

[3] Planted grass yields are averaged across planted grass and grass and legume mixtures and burn and mow treatments. Prairieclover yields are averaged across burn and mow treatments.

[4] Combined yields are averaged across planted grass and grass and legume mixtures and burn and mow treatments.

Table 4. Yield of big bluestem (BB), indiangrass (IN), little bluestem (LB), sideoats grama (SG), switchgrass (SW), and purple prairieclover (PPC) and combined yield of grass (G) and grass and legume (GL) mixtures in August 1997 at a rangeland site near Tilden, Nebr. that was treated with herbicides, burned (B) or mowed (M), and seeded with grass or grass and legume mixtures.[1, 2]

Herbicide	Rate		Planted species[3]				
	Fall	Spring	BB	IN	SG + LB +SW	PPC	Combined yield[4]
	(g a.i. ha^{-1})		(Mg ha^{-1})				
Non-Treated	0	0	0 a	0.1 a	0.2 a	0 a	0.3 a
Glyphosate	1600	0	0.4 b	0.2 a	0.5 a	0.2 b	1.2 b
Imazapic + glyphosate	140 1600	0 0	0.5 b	0.9 b	0.4 a	0.1 b	1.9 c
Imazapic + glyphosate	140 1600	70 0	0.8 b	1.3 b	0.7 a	0.3 b	3.0 c
Imazapic + glyphosate	210 1600	0 0	0.6 b	0.9 b	0.8 a	0.2 b	2.4 c
Imazapic + glyphosate	210 1600	70 0	0.7 b	1.4 b	0.5 a	0.2 b	2.6 c

[1] Herbicides were applied in October 1995 (Fall) and June 1996 (Spring). Burn or mow treatments were applied and grass or grass and legume mixtures were planted in April 1996.

[2] Means followed by the same letter within a column are not significantly different ($P \leq 0.05$). Non-transformed means are presented, but mean separation test is based on analysis of transformed data.

[3] Planted grass yields are averaged across planted grass and grass and legume mixtures and burn and mow treatments. Prairieclover yields are averaged across burn and mow treatments.

[4] Combined yields are averaged across planted grass and grass and legume mixtures and burn and mow treatments.

imazapic was applied with glyphosate at Mason City and Tilden, respectively (Table 2), compared with 4% or lower frequencies where no herbicide or only glyphosate was applied. Purple prairieclover yields were greater at both sites where herbicides had been applied and contributed at most 20% and usually less than 10% to the combined herbage yield (Tables 3 and 4). Illinois bundleflower was common at both sites within the first 3 months after planting, but did not persist. Leadplant was rarely observed during the study.

Successful establishment of only 1 of the 3 planted legume species in this study highlights potential problems using native legumes in rangeland revegetation programs. High cost, low availability, and variable quality of native legume seeds further constrain their use. Legumes may improve N availability in degraded rangeland ecosystems, while providing a sustainable and higher quality forage resource. Posler et al. (1993) found that certain legumes native to the central Great Plains, e.g., Illinois bundleflower, roundhead lespedeza (*Lespedeza capitata* Michx.), and catclaw sensitivebriar [*Mimosa quadrivalvis* var. *nuttallii* (DC.) LS. Beard *ex* Barneby], improved forage yield and crude protein content when seeded with native warm-season grasses. Clearly, more information is needed about native legume compatibility with warm-season grasses, contribution to nitrogen fixation, seed production, and establishment methods before they can be recommended for use in rangeland improvement strategies.

Effects of herbicides on yields of resident cool- and warm-season grasses and forbs were inconsistent at both sites. At Mason City, cool-season grass yields ranged from 0.8 to 1.3 Mg ha^{-1} where imazapic was applied with glyphosate compared with 1.0 Mg ha^{-1} or more where glyphosate or no herbicide was applied. Warm-season grass and forb yields were not affected by herbicides and ranged from 0.3 to 0.5 Mg ha^{-1}. At Tilden, cool-season grass yields were not affected by herbicide treatments and ranged from 0.3 to 0.8 Mg ha^{-1}. Warm-season grass yields ranged from 0.6 to 0.8 Mg ha^{-1} where imazapic was applied with glyphosate and were < 0.3 Mg ha^{-1} where no herbicide or only glyphosate was applied. Yields of the warm-season grasses were less than 0.2 Mg ha^{-1} where grass or grass and legume mixtures were planted and were 1.3 Mg ha^{-1} where no species were planted. This response of the resident warm-season grasses resulted from remnant native grasses at Tilden that were released after leafy spurge and other resident vegetation was suppressed by the herbicides.

Total vegetation yield (planted species yield + resident vegetation yield) responses to the treatments varied by site. At Mason City, the interaction of herbicide and planting treatments was significant ($P \leq 0.05$) (Table 5). Yields, ranging from 2.0 to 2.7 Mg ha^{-1}, were similar across planting treatments where no herbicide or only glyphosate was applied. In contrast, total yields from imazapic-treated areas were greater and ranged from 4.1 to 7.0 Mg ha^{-1} where grass or grass and legume mixtures were planted, while yields where no species were planted ranged from 2.3 to 3.2 Mg ha^{-1}. These substantive yield increases provide evidence for the suppression of existing vegetation by imazapic applied with glyphosate, which facilitated establishment of the planted species. Moreover, increased dry matter yield where the planted grasses were successfully established demonstrates that the productivity of the leafy spurge-dominated plant community was far lower than the potential for the site.

Total vegetation yield at Tilden was influenced by herbicides, but not by plant-

Table 5. Total yield of vegetation on rangeland sites near Mason City and Tilden, Nebr. in August 1997 that were treated with herbicides, burned or mowed, seeded with grass (G) or grass and legume mixtures (GL) or not seeded (NS).[1]

Herbicide	Rate		Mason City[2]			
	Fall	Spring	G	GL	NS	Tilden[2]
	(g a.i. ha^{-1})		(Mg ha^{-1})			
Non-Treated	0	0	2.1	2.0	2.3	1.1
Glyphosate	1600	0	2.3	2.4	2.7	2.3
Imazapic + glyphosate	140 1600	0 0	4.1	5.0	2.4	3.0
Imazapic + glyphosate	140 1600	70 0	4.7	5.8	3.2	4.0
Imazapic + glyphosate	210 1600	0 0	4.8	5.1	2.7	3.2
Imazapic + glyphosate	210 1600	70 0	7.0	4.7	3.0	3.3
LSD (0.05)				1.2		0.9

[1] Herbicides were applied in October 1995 (Fall) and June 1996 (Spring). Burn and mow treatments were applied and grass and grass and legume mixtures were planted in April 1996.

[2] Measured attributes are averaged across burn and mow treatments.

[3] Measured attributes are averaged across planting treatments and burn and mow treatments.

ing treatments. Total yields where imazapic was applied with glyphosate ranged from 3.0 to 4.0 Mg ha^{-1} compared with a yield of only 1.1 Mg ha^{-1} where no herbicide was applied (Table 5). Total yields were increased where imazapic was applied at 70 g a.i. ha^{-1} in June 1996 compared to yields where glyphosate was applied in October 1995. Total yields on areas treated with imazapic at 140 g a.i. ha^{-1} combined with glyphosate in October 1995 were greatest where imazapic was applied again in June 1996. Perhaps suppression of certain species in the resident vegetation caused by the June 1996 imazapic treatment favored some of the planted or resident species. The reasons for this positive response were not evident from yields of the planted species (Tables 3 and 4) or resident vegetation components.

Imazapic and glyphosate were essential components of treatments applied before planting to improve establishment of native grass and legume stands on the leafy spurge-infested grasslands evaluated in this study. Applying these herbicides together reduced leafy spurge and other resident vegetation, which facilitated establishment of the planted native species in less than 2 years. Planted species yields were increased substantially and leafy spurge density and yield were reduced by imazapic applied with glyphosate compared with glyphosate applied alone or no herbicide. Increases in total yields where native species were seeded at Mason City and where imazapic was applied with glyphosate at Tilden indicate that the inherent productivity of the site was not being fully expressed by the plant community dominated by leafy spurge, Kentucky bluegrass, and smooth bromegrass. These yield increases reflect the considerable contribution of the warm-season native plants, which appeared to use site resources more efficiently than the cool-season plants that dominated the leafy spurge-infested communities. This strategy took less than 2 years to substantively improve the forage resource and reduce leafy spurge. These plant stands should be evaluated over several years to determine changes in species composition and productivity, and rate of leafy spurge recovery.

Established mixtures of native species have the potential to more fully utilize grassland resources and preempt resource use by leafy spurge and the other less desirable species. By maximizing resource capture, the more diverse reestablished grassland community could be more resistant to invasion by less desirable species. Tilman et al. (1996) determined that plant productivity and nitrogen use were greater in more diverse plant species mixtures than less diverse mixtures. This supports the concept that differences in resource use by multiple plant species allows more diverse plant communities to more fully use resources than less diverse plant communities and improve overall productivity (Frank and McNaughton 1991, McNaughton 1993, Naeem et al. 1994). More diverse grassland communities also should be more resilient (Tilman and Downing 1994) and better able to sustain stable ecosystem processes over a range of disturbances, e.g., grazing, fire, and periodic droughts, and return to a desirable state once disturbances moderate.

Our goal was to provide rangeland managers with strategies that extend beyond controlling undesirable vegetation and lead to restoring degraded rangeland communities by reintroducing desirable native plant mixtures. Establishing mixtures of desirable species, as demonstrated in this study, represents an important step in the process of recapturing the productive potential of leafy spurge-infested sites in the central Great Plains. Once these desirable species establish, management systems must be used that shift the competitive advantage to desirable species and away from invasive species. Chemical and biological controls will continue to be important components of these management systems because of the continued threat leafy spurge will pose to these restored communities. The strategy developed in this study has the potential to provide the means to redirect the successional trajectory of the leafy spurge-infested communities towards a more desirable community comprised of native prairie flora with improved carrying capacity and native plant diversity, and decreased leafy spurge abundance.

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Statistical analyses of fluorometry data from chloroform filtrate of lamb feces

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Abstract

Accurately identifying the botanical composition of free-ranging animal diets remains a challenge. Currently accepted procedures are time consuming, many requiring painstaking sample preparation while none produce data useful for real-time management. Automated procedures focusing on detection of chemical and/or physical plant properties using specific molecules called fluorophores offers possibilities for determining the species composition of herbivore diets. This study was designed to evaluate fluorometry techniques in herbivore diet determinations using fecal samples obtained from 13 lambs fed a basal diet of tobosa hay (*Pleuraphis mutica* Buckley), and containing 4 different levels (0, 10, 20, and 30%) of tarbush (*Flourensia cernua* D C.) leaf material. Chloroform ($CHCl_3$) filtrate obtained from the lamb's feces was exposed to UV light from a xenon arc lamp. This caused fluorophore molecules in the filtrate to have their outer shell electrons move to a higher energy state as a result of UV light excitation. After excitation by UV light at 310, 320, 330, 340, 350, and 355 nm, the fluorophores returned to their ground state giving off light (fluorescence). This fluorescence intensity (counts) varied and when captured using appropriate electronics, produced 1,024 pairs of light intensities (counts) and fluorescent wavelengths between 175 and 818 nm in 0.63 nm increments. Previous research indicated differences among diets could be determined using distinct peaks in the red and blue regions of the visible light spectrum and a univariate (1 variable at a time) analysis. This research demonstrates the entire fluorescence data set can be used to determine differences among diets using multivariate statistics. Sequences of 5 increasingly complex statistical techniques were used to distinguish among diets: 2-dimensional plots, polynomial regression models, confidence interval plots, discriminant analysis, and 3-dimensional plots. Two-dimensional plots indicated 2 spectral fluorescence peaks, 1 in the blue-green (420–600 nm) and 1 in the red (640–720 nm) region of the visible

Resumen

El identificar en forma certera la composición botánica de la dieta de animales en libre pastoreo sigue siendo un reto. Los procedimientos actualmente aceptados consumen mucho tiempo y muchos requieren una laboriosa preparación de la muestra, mientras que ninguno produce datos útiles en términos de manejo real de tiempo. Los procedimientos automatizados enfocados a la detección de propiedades físico-químicas de las plantas mediante el uso de moléculas especificas llamadas fluroforos ofrecen posibilidades alentadoras para determinar la composición de especies de la dieta de los herbívoro. Este estudio se diseño para evaluar las técnicas de flurometría en la determinación de la dieta de herbívoros utilizando muestras fecales obtenidas de 13 corderos alimentados con una dieta basal de heno de toboso (*Pleuraphis mutica* Buckley) y conteniendo cuatro diferentes niveles (0, 10, 20, y 30%) de hojas "Tarbush" (*Flourensia cernua* D C.). Un filtrado de cloroformo ($CHCL_3$) obtenido de las heces de los corderos se expuso a la luz ultravioleta (UV)de una lampara de arco de xenón. Esto causo que los electrones de las órbitas exteriores de las las moléculas de los fluoroforos del filtrado cambiaran a un estado de alta energía resultante de la excitación por la luz UV. Después de la excitación por la luz UV a 310, 320, 330, 340 y 350 nm, los fluoroforos regresaron a su estado inicial quedando sin fluorescencia. Esta intensidad de fluorescencia (conteos) variaron, cuando son capturados con los aparatos apropiados, produjeron 1,024 pares de intensidades de luz (conteos) y longitudes de onda fluorescente entre 175 y 818 nm con incrementos de 0.63 nm. La investigación previa indica que la diferencia entre dietas pude ser determinada utilizando distintos picos en las regiones azul y roja del espectro de luz visible y un análisis univariado (1 variable a la vez). Esta investigación demuestra que el conjunto completo de los datos de fluorescencia puede ser utilizado para determinar diferencias entre las dietas mediante el uso de estadística multivariada. Se utilizaron las secuencias de 5 técnicas estadísticas que incrementan en complejidad para distinguir entre las dietas: gráficas bidimensionales, modelos de regresión polinomial, gráficas de intervalos de confianza, análisis discriminante y gráficas tridimensionales. Las gráficas bidimensionales indicaron 2 picos de espectro de fluorescencia, 1 en la región azul-verde (420–600 nm) y 1 en la región roja (640–720 nm) del espectro visible. Debido a la naturaleza asimétrica de estos picos se desarrollaron polinomiales de quinto orden para diferenciar entre 4 dietas. La confiabilidad estadística fue alta cuando se discrimino entre dietas que

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spectrum. Because of the asymmetrical nature of these peaks, fifth-order polynomials were developed to differentiate among the 4 diets. Statistical reliability was high when discriminating between diets containing no tarbush leaf and the diets containing 30% tarbush leaf; however, it was not possible to statistically separate diets containing intermediate (10 and 20%) amounts of tarbush leaf material from each other or from the 2 extremes (0 and 30% tarbush leaf). These results suggest spectral signatures arising from fluorometry data may be useful for differentiating among botanical composition diets that differ in plant form, but that a multivariate approach may require large sample sizes.

Key Words: **Cattle, botanical composition, fluorescence, xenon fluorometry, fecal fluorophores**

no contenían hojas de "Tarbush" y dietas conteniendo 30% de hojas de "Tarbush"; sin embargo, no fue posible separar estadísticamente las dietas que contenían cantidades intermedias (10 a 20%) de hojas de "Tarbush", no se pudieron separar entre ellas o de las otras 2 dietas extremos (0 y 30% de hojas de "Tarbush". Estos resultados sugieren que firmas espectrales que surgen de los datos de la flurometría pueden ser útiles para diferenciar entre la composición botánica de dietas que difieren en la forma de la planta, pero se puede requerir un análisis multivariado para tamaños de muestra grandes

Determining the components comprising free-ranging herbivore diets is crucial to evaluating the nutritional well being and implementing herbivore management as well as maintaining positive plant relationships within ecological communities. Therefore, it is essential for managers to not only know what kind and amount of forages are available, but also which species are actually being eaten.

Diets are currently determined using various techniques. Probably the oldest and least automated technique is that of direct observation of foraging animals (Bjugstad et al. 1970). The bite count procedure, as it is frequently called, is still used (Doherty et al. 1999); yet, it is often inappropriate for some animal species and landscapes, and is always of concern scientifically because of the ever-present effect of observer influence. All other animal-based techniques require sampling digesta from 1 or more locations along the digestive tract (Holechek et al. 1984). The microhistological technique is the predominant method currently used for identifying dietary botanical composition of free-ranging animals (Bennett et al. 1999, Bontti et al. 1999), with feces being the most commonly used samples since they represent a broad spatial and temporal range of dietary intakes (Norbury and Sanson 1992). Plant fragments too small to identify taxonomically, the overestimation of indigestible materials and the underestimation of readily digested materials such as leaf material, are just some of the problems that beset microhistological analysis. A major limitation to this technique as a management tool is the amount of time required for sample preparation and analysis thus preventing its usefulness in making real-time management decisions. Two recent automated techniques for determining botanical composition of animal diets having shorter analytical time requirements are near infrared reflectance spectroscopy (NIRS); (Garcia-Criado et al. 1991, Walker et al. 1998) and laser induced fluorescence (LIF); (Anderson et al. 1996, 1998). Although NIRS (Foley et al. 1998) and fluorometry (Lakowitz 1983, Guilbault 1990), of which LIF is one type, both rely on molecular properties, they differ in several important ways (Table 1).

The Fluorometric Technique

Fluorometry involves capturing light emitted from an excited molecule. All materials will emit fluorescence if excited with the proper excitation wavelength (Brach et al. 1977). Excitation is accomplished with an energy source, such as a xenon arc lamp or laser. This source, when focused at specific wavelengths and directed at a material, excites outer shell electrons from a ground state to a higher energy state. After excitation the electrons fall back to their ground state, many in a cascade fashion, and give off energy in the form of heat and light. The light emitted as a result of excitation has a longer wavelength than the excitation light and is termed fluorescence or more generally luminescence. This emitted light, when captured by a photo diode array, produces a unique spectral fluorescence fingerprint. These fluorophores and their unique individual fluorescence characteristics form the basis for identification. The objective of this research was to evaluate several statistical approaches using the entire spectral fingerprint to determine differences among fluorophores in a chloroform filtrate of feces from lambs fed differing diets.

Materials and Methods

Feces from 13 ruminally cannulated Polypay x Rambouillet lambs were fed a basal diet of tobosa (*Pleuraphis mutica* Buckley) hay with 0, 10, 20, and 30% tarbush (*Flourensia cernua* D C.) leaf was added to provide 4 dietary treatments. The feces collected were taken in conjunction with a metabolism study previously reported by King et al. (1996). Collection of the samples used in these fluorometry analyses and the sample preparation procedures has been previously described by Anderson et al. (1996) who used laser-induced fluorescence (LIF) to establish differences among these same diets.

This study differed from previous research (Anderson et al. 1996) in 3 ways. First, chloroform ($CHCl_3$), an organic polar solvent having a dipole moment

Table 1. Comparison of near infrared reflectance spectroscopy (NIRS) and fluorometry.

Characteristics	NIRS	Fluorometry
Measures	Vibrational energies (>700 nm)	Electron transitions (190 to 800 nm)
Pattern recognition	Focuses on blended chemical structures (many 2D response curves)	Focuses on specific chemical structures (specific 2D curves to 5D[1] response surfaces)
Sample state	Choice of specific solvents required (many materials absorb)	Many polar & non-polar solvents available (fewer materials fluoresce)
Post processing data	Complex algorithms "trainable" for indirect determination of alternative characteristics	Simple algorithms "trainable" for indirect determination of alternative characteristics

[1] Fluorescence lifetime represents the fourth dimension and rotational anisotropy* (the rate at which the fluorophore rotates in a liquid or gaseous solvent based on the fluorophore's size and the solvent's viscosity) represents the fifth dimension.

* Lakowitz, J. R. 1983. Principles of Fluorescence Spectroscopy. Plenum Press, New York, NY.

slightly less than that of water, containing fecal pellet filtrate was exposed to UV light from a xenon arc lamp instead of a laser. Second, the continuous fluorescence spectrum for 6 excitation wavelengths (310, 320, 330, 340, 350, and 355 nm) was used to determine differences among the diets instead of only evaluating individual peak features. Third, the fecal pellets were exposed at room temperature to chloroform for 24 hours, a shorter period of time than previously used, before the $CHCl_3$ extract was filtered through No. 4 Whatman Filter Paper. All pellets were intact and immediately removed before filtration except for one, a 100% tobosa diet fecal pellet in which the pellet had been ground through a Wiley mill to pass a 40-mesh (0.5 mm) screen before being placed in the chloroform. We did not consider the physical condition of the fecal material to be of concern since Anderson et al. (1996) demonstrated similar spectral signatures using feces from these same lambs when comparing ground and intact sheep fecal pellets. For this study, fecal pellets from only 13 of the original 16 lambs were available (King et al. 1996, Anderson et al. 1996). Lambs 1–3 received only the basal diet consisting of tobosa hay, lambs 4–6 received a diet consisting of 90% tobosa hay and 10% tarbush leaf, lambs 7–9 received a diet consisting of 80% tobosa hay and 20% tarbush leaf and lambs 10–13 received a diet consisting of 70% tobosa hay and 30% tarbush leaf.

Fecal filtrate was prepared and evaluated using a fluorometer at Sandia National Laboratory, Albuquerque, N. M. The fluorometer had as an excitation source a 150 watt, high-pressure xenon arc lamp (Oriel Model 68805 arc lamp with xenon bulb Model 6254). White light from the xenon lamp was focused into an F/4, 1/8 meter double monochromator (CVI Model 120, 200–400 nm range, 5 nm steps, 7 nm bandwidth) to reduce scattered light outside of the pass band of the monochromator. Light from the monochromator was then imaged into the center of an RF-3010-T FUV ultraviolet quartz sample cell (Spectrocell, Oreland, Penn). Scattered light and fluorescence from the chloroform filtrate was detected at 90 degrees to the incident excitation source. Excitation light was imaged into the entrance slit of an F/4, 1/8 meter imaging spectrometer (ISA Jobin Yvon, Edison, N. J., 200–700 nm range, 5 nm resolution). A 1,024-element intensified Reticon array (Model 1420, EG&G Princeton Applied Research, Trenton, N.J.) detected the light at the image plane. The detection spectrometer had 5 nm resolution. A calibrated D_2 lamp was used to determine the response of the detector system in the spectral range 200-400 nm. The spectrum of the D_2 lamp was calibrated by the manufacturer in accordance with the National Institute of Standards and Technology (NIST) standards. The relative output of the xenon lamp through the monochromator was measured using an Ophir Model PD-300-UV colorimeter.

Five excitation wavelengths (310, 320, 330, 340, and 350 nm) were selected for evaluation by 1 author (Tisone) based on his experience with fluorescence spectra. These 5 wavelengths produced the most visually prominent and distinct fluorescence features from among the 200 to 400 nm range of excitation wavelengths associated with response surfaces. A sixth excitation wavelength (355 nm) was also selected, corresponding to the single excitation wavelength previously used to produce LIF on samples of this same fecal material as previously reported (Anderson et al. 1996). Light intensity counts at each excitation wavelength were measured at fluorescent wavelengths between 175 and 818 nm in 0.63 nm increments. This resulted in a total of n = 1,024 pairs, each consisting of a fluorescent wavelength and an intensity count.

In previous work, Anderson et al. (1996) used LIF information from distinct peaks in the red and blue-green regions of the visible light spectrum to conduct statistical analyses. Responses were analyzed by analysis of variance using intensity counts and wavelengths for each peak and the red/blue count ratio. In addition, only univariate (i.e., 1 response at a time) statistical analyses were conducted.

This study examined the 4 dietary treatments using the entire spectrum of fluorescence light intensities, necessitating a more complex statistical sequence requiring 5 analyses. First, bivariate plots of light intensities versus fluorescence wavelengths were examined to decide on appropriate regression models. Next, regression models were fitted and the fitted regression coefficients were extracted for use in the next 3 statistical techniques to discriminate among diets. Given that a regression model is a good fit, the regression coefficients contain all statistical information about the shape of the response curve. Thus, the dimensionality of the problem was reduced from 2n (in this case 2,048) down to k = the number of regression coefficients. In addition, 2 of the last 3 techniques (discriminant analysis and 3-dimensional plots) add a multivariate component to the problem of distinguishing among diets by using more than 1 response at a time. The sequence of the 5 interrelated statistical techniques is now discussed in detail.

Two-dimensional Plots

Fluorescent light intensity (counts) was plotted against fluorescent wavelengths for each of the 6 excitation wavelengths using the GPLOT procedure in SAS (SAS Institute 1990b, 1990c). All data were plotted on the same scale to help visually distinguish similarities and differences among the 4 tarbush leaf treatments and to decide on appropriate regression models. Because of the consistent bimodal nature of the x-y plots with individual peaks of different magnitudes in the blue-green and red regions of the visible spectrum across all diets and animals, we decided to fit a polynomial to each of these regions for each of the 6 excitation wavelengths. A fifth-order polynomial was chosen because of slope asymmetry among the individual peaks.

Polynomial Regression Models

The fifth-order polynomial regression model (Neter et al. 1996) is given by

$$Y_i = \beta_0 + \beta_1 X_i + \beta_2 X_i^2 + \beta_3 X_i^3 + \beta_4 X_i^4 + \beta_5 X_i^5 + \epsilon_i , \qquad \textbf{(1)}$$

where Y_i is the intensity count at fluorescent wavelength i, for i = 1 to 1,024,

$\beta_0, \beta_1, \ldots, \beta_5$ are (unknown) regression parameters,

X_i is the i^th fluorescent wavelength which is a fixed constant and ranges from 175 to 818 nm,

$X_i^2, \ldots X_i^5$ are the higher powers of fluorescent wavelengths, and

ϵ_i are errors which are independent and identically distributed as $N(0, \sigma^2)$.

The REG procedure in SAS (SAS Institute 1989b) was used to model the data. There were 13 fitted models for each of the 6 excitation wavelengths and 2 regions of the visible spectrum (blue, green, or red), 1 for each lamb, with each model containing 6 regression coefficients. These regression coefficients were output for use in succeeding statistical analyses.

Confidence Interval Plots

Confidence interval plots represent a univariate statistical technique. After polynomials models were fitted, similarities and differences among the 4 tobosa diet models were examined using the individual regression coefficients (e.g., we compared intercepts for all 13 models of samples in chloroform). To statistically compare regression coefficients, it was necessary to have information about the reliability or precision of the estimates. Therefore, confidence intervals incorporating information from both the regression coefficient and its variability were used to compare coefficients for a particular term (e.g., the intercept) across diets. To view these diet comparisons graphically, confidence interval plots for each term were constructed (intercept, linear term, etc.) for each excitation wavelength. Identifiers for the 13 lambs fed with the 4 diets were represented along the vertical (Y) axis, and first-order regression coefficient estimates with their 95% confidence intervals were plotted on the horizontal (X) axis. For each fluorescent region (blue, green or red) within each excitation wavelength, there were 6 such plots, 1 for each regression coefficient. The plots were constructed using the PLOT procedure in SAS (SAS Institute 1990a). These plots provided a subjective, graphical way to compare the treatments univariately (i.e., 1 regression coefficient at a time). Discriminant analysis was used to compare treatments using all coefficients at the same time to distinguish more objectively among treatments.

Discriminant Analysis

Discriminant analysis, also known as discriminant function analysis, is a multivariate technique designed to address problems arising due to classification. In plant taxonomy, discriminant analysis has been used to classify an individual into 1 of several related species (Morrison 1976, Johnson and Wichern 1988). In general, data from individuals from several known, mutually exclusive classes are used to develop rules (discriminant functions) which will then allow classification of an unknown individual into 1 of the classes.

Implementation of discriminant analysis involves several steps. First, a statistical metric distance to the sample mean of each class (Mahalanobis distance) is determined for every individual in the data set. These distances are based on the individual's multivariate measures and are scaled relative to the variability associated with each variable. The individuals' true classifications and these metric distances are then used to develop formulas for estimating the probability that any individual belongs to a particular class. Using these formulas, the probability that an individual (whose classification is unknown) belongs to a class can be estimated for each class based on the individual's distances to the class means. The individual is then predicted to belong to the class for which the individual has the highest probability of belonging.

Pairwise generalized-squared distances are a unitless measure of the distances between class means—again, scaled relative to the variability in each variable. The magnitudes of these squared distances can give insight into the potential for separating 2 treatments.

To evaluate how well the discriminant analysis classified an individual, cross-validation was used. In the cross-validation procedure, 1 of the individuals is deleted while the remaining individuals are used to build the discriminant function. The deleted individual is then classified based on this new discriminant function. This process is repeated for each individual in the data set, and the number of mis-specifications are totaled to obtain the misclassification rates for each class

In these data, there were 4 classes ($c = 4$) representing the 4 diets, 6 classification variables (the intercept and the 5 estimated regression coefficients from the fifth-order polynomial model), and $n = 13$ lambs (4 for 70% tobosa mixed with 30% tarbush leaf, and 3 each for the remaining three diets). Discriminant analysis was used to develop classification rules, classify each lamb using cross-validation, and then determine if a lamb was properly classified into the correct diet class, all based on the values of the polynomial regression coefficients. The DISCRIM procedure of SAS (SAS Institute 1989a) was used to perform these analyses.

Having 13 observations limited the number of variables that could be examined at one time using discriminant analysis.

Three-dimensional Plots

Finally, 3-dimensional plots of the polynomial regression coefficients were used to study the spatial relationships among the 4 diet treatments graphically (JMP software, SAS Institute 1995). All subsets of 3 coefficients were picked and plotted on 3 axes. Changing the orientation of the axes (i.e., by rotating the axes at different angles) helped in understanding how the lambs were assigned to the various classifications, and which variables effectively separated the treatment groups spatially. This provides information regarding the utility of including each of the variables (regression coefficients) in the discriminant analysis. After choosing the coefficients that facilitated separation of the observations, the discriminant function analyses were performed again, using the DISCRIM procedure in SAS. Using variables that do not add useful information reduces the ability of many procedures to correctly distinguish among individuals from different treatments.

Results and Discussion

Two-dimensional Plots

Initially, plots of the fluorescent intensity counts versus fluorescent wavelengths were evaluated. In general, the feces from all 13 lambs at all 6 excitation wavelengths had a sharp distinct tall peak in the red (640–720 nm) and a relatively short broad peak in the blue-green (420–600

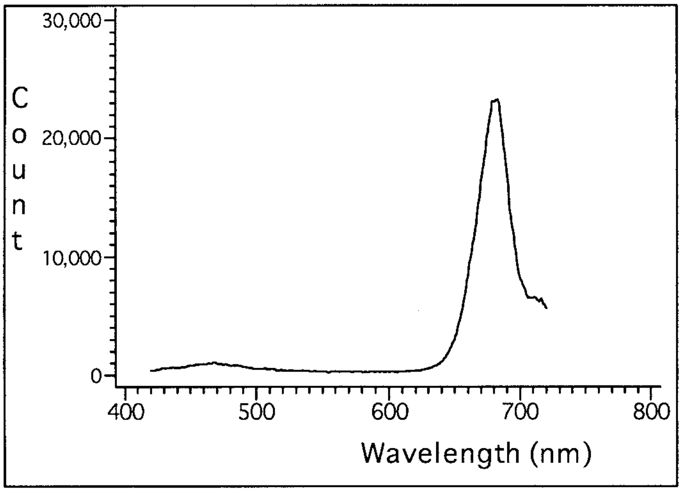

Fig. 1. Two dimensional plots of a raw fluorescence signature obtained from chloroform filtrate excited with a xenon light at 355 nm, obtained from lamb 1's feces representing a 100% tobosa hay diet. Plot represents fluorescence intensity (counts) vs. fluorescence wavelengths between 420 and 720 nm.

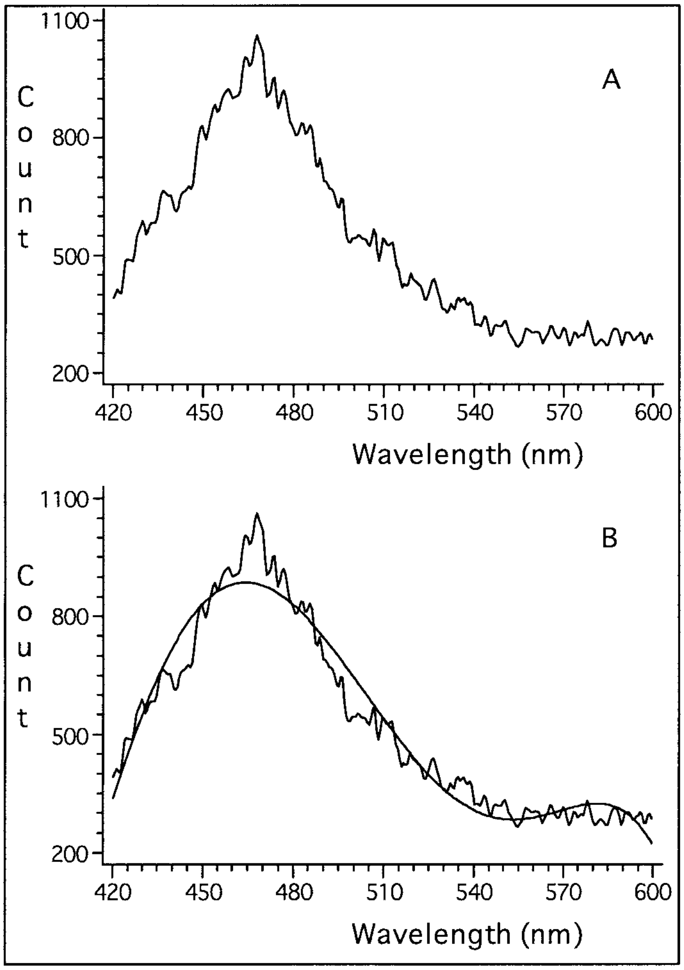

Fig. 2. Two dimensional plots of a raw fluorescence signature obtained from chloroform filtrate excited with a xenon light at 355 nm, obtained from lamb 1's feces representing a 100% tobosa hay diet. Plot (A) is the same data as for Fig. 1 but only for the blue-green region (420–600 nm) of the visible spectrum. Plot (B) represents a fifth-order polynomial superimposed over the blue-green region of the fluorescence spectrum.

nm) region of the visible spectrum. This bimodal characteristic was similar to that previously reported by Anderson et al. (1996) for these same feces when excited with Laser-Induced Fluorescence. Figure 1 depicts the fecal spectral signature from lamb 1 fed only the basal diet consisting of tobosa hay, excited at 355 nm over the range 420 to 720 nm. Figure 2A is from the same data for only the blue-green region. The curves were bimodal among all plots of the 6 different excitation wavelengths.

Of the 6 excitation wavelengths for which data were collected, only the extreme and middle excitation wavelengths (310, 330, and 355 nm) were used in further statistical procedures. As the other 3 excitation wavelengths were at intermediate levels (320, 340, and 350), they should not contribute much additional information in the diet characterizations. The sharp peaks (high counts) in the red region, were possibly from chlorophyll a (Krause and Weis 1984, Lang et al. 1991) and the relatively low peaks (low counts) in the blue-green region were from fluorophores possibly associated with cell wall bound ferulic acid (Lichtenthaler and Schweiger 1998). Therefore, the 2 regions were modeled separately.

Polynomial Regression Models

Polynomial regression is used when the true curvilinear response function is a polynomial function, but can also be used when the curvilinear response is unknown or complex, because a polynomial curve is often a good approximation of the true function (Neter et al. 1996). In this study, polynomial regression was used because the true curvilinear response was unknown. The 2-dimensional plots suggested a fifth-order polynomial model would capture most of the peak curvatures in both the red and blue-green regions of the fluorescence spectrum, including a commonly visible "shoulder" in the red region between 700 and 720 nm. Because of the magnitude of the X-values (fluorescent wavelengths), there was severe collinearity (linear relationships) among the predictors, X, X^2, …X^5. That is, there were high pairwise correlations between X and X^2, etc. This caused the polynomial regressions to be unstable, and resulted in the regression procedure incorrectly reporting coefficient estimates that were "biased" and "not unique." This is a common computational problem with polynomial models and was solved by centering the data at 0 (by subtracting the mean of the range of wavelengths) and scaling the range of the data to be approximately between –2 and +2 (by dividing by an appropriate constant) (Aiken and West 1991). For example, for the 420 to 600 nm range, the origin was shifted by subtracting 510 and the resulting deviations were divided by 45.

For each of the replicates at the excitation wavelengths of 310, 330, and 355 nm, a fifth-order polynomial equation was developed. After scaling, the fitted models had high R-square values, ranging from 0.908 to 0.998. Most of the regression coefficients were significant at the 5% level (e.g., of the 13 fitted models for the blue-green region at 355 nm, only 4 of 78 regression coefficients were not significant, see Table 2).

Summaries from the fitted model with estimated regression coefficients, Mean Square Error, and R-square for the blue-green and red regions at excitation wavelength 355 nm are given in Table 2. Figure 2B is a plot of the same data from Figures 1 and 2A with the fitted polynomial model from Table 2 superimposed.

Confidence Interval Plots

These plots visually depict how the 4 diets differed or were similar with respect to each term in the model. Coefficients that were similar had overlapping 95% confidence intervals while coefficients that were different had non-overlapping 95% confidence intervals. The latter was the case for all regression coefficients except the fourth-order term. The control diet (0% tarbush leaf) and the diet containing 30% tarbush leaf material, were readily distinguishable most of the time (for the blue-green region at 355 nm, 5 out of 6 confidence intervals plots were readily distinguishable). Five of the 6 plots from samples excited at 355 nm in the blue-green region indicated separation of the control diet from the diet containing the maximum amount of tarbush leaf material (30%), while neither of the other 2 diets containing 10% and 20% tarbush leaf material were visually distinguishable in any of the 6 plots. The models developed for the blue-green region of the fluorescence spectrum showed more visual separation than the models depicting the red region. Similar results were obtained for the other excitation wavelengths.

Plots of confidence intervals for each regression term suggested a possibility of separating the control diet from the diet containing 30% tarbush leaf material. To illustrate, Figure 3 shows a plot of the 95% confidence intervals for the first-order regression coefficient estimates for excitation wavelength 355 nm with emission in the blue-green spectral region. The vertical axis identifies the 13 lambs and the diets to which they had been randomly assigned. This plot shows the first-order coefficients are reasonably differentiated between the 70% and 100% tobosa diets, but not differentiated between the 80% and 90% tobosa diets. The extreme diets are generally differentiated from the middle diets, but not completely. For example, the confidence intervals for lamb 12 (consuming 30% tarbush leaf) and lamb 9 (consuming 20% tarbush leaf) overlap. This and similar plots suggest that first-order regression coefficient estimates are useful in separating lamb diets consisting of 30% tarbush leaf content from diets not containing tarbush leaf. However, at intermediate levels of tarbush leaf, it is not apparent that the first-order coefficients assist in separating diets—at least with these sample sizes.

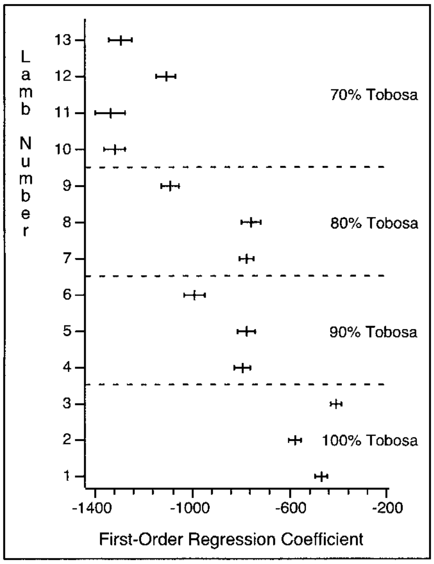

Fig. 3. First-order regression coefficient estimates of fluorometry data obtained from chloroform filtrate of fecal samples from 13 different lambs fed a basal diet of tobosa hay containing 4 levels (0, 10, 20, and 30%) of tarbush leaf. The middle vertical line on each symbol represents the linear coefficient point estimate, while the outer vertical lines represent the 95% confidence interval. The diets having estimates that are furthest apart are the most statistically dissimilar.

Table 2. Estimated regression coefficients of fluorescence data in the blue-green (420–600 nm)[1] and red (640–720 nm)[1] regions of the visible spectrum obtained from the excitation of chloroform filtrate of lamb fecal pellets excited with a xenon lamp focused at 355 nm using four diets differing in tarbush leaf content with mean square error (MSE) and coefficient of determination (R^2). Regression coefficients without "ns" below the number are significant ($\alpha = 0.05$).

Tarbush leaf in a basal diet of tobosa hay	Lamb	Intercept	Regression coefficients 420 to 600 nm						
			Linear	Quadratic	Cubic	Quartic	Quintic		
			X	X^2	X^3	X^4	X^5	MSE	R^2
(%)									
0	1	538.5	–471.6	83.6	190.6	–37.5	–20.0	2769.8	0.950
0	2	673.3	–578.3	–108.6	180.6	–39.9	–17.6	3321.8	0.972
0	3	531.1	–410.9	92.2	130.3	–34.2	–10.7	1946.4	0.964
10	4	869.1	–795.2	10.9 ns	373.5	–41.7	–44.9	5499.7	0.961
10	5	894.7	–775.7	–39.8	420.4	–33.1	–56.6	7452.2	0.940
10	6	1173.3	–993.8	–91.3	503.4	–31.3	–66.9	9968.8	0.955
20	7	922.8	–777.4	7.3 ns	332.8	–38.0	–38.4	4674.6	0.969
20	8	858.2	–759.4	–181.7	518.8	–4.4 ns	–81.3	8776.6	0.926
20	9	1362.8	–1089.9	–38.7	439.6	–32.1	–54.3	6603.2	0.980
30	10	1671.6	–1319.6	–230.6	623.1	–12.9	–82.9	9882.2	0.977
30	11	1364.8	–1339.0	–155.4	754.9	–39.5	–106.2	17674.0	0.952
30	12	1262.2	–1108.3	0.4 ns	456.6	–51.8	–52.1	7382.3	0.977
30	13	1578.0	–1296.4	–115.3	585.4	–41.7	–72.5	10668.0	0.975
			Regression coefficients 640 to 720 nm						
0	1	16984	13552.0	–4186.6	–6147.6	221.6	816.7	309413	0.995
0	2	11825	7191.7	–4017.1	–3382.7	435.9	460.9	45696	0.998
0	3	13844	9634.1	–4230.0	–4546.9	392.6	623.7	83045	0.997
10	4	15021	12690.0	–2870.1	–5613.3	7.3 ns	729.0	385263	0.992
10	5	14882	13094.0	–2645.5	–5733.7	–56.8 ns	733.0	380007	0.992
10	6	11349	6807.9	–3352.6	–3175.1	–319.3	440.9	70632	0.996
20	7	15333	11412.0	–4140.8	–5288.1	292.3	712.8	209464	0.995
20	8	8164	7997.7	249.6 ns	–2990.6	–427.6	326.8	351623	0.983
20	9	9066	4798.7	–3092.1	–2291.9	353.7	319.5	23722	0.998
30	10	10036	5350.6	–3354.6	–2571.9	375.9	359.9	24450	0.998
30	11	11945	9004.7	–2249.7	–3932.5	7.0 ns	508.4	192165	0.993
30	12	14341	10765.0	–3970.5	–5196.9	303.3	725.7	227452	0.994
30	13	9699	6125.5	–2886.0	–3087.8	277.5	444.4	41928	0.997

[1] Weast, R.C. (Ed). 1967 Handbook of Chemistry and Physics, 48th ed. CRC Press, Cleveland, Ohio, pp. E-133.

Discriminant Analysis

Among the 4 dietary treatments, discriminant function analysis provided a means for detecting differences in multidimensional space, as opposed to the confidence-interval plots that examined 1 dimension at a time. In this approach, the 13 lambs fed the 4 diets were treated as observations and the 6 regression coefficients were treated as variables. Each of the 3 excitation wavelengths (310, 330, and 355 nm) was individually evaluated for both the blue-green and red regions of the visible spectrum. The number of lambs sampled (13) was not high compared to the number of variables (6); therefore, no sharp demarcation was possible between intermediate diets. However, it was possible with discriminant analysis to delineate between control diets and those containing 30% tarbush leaf material.

Pairwise generalized squared distances and misclassification rates give insight and

Table 3. Misclassification results from discriminant analysis performed on polynomial regression coefficients obtained from fluorometry data of fecal chloroform filtrate differing in tarbush leaf content exposed to 355 nm xenon light. The values represent number of lambs classified incorrectly into a particular diet category by the discriminant analysis procedure when using spectral characteristics from both the blue-green (420–600 nm[1]) and red (640–720 nm[1]) regions of the visible spectrum.

Tarbush leaf in a basal diet of tobosa hay	Wavelength							
	420 to 640 nm				640 to 720 nm			
	30	20	10	0	30	20	10	0
(%)	(Count				(Count)			
30	3	1	0	0	2	2	0	0
20	0	0	2	1	1	1	1	0
10	0	3	0	0	1	1	1	0
0	0	0	0	3	0	1	0	2

[1] Weast, R.C. (Ed). 1967 Handbook of Chemistry and Physics, 48th ed. CRC Press, Cleveland, Ohio, pp. E-133.

help to illustrate our conclusions. The generalized squared distance between the control diet and the diet containing 30% tarbush leaf material, 106.62, was much larger than the distances between the other treatments, ranging between 5.48 and 41.58. Misclassification rates in Table 3 (listed for analysis of the blue-green and red regions of the visible spectrum at an excitation wavelength of 355 nm) show that all 3 lambs fed the control diet containing no tarbush leaf (100% tobosa hay) were correctly classified, and 3 out of the 4 lambs fed the diet containing 30% tarbush leaf were correctly classified. Cross-validation (the CROSSLIST option in the DISCRIM procedure in SAS 1989a) indicated the lambs fed the diets containing 10% and 20% tarbush leaves were likely to be misclassified—in general interchangeably. This indicated there was no sharp spectral separation at the excitation wavelength evaluated between the diets containing 10% and 20% tarbush leaf material.

Out of 7 misclassifications given in Table 3, five were strongly misclassified, with maximum classification probabilities greater than 0.95. For example, for 1 lamb fed 10% tarbush leaf which was misclassified to the diet containing 20% tarbush leaf, the maximum classification probability was 0.97 while the probability of correctly classifying that lamb was much lower at only 0.02. Two of the misclassifications were borderline with a maximum classification probability of 0.55, but with only a slightly lower probability (0.45) for being correctly classified to the diet containing 10% tarbush leaf. Even with the small sample size for each treatment, it was still possible to separate the control diet from the diet containing 30% tarbush leaf material. The misclassification results from the red region of the visible spectrum for an excitation wavelength of 355 nm are also provided in Table 3. Misclassification results for the red and blue-green regions of the visible spectrum for excitation wavelengths 310 and 330 nm were also calculated but are not reported.

Three-dimensional Plots

Based on the 3-dimensional plots of polynomial regression coefficients taken 3 at a time, it was observed that regression coefficients for the fourth-order term were giving the least useful information to graphically separate the regression coefficients. Therefore, the decision was made to replace the quartic term with a new variable, the red-to-blue count intensity ratio. This decision was based on the previous work by Anderson et al. (1996, 1998), who found the red-to-blue count ratio to be useful in distinguishing among materials when using maximum fluorescence intensity values. The maximum intensity of both blue-green and red regions was found for each of the lamb's 13 data sets and the ratio of these 2 maximum peak intensities was calculated using the MEANS procedure in SAS (SAS Institute 1990a). After including this new variable (an intensity ratio) and deleting the fourth-order regression coefficient, discriminant function analysis was again performed. Unfortunately, the addition of the red-to-blue maximum count intensity ratio did not improve diet separation. For all cases (i.e., for both red and blue-green regions and for each of the excitation wave lengths 310, 330, and 355 nm), separation of the extreme diets (those containing no tarbush leaf and those containing 30% tarbush leaf) was possible only for the red region at 310 nm. The 2 intermediate diets containing 10% and 20% tarbush leaf material were still indistinguishable in all cases.

Conclusions

It was possible to discriminate 30% differences (0% and 30%) but not smaller differences (10% and 20%) among chloroform filtrates from lamb feces that differed in tarbush leaf content using a series of 2-dimensional plots, confidence interval plots, discriminant analysis, and 3-dimensional plots. Statistically, feces from control lambs fed no tarbush leaf material (0%) had bimodal spectral signatures between 400 and 800 nm that were different from feces obtained from lambs that had been fed the basal diet but which contained 30% tarbush leaf material. However, lambs fed a tobosa hay basal diet containing 10% and 20% tarbush leaf material could not be statistically separated.

Univariate analyses on single-peak information in Anderson et al. (1996) similarly distinguished between the control and 30% tarbush leaf material in diets but also distinguished among intermediate diets. These single peaks were in the blue and red regions of the visible spectrum and made it possible to discriminate among the 4 diets in a linear fashion (a = 0.05).

Multivariate techniques are, in general, more powerful than analogous univariate techniques but do require larger sample sizes to compensate for simultaneously fitting more parameters. In this set of analyses, the number of observations (lambs) was small (n = 13) relative to the number of variables and groups being used (t = 6, c = 4). The small sample size likely resulted in the inability of multivariate analyses to separate the 10% and 20% tarbush leaf diets from the 2 extreme diets. However, these analyses do provide information about the entire fluorescence spectrum, summarizing that information in just 6 regression coefficients for each lamb and spectral region. In situations where more animals are available from which to obtain fecal samples, we expect this sequence of statistical techniques will be able to distinguish among diets.

These results suggest fluorometry in conjunction with multivariate statistical techniques show promise in distinguishing among fecal samples representing different diets, especially if numbers of animals sampled remains relatively large. It is the opinion of the authors that 20 to 30 animals allocated among the 4 diets would have substantially improved our ability to discriminate among the different diets.

Future Work

Calibration procedures following NIST standards should be conducted to evaluate long term instrument stability by comparing data taken from sub samples of a single sample that are randomly evaluated over time. Furthermore, a set of reference standards representing the materials being evaluated should be periodically evaluated to determine if spectral output changes among runs. If spectral fluorescence variability increases as a result of increased hours of xenon arc lamp use, this would be detected and appropriate data adjustments could be made. This information will be necessary to establish proper fluorometry protocol for determining botanical composition among sample mixtures.

Degradation of a xenon arc lamp does not occur over short periods of time. Therefore, this potential source of variability was not considered important in these data since it took only a few minutes to obtain data on each sample and the entire procedure lasted only a few hours.

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A proposed method for determining shrub utilization using (LA/LS) imagery

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Abstract

Utilization of plant above ground biomass has continued to be a critical yet difficult assessment in rangeland monitoring. Shrub size and woody structure further compound the measurement of shrub biomass utilization. This study was designed to determine the potential utility of low altitude / large scale (LA/LS) imagery in assessing shrub utilization. A near monoculture of *Ceriotoides lanata* (Pursh) J.T. Howell (winterfat) located in the western desert shrubland of Utah was used to evaluate this technique. Four, 3.1 by 3.1 m plots were identified and the shrubs within the plots were defoliated by hand-picking at about 10% intervals with imagery of the plots obtained between pickings. Imagery was obtained using a radio controlled airplane (drone) fitted with a 35 mm camera. Images were evaluated using image processing software and the resulting reflectance data correlated with defoliation percentages (weight basis) for each plot. Reflectance data from images correlated highly with defoliation percentages ($r^2 >$ 0.9). This technique of using LA/LS imagery shows promise for a quick and accurate tool in assessing utilization of shrubs.

Key Words: remote sensing, vegetation inventory, photography

Resumen

La utilizaciónde la biomasa vegetal aérea continua siendo un criterio critico pero difícil de evaluar en el monitoreo de pastizales. El tamaño del arbusto y la estructura leñosa componen las medidas de la utilización de biomasa de arbustos. Este estudio se diseño para determinar la utilidad potencial de las imágenes de baja altitud/amplia escala (LA/LS) para evaluar la utilización de arbustos. Para evaluar la técnica se utilizó una población casi pura de *Ceriotides lanata* (Pursh) J.T.Howell (winterfat) localizada en un matorral desértico de Utah. Se identificaron 4 parcelas de 3.1 x 3.1 m y los arbustos dentro de ellas fueron defoliados manualmente en intervalos aproximados del 10% y en ellas se tomaron imágenes entre defoliación y defoliación. Las imágenes se obtuvieron utilizando un aeroplano controlado por radio (zumbido) equipado con una cámara de 35 mm. Las imágenes se evaluaron utilizando programas de computadora para procesar imágenes y los datos de reflectancia resultantes se correlacionaron con los porcentajes de defoliación (en base a peso)de cada parcela. Los datos de reflectancia de las imágenes se correlacionaron altamente con los porcentajes de defoliación ($r^2 >$ 0.9). Esta técnica de utilizar imágenes LA/LS promete ser una herramienta rápida y certera para evaluar la utilización de arbustos.

Plant utilization is commonly measured as part of a sustainable natural resource management plan. Many utilization techniques have been developed and used on rangelands, some of which are complex and require extensive experience. After significant review of browse utilization techniques, Bonham (1989) concluded that, “Estimation of browse utilization is one of the most difficult vegetation characteristics to determine” The object of this research was to develop a simple, fast, and inexpensive method of measuring shrub utilization using low altitude/large scale (LA/LS) imagery.

Walker and De Vore (1985) described how LA/LS imagery is effective in discerning shadows of small objects in archeological work. Shadows produce “texture” in images. Leaves, stems, and flowers all produce shadows and bright spots depending on how they are lighted by the sun. This produces dark and light spots on images. With lots of small objects, such as leaves and stems intercepting light (bright) and casting shadows (dark) an image will have a “salt and pepper” appearance or texture. Olthof and King (1997) found using this textural information in LA/LS imagery increased their ability to accurately estimate the Leaf Area Index in forests. When leaves and small stems are removed there are fewer bright and dark specks in the image and the image texture becomes “soft” or “fuzzy”. It is proposed that by measuring this change in texture caused by defoliation (grazing) the amount of foliage removed can be estimated.

Methods and Materials

A near monoculture of winterfat *(Ceriotoides lanata* (Pursh) J.T. Howell) was selected for study during the summer of 1995 in Rush Valley, Tooele County, Utah"). Using a 1-m circular quadrat with 15 replications, the canopy cover of winterfat on the site covering 50 ha was estimated to be about 35%. Three, 3.1 by 3.1 m plots were delineated adjacent to each other in the most uniform stand of winterfat. A wooden stake marked each corner of each plot. Yellow nylon line was attached to the stakes and marked the perimeter of the plots. To make identification of plot corners easier to see in images, paper plates, measuring 23 cm in diameter were centered on each stake at a height of 45 cm.

Plots were defoliated by hand to simulate grazing. The plots were picked 10 times removing approximately 10% of current

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year's growth each time. At the end of 10 picking events all of the current years growth was removed. The harvested plant materials were placed in separate paper sacks for each plot and picking event. After drying in a forced air dryer at 38°C for 7 days, weights were obtained for each plot and picking event. After each picking event a white paper plate was placed between plots to document picking periods (the first picking event had 1 plate, the second 2, the third 3, etc.). Plots were then photographed from the air.

Two drones were used to photograph the plots. One drone was fitted with 2 digital cameras; one, was a 3 color (Red, Blue, and Green) sensor and the other a black and white sensor which was filtered with a wratten 25 filter to record reflected near infra-red (NIR) light. This drone was flown before the first picking and after each of the 10 pickings. It was intended that vegetation indexes could be obtained from the red and NIR bands of the digital cameras and provide measurements of defoliation. The second drone was fitted with a 35 mm SLR film camera and loaded with a 36-exposure roll of Kodak Gold ISO 200 film. Pictures acquired with this drone were intended primarily to document the work and only flown during the 2nd, 4th, 5th, and 9th pickings.

The work was done on 12 July 1995 between 1000 hours and 1200 hours. This period of time would provide the best sun angle (almost vertical) for aerial photographs. The drones flew at an altitude 122 m. Drone pilots were directed by the ground crew when to trigger their cameras by signaling when the drones were directly over the plots. The images from the digital cameras were viewed at the site on a laptop computer. It was found that none of the digital images recorded the plots. It was determined that the automatic exposure sequence of the digital cameras was not consistent between cameras or exposures. Therefore we were unable to time the cameras' exposures and obtain usable digital images of the plots.

Film from the drone was developed at a commercial film processor. Differences between the early pickings and later pickings were apparent in the photographs. It was determined that we would evaluate the photographs. One image from each of the 4 photographed picking events were selected and enlarged to 20.3 by 25.4 cm. Enlarged photographs were then scanned in a flat bed color scanner set at a resolution of 900 dots per inch. The images were cropped to show just the plots and saved in a tagged-image file format (TIFF) for computer processing.

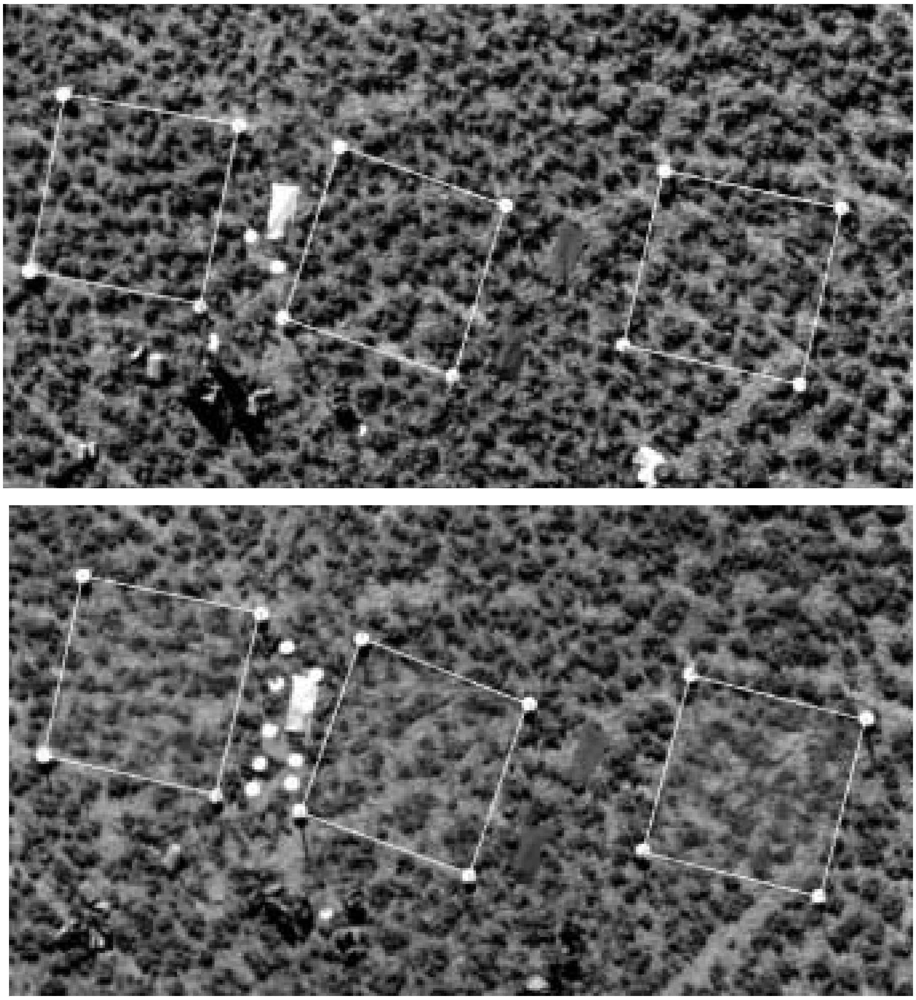

Fig. 1. Aerial images of winterfat study plots in Utah's west desert: a). Lightly Defoliated (2 picking events, about 20% defoliation); b). Heavily Defoliated (9 picking events, about 80% defoliation).

The TIFFs were imported into image processing software package (IDIRSI, Clark University 1995) for image analysis. This analysis produced red, blue, and green bands from each TIFF image. All images were colored balanced to match the first image by selecting the same area in each image and using IDRISI's regression procedure to obtain slope and y intercept values to adjust color. To balance the effect of time on shadows the images were balanced using a linear stretch routine in IDRISI. This procedure also neutralized effects of harsh shadows caused by direct sunlight.

The difference between the early and late images (non-defoliated vs. defoliated) was depicted in the photograph's texture. Non-defoliated plots had many variations in shadow and light making the image speckled. Photographs of defoliated plots appeared soft and somewhat fuzzy, because the many variations of shadow and light were removed by removing the vegetation which created them (see Figs. 1a. and 1b). After visually analyzing the images, it was decided that the most efficient method to interpret them was to evaluate reflectance profiles for each plot and picking event. Reflectance profiles show the amount of reflected light recorded in an image as a profile with high reflectance values (white objects) forming peaks and low reflectance values (shadows) forming valleys (see Figs. 2a and 2b). Profiles were selected on diagonal lines of the plots as marked by paper plates at the corners. This ensured that each profile was of the same area in each image for each plot. The profile's y-axis records the gray scale reflectance from 0 (dark shadow) to 215 (bright reflectance of white light) for the paper plates. The x-axis was the distance from corner to corner.

Profiles were evaluated by determining the percentage of the line that has a Grey Scale Reflectance value of 21.5 or higher. This is the reflectance level of soft shad-

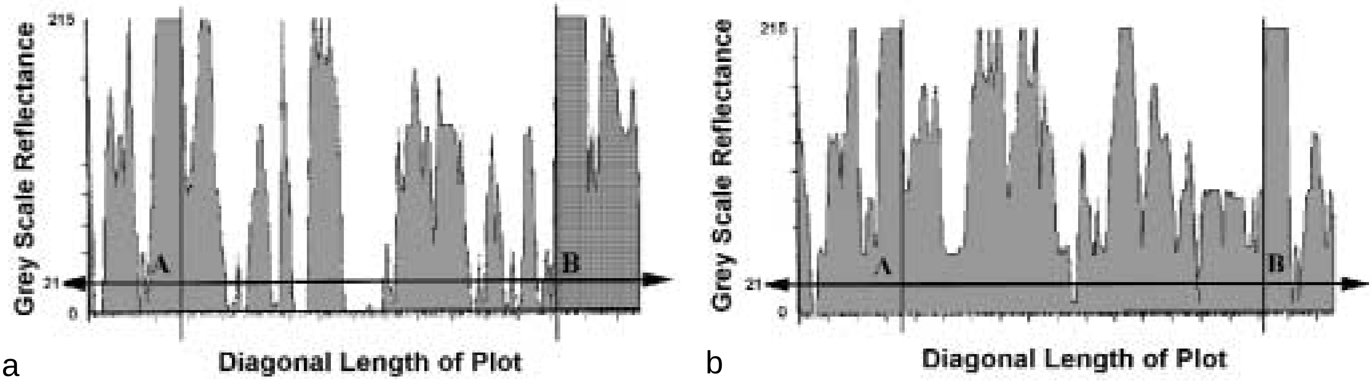

Fig. 2. Reflectance profile of winterfat study plots in Utah's west desert area after: a). 2 picking events (about 20% defoliation); b). 9 picking events (about 80% defoliation). The value of 215 represents total reflectance (bright white) where 0 is no reflectance (deep shadow). Line intercept values are measured as a percent reflectance running between points "A" and "B" along the reflectance value of 21.5. Fig. 2a shows more shadows than Fig. 2b which has very little shadow along the "AB" line.

ows caused by small twigs, leaves, and diffuse objects. (The value of 21.5 was determined by querying the reflectance values of soft shadows in the images.) Reflectance values below 21.5 are harsh shadows from large stems, rocks, and other solid objects. Vertical lines were first drawn at the plot corners. The high reflectance values (215), which are flat, were produced by the paper plates and identify the plot corners. Next, a line is drawn parallel to the x-axis at the y-value of 21.5. The total length of the gray area that intercepted the line at 21.5 was measured and divided by the total length of the line to give a "Percent Reflectance". Percentages were used to negate the differences in scale of the different photographs. Profiles were determined for each plot in the 4 photographs producing 12 profiles.

The total dry weight of plant material removed from each plot was determined by summing all dry weights from each picking event for the plot. Percent dry weights for each picking event was then calculated based on the total plant material removed from the plot up to and including the current picking event ("Percent Utilization").

"Percent Reflectance" values were then regressed against the corresponding "Percent Utilization" values of the picked vegetation for corresponding plots and picking events using Pearson's Correlation procedures (Conover 1980).

Results and Discussion

The purpose of this project was to find a simple method of measuring changes in vegetation cover or browse available. After visually studying aerial photographs of treated plots, it was apparent that there were changes due to successive defoliation (compare Fig. 1a. Lightly Defoliated and Fig. 1b. Heavily Defoliated). The most notable changes were in the textural characteristics of the defoliated plots (Fig. 1b). Areas outside of the treated plots have a rough, specked appearance. The defoliated plots appear soft or fuzzy because shadows have been removed by defoliation.

Percent Reflectance had high positive correlation with Percent Utilization (Fig. 3, r^2 = 0.9365). This indicates that photographs using this methodology can be used to measure utilization in winterfat communities. Of significance for the range manager, is the area of the curve between 20 and 80 percent utilization. It is in this range that critical decisions are made as to when livestock are removed from the

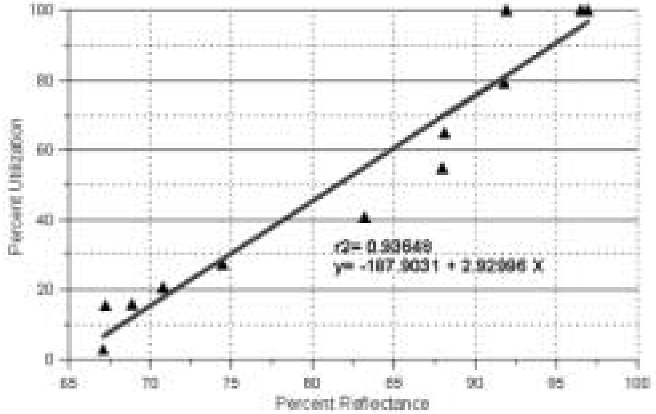

Fig. 3. Reflectance plotted against percent utilization with the respective regression equation, line and strength.

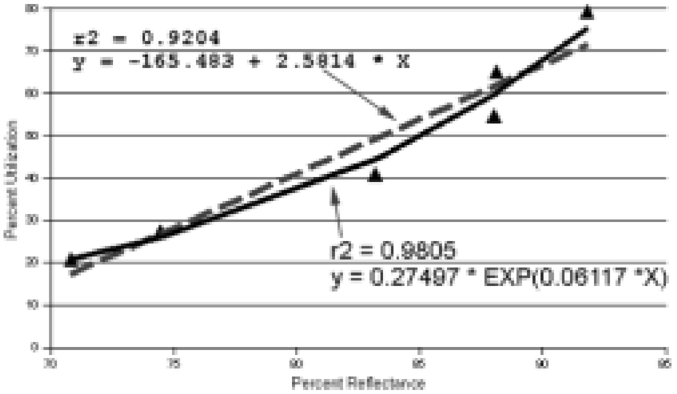

Fig. 4. Reflectance plotted against percent utilization (between 20 and 80%) with the respective regression equation lines and strengths.

range site. The best exponential fit in this critical range has an even higher correlation value (Fig. 4, $r^2 = 0.9805$).

This study demonstrates the value of using LA/LS imagery in measuring shrub utilization in winterfat communities. This procedure could likely be extended to other shrub and herbaceous communities. A recommended procedure would be to place several pairs of posts to designate permanent transect lines. Next a small enclosure would be needed next to each transect line. This enclosure would serve as a control to adjust images taken at various times as well as provide an undisturbed site for comparisons. At the time of photographing the posts would be fitted with a white highly reflective target to delineate transects on the images. Profiles would then be obtained and processed as discussed in this paper. Consecutive flights would be made throughout the grazing season or seasons to measure utilization of the site.

Conclusions

This work demonstrates that LA/LS may be a useful tool in range management to accurately measure utilization of desert shrubs. The LA/LS imagery could become a primary method for measuring utilization and change in rangeland areas. Since the method measures change in shadow, which in turn is related to the vegetative cover, the method has promise for measuring change in any vegetated area. Unlike many of the traditional utilization methods of monitoring, this method requires little time, is non-destructive, and the data is permanently recorded.

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Low density of prickly acacia under sheep grazing in Queensland

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Abstract

Populations of an introduced woody weed, prickly acacia (*Acacia nilotica* (L.) Delile ssp. *indica* (Benth.) Brenan syn. *Acacia arabica* (Lam.) Willd. ssp. *indica* Benth.), were surveyed at 4 sites in central Queensland. There is a significantly lower frequency of plants of < 3 m in height within populations which have been grazed by sheep, indicating that browsing by sheep reduces regeneration. There were higher losses of seedlings at a sheep-grazed site than at cattle-grazed sites. These results support previous assertions that prickly acacia is regenerating more successfully on cattle properties, because cattle both disperse seeds and are less effective herbivores. In regions of low annual rainfall, prickly acacia is capable of forming dense stands (up to 2,700 shrubs ha^{-1}) in lowland landscape types. Stands are less dense in upland landscapes (maximum of 718 shrubs ha^{-1}). Of most concern is that in regions of high annual rainfall prickly acacia can form extremely dense thickets across most landscape types (up to 3,400 shrubs ha^{-1}). We suggest that prickly acacia is most likely to become a management problem on cattle properties, and an extreme problem in high annual rainfall areas. The inclusion of sheep in livestock rotations may be an effective control measure in the Mitchell Grasslands, but this may not always be possible. A high priority is to prevent prickly acacia from expanding its range into equivalent high rainfall areas within Queensland, and also in the Northern Territory, northern New South Wales, and Western Australia. This could be achieved by quarantining livestock which have come from infested properties until seeds have passed through the digestive tract, after about 6 days. Management strategies at the property level should aim to prevent further spread of prickly acacia by controlling cattle movements between paddocks during periods when cattle are ingesting pods and seeds.

Resumen

En 4 sitios de la región central de Queensland se muestrearon poblaciones de una maleza leñosa introducida, “Prickly acacia” (*Acacia nilotica* (L.) Delile ssp *indica* (Benth.) brenan syn *Acacia arabica* (Lam) Willd. ssp *indica* Benth.). Dentro de poblaciones que han sido apacentadas por ovinos hay una frecuencia significativamente menor de plantas de < 3 m de altura, indicando que el ramoneo por ovinos reduce la regeneración. Hubo mayores perdidas de plántulas en los sitios apacentados por ovinos que en los sitios apacentados por bovinos. Estos resultados avalan afirmaciones previas respecto a que el “Prickly acacia” se esta regenerando mas exitosamente en los ranchos que son explotados con bovinos porque dispersan las semillas y son herbívoros menos efectivos. En regiones de baja precipitación anual el “Prickly acacia”es capaz de formar poblaciones densas (hasta 2,700 arbustos ha^{-1}) en tipos de paisaje de tierras bajas. Las poblaciones son menos densas en terrenos altos (máximo 718 arbustos ha^{-1}). La preocupación mas frecuente es que en regiones de alta precipitación anual el “Prickly acacia” forme poblaciones extremadamente densas en la mayoría de los tipos de paisaje (hasta 3,400 arbustos ha^{-1}). Sugerimos que el “Prickly acacia” es mas probable que llegue a ser un problema de manejo en las propiedades de bovinos y un problema extremo en áreas con alta precipitación anual. La inclusión de ovinos en las rotaciones de ganado puede ser una medida de control efectiva en los pastizales Mitchell, pero esto no siempre es posible. Una alta prioridad es el evitar la expansión del rango del “Prickly acacia” a áreas equivalentes de alta precipitación dentro de Queensland, del Territorio del Norte, del norte del Nuevo Sur de Galeso y el oeste de Australia. Esto se puede lograr cuarentenando el ganado que viene de propiedades infestadas hasta que las semillas hayan pasado a través de tracto digestivo, aproximadamente después de 6 días. Se deben promover estrategias de manejo a nivel de propiedad para prevenir la dispersión del “Prickly acacia” mediante el control de los movimientos de ganado entre potreros con bovinos que están consumiendo vainas y semillas.

Key Words: Life-stage profiles, rainfall, population dynamics, regeneration, cattle, woody weeds

Prickly acacia (*Acacia nilotica* (L.) Delile ssp. *indica* (Benth.) Brenan syn. *Acacia arabica* (Lam.) Willd. ssp. *indica* Benth.) was introduced into the Mitchell Grass Plains of western Queensland in the 1890s as a source of shade and fodder (Barker

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1996). From western Queensland, prickly acacia has spread as far as Cooktown in far north Queensland, south to Coonamble in New South Wales, west to the Barkly Tablelands and Arnhem Land in Northern Territory and east to the coast of Queensland, an area approaching 4 million km^2. It is now listed as a category 1 weed for northern Australia, that is: a terrestrial species which has extensive continental distribution and is capable of destroying an ecosystem (Humphries et al. 1991).

Rapidly increasing populations of both native and exotic shrubs, often called "woody weeds", which cause disruption of ecosystems and reduction of rangeland productivity have been well documented in the USA (Hennessy et al. 1983, Archer 1989, 1984, Brown and Archer 1989), southern Africa (Skarpe 1990, Holmes and Cowling 1997) as well as in Australia (PNSW 1901, Moore 1969, Harrington et al. 1984, Humphries et al. 1991). Efforts to control shrubs by clearing and poisoning have generally proved unsuccessful and uneconomic. Such methods are expensive for the degree of control achieved, and there is only a short to medium term benefit in increased livestock returns per hectare, particularly on properties where stocking rates are low regardless of shrub densities. Control strategies are more likely to be implemented if they are economical and aligned with existing management practices, and more likely to be successful if based on ecological principles (Harrington 1979, Adamson and Fox 1982, Jacoby 1985). Any alteration in the establishment of new individuals into the population can have dramatic effects on the long-term survival of plant populations (Harper 1977). The survivorship of seedlings is crucial to shrub regeneration so it is logical to examine this portion of the life cycle of a plant when developing a management strategy.

A widespread change from sheep to cattle-based enterprises in the Richmond Shire may have contributed to the increase of prickly acacia since 1973/74 (Carter 1994). Originally, leases in the western districts were only legally permitted to carry sheep. This requirement was relaxed during the 1960s and 70s and increased cattle prices encouraged many landholders to switch from sheep to cattle-based enterprises. Both sheep and cattle are known to eat the pods of prickly acacia but cattle chew seeds very ineffectively compared to sheep, pass a larger proportion of viable seeds in their dung and hence are more effective dispersal agents than sheep. Cattle pass about 81% of ingested seed intact of which 15% are germinable (Harvey 1981), giving 41% germinability from those ingested (Barker 1996). Sheep pass < 1% of prickly acacia seeds intact of which 33% are germinable (Harvey 1981, Carter et al. 1991, Barker 1996). Sheep tend to regurgitate large numbers of seeds during ingestion of the pods (35%) and rumination (14%) (Carter and Cowan 1993) hence depositing the seeds close to source and contributing little to increased range of prickly acacia. Cattle have been shown to disperse the seeds of mesquite (*Prosopis*) in North America (Brown and Archer 1987). The gut bacterial flora of large herbivores has been shown to destroy larvae of beetles from the family Bruchidae which would otherwise consume the seeds in which they are present (Miller 1994). This means that large herbivores not only act as dispersal agents, they also protect the seed from one of the potentially most important predators. The process of digestion also scarifies the seeds, thus increasing germinability of deposited seeds and further increasing the potential of large herbivores to spread prickly acacia.

The objective of this study was to survey existing populations of prickly acacia and to determine if the species of livestock used for rangeland enterprises (sheep and cattle) are each associated with differences in seedling survival and population densities of prickly acacia.

Materials and Methods

Background

Prickly acacia was deliberately introduced to western Queensland at least by 1926, when it was recommended as a shade and fodder species by the Queensland Department of Agriculture and Stock (Barker 1996). It was not listed as a significant exotic in western Queensland in 1938 (Blake 1938). Although prickly acacia became naturalized along creeks and boredrains (artificial drains where artesian water from the Great Artesian Basin is channelled for livestock), it did not appear to cause widespread concern until the 1970s. There were several above-average rainfall years in the early 1970s, including 1973 and 1974 when the annual rainfall was around twice the average (ABM 1996). These periods of high rainfall are associated with La Niña phases of the El Niño-Southern Oscillation (ENSO) patterns which control the climate of the Pacific Ocean and eastern Australia (Nicholls 1991). During 1974 much of the low-lying country in western Queensland was flooded for weeks and local pastoralists report that there was a mass germination of prickly acacia following these floods. Pods are indehiscent, so the seeds remain in the pods unless consumed by herbivores. We have observed that pods are capable of floating for up to 30 hours in water with 67% subsequent germination so the floods may have served a dual purpose of dispersing seeds and also scarifying them by softening the seed-coat and leaching growth inhibitors.

The Study Area

Eight sites in prickly acacia stands were chosen in central Queensland; locations and rainfall are shown in Fig. 1 and Table 1. Average annual rainfall data from the nearest recording centres to each site (Giru, Bowen, Hughenden, Richmond and Julia Creek) were obtained from the Australian Bureau of Meteorology, and had been collected for 60–100 years, depending on the time of establishment of the recording stations at these centres (ABM 1996). Two high rainfall (989 and 1,164 mm) sites were near the coast south of Townsville (Giru and Bowen). It is very difficult to determine the original vegetation at these sites because of the large degree of alteration to the vegetation cover through cultivation for sugar cane, introduction of pasture species for cattle-grazing, and invasion by woody weeds including prickly acacia and others such as paloverde (*Parkinsonia aculeata* L.). The sites appear to have originally been teatree (*Melaleuca* spp.) swampy woodlands. The remaining 6 sites were at inland, low annual rainfall (420–487 mm) areas in central western Queensland between Hughenden and Julia Creek. These sites were originally open plains dominated by Mitchell grass (*Astrebl*a spp.). The landholders supplied information on grazing histories for the previous 20 years or more. The 2 coastal sites (Giru and Bowen) and one of the Hughenden sites (Marathon Station) have been exclusively grazed by cattle for ≥ 25 years. The remaining Hughenden site (Nocoleche Station) is grazed by cattle. The 2 sites at Richmond (Allaru Station) are grazed predominantly by sheep, with very occasional access by cattle to the site. The 2 sites at Julia Creek (Garomna Station) have been grazed by sheep only, and one was unstocked during the seedling study.

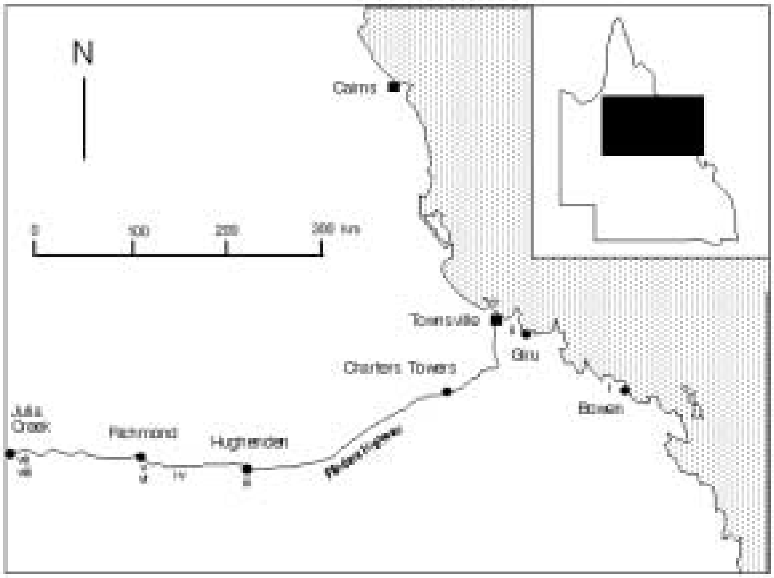

Fig. 1. The study area in central Queensland (inset) showing the location of 8 sites in prickly acacia (*Acacia nilotica*) populations. The sites at Giru, Bowen, and Hughenden are grazed by cattle, and the sites at Richmond and Julia Creek are grazed by sheep. The coastal sites, Giru and Bowen have about double the annual rainfall (around 1000 mm) of the inland sites (around 450 mm) (see Table 1).

Population Structures & Population Densities

Size structure profiles of each population were developed from 20 individuals located by a "random walk" transect method (Kent and Coker 1992, Silvertown and Lovett-Doust 1993) and the results plotted as frequency distributions. Differences between sheep and cattle grazed sites were analysed by t-test. At 6 of the sites, the height of the nearest tree within each of the 4 compass quadrants was measured each 20 m along a 400 m transect, giving a size profile for each population based on 80 individuals per site. Density of prickly acacia at each landscape type within each site was calculated as follows. The distance to each of the trees in each quadrant was measured using a point-centred quarter plotless sampling technique. These were later used to calculate plant densities (D) using the formula:

$$D = 20 \Big/ \sum_{m=1}^{20} \left(\sum_{n=1}^{4} d_{m,n} / 4 \right)^2 \qquad \textbf{(1)}$$

where d is the distance to the trunk of the nearest tree in each quadrant n, and m is the tree number (Cottam and Curtis 1956, Greig-Smith 1983). Differences in population densities between sites and landscape types within sites were analysed by ANOVA.

Seedling Survival

Following rain in January 1995, cohorts of acacia seedlings were observed at Giru, Bowen, Nocoleche, Allaru, and Garomna North. At each site over 60 seedlings were located and their positions recorded using a measuring tape placed between 2 permanent marking stakes.

Seedling location was recorded as a pair of coordinates, distance along the tape in m and distance and direction at right angles from the tape in cm. Seedlings were tagged with plastic poultry leg-rings. Two rings were placed on each plant, in different combinations of 6 colours so that individuals could be found and identified easily. The cohorts were visited every 3 weeks and individuals which had died due to desiccation recorded. In this case, the plant was still present with the rings intact. Where rings were scattered and the seedling missing from its recorded position, it was assumed that the seedling had been either trampled or grazed, thus allowing the rings to come off. These seedlings were recorded as missing since it was usually not possible to determine with certainty whether they had been trampled or grazed. Cohorts were followed until July 1995. The experiment was located opportunistically rather than by design. It is therefore not replicated and the results were not statistically analysed, but presented in summarized format only.

Results

Population Densities

Densities of prickly acacia at 6 sites are given in Table 2. Prickly acacia can form very dense stands, especially in high annual rainfall regions of coastal Queensland such as Bowen (3,381 shrubs ha^{-1}). Extremely dense stands were also recorded at Giru (5,059 shrubs ha^{-1}), a high rainfall site which had been chained approximately 15 years previously (C. Burry pers. comm.). At the high annual rainfall sites, shrub densities were highest on well-drained sites (uplands and plains) whereas a poorly drained floodzone supported lower density shrubs ha^{-1}. Prickly acacia has also formed dense stands at low annual rainfall in the Mitchell grasslands of inland Queensland, but only in and adjacent to boredrains (shallow earth channels built to carry water flowing from uncapped artesian bores for livestock) and in creeklines which receive extra water from surface flow. Densities were as high as 1,150 shrubs ha^{-1} on the bank of a boredrain at Allaru North but on upland landscapes the maximum was 354 shrubs ha^{-1} at Marathon.

Table 1. Locations (recorded by GPS) and precipitation data of 8 prickly acacia (*Acacia nilotica*) sites in central Queensland.Rainfall data were obtained from the Australian Bureau of Meteorology (ABR 1996).

Site	Coordinates	Nearest Rainfall Recording Station	Median Rainfall	Years of Rainfall Records
			(mm)	(years)
Giru	20° 28'14" S 147° 7' 5" E	Giru PO	1164	1929–1993
Bowen	20° 3' 45" S 148° 12' 23" E	Bowen PO	988	1871–994
Nocoleche	20° 54' 39" S 144° 10' 33" E	Hughenden PO	483	1884–1994
Marathon	20° 54' 44" S 143° 34' 00" E	Richmond PO	425	1890–1994
Allaru North	20° 45' 16" S 143° 09' 10" E	Richmond PO	"	"
Allaru South	20° 46' 8" S 143° 9' 10" E	Richmond PO	"	"
Garomna North	20° 40' 7" S 141° 47' 28" E	Julia Creek PO	422	1913–994
Garomna South	20° 42' 8" S 141° 50' 51" E	Julia Creek PO	"	"

Table 2. Mean densities (shrubs ha^{-1}) of prickly acacia (Acacia nilotica) at 6 sites in northern Queensland. Densities differ significantly (F = 6.84, df = 5, 113, p = 0.0001) by anova. Numbers of trees within each landscape type are shown in brackets. Densities between coastal sites (Giru and Bowen are significantly different from those at the inland sites (Nocoleche, Marathon, Allaru North and Garomna North) (t = 4.182, df = 117, p = 0.0001).

Site	Landscape type (n = no. of trees)	Density	Site Mean
		(shrubs ha^{-1})	
Giru	upland/plain (n = 10)	5059	
	floodzone (n = 7)	220	
	swamp (n = 3)	2642	3696
Bowen	upland/plain (n = 20)	3381	3381
Nocoleche	bank (n = 4)	339	
	creek (n = 5)	497	
	floodplain (n = 1)	610	
	upland/plain (n = 10)	181	313
Marathon	puddle/gilgai (n = 6)	192	
	bank (n = 5)	354	
	creek (n = 2)	64	
	upland/plain (n = 6)	354	272
Allaru North	bore-drain (n = 4)	1039	
	bank of drain (n = 6)	1150	
	upland/plain (n = 10)	253	679
Garomna North	creek-bed (n = 7)	613	
	bank (n = 3)	385	
	upland (n = 9)	80	359

Population Structures

Population profiles show a higher frequency of individuals between 100 and 300 cm high at cattle-grazed as compared with sheep-grazed sites (Figs 2 and 3). This is also apparent when expressed as a percentage of the total population (Table 3) and is statistically significant by t- test (p = 0.0284). The few individuals under 300 cm present at the 4 sheep-grazed sites were heavily browsed and dwarfed, and may have been considerably older than expected for those height classes. These are indistinguishable from recent recruits in the histograms, highlighting a problem of using height as a surrogate for age. The browsed dwarfs were particularly noticeable at Garomna (both North and South) and Allaru South. In many cases these had died. Individuals between 100 and 300 cm high were almost entirely absent from the remaining sheep-grazed site (Allaru North). Individuals below 300 cm at the cattle-grazed sites (Giru, Bowen, Nocoleche and Marathon) showed little sign of browsing.

Seedling Survival

Prickly acacia seedling losses were highest at the sheep-grazed site, Allaru North (88%) (Fig. 4). Some plants were missing from their recorded positions and this could have been due to either trampling or grazing. However in some cases the nipped off stem of the seedling was located, indicating that at least some of the losses were caused by grazing. Seedling losses were between 16 and 23 % at cattle-grazed sites. Most mortality appeared to be due to trampling because there were hoofmarks present in most cases and the rings were often found kicked some distance away. Losses to grazing, presumably by insects, were very low (3%) at the site which was ungrazed by sheep or cattle for the duration of the study, Garomna North.

Discussion and Conclusions

Prickly acacia populations are capable of reaching extremely high densities (over 3,000 shrubs ha^{-1}) on high annual rainfall (> 900 mm year^{-1}) sites where they have formed impenetrable thickets, presenting a serious management problem. Populations of this density were not recorded in the low annual rainfall (< 500 mm year^{-1}) rangelands to the west, the highest densities recorded in boredrains are about one fifth (just over 1,000 shrubs h^{-1}) of those

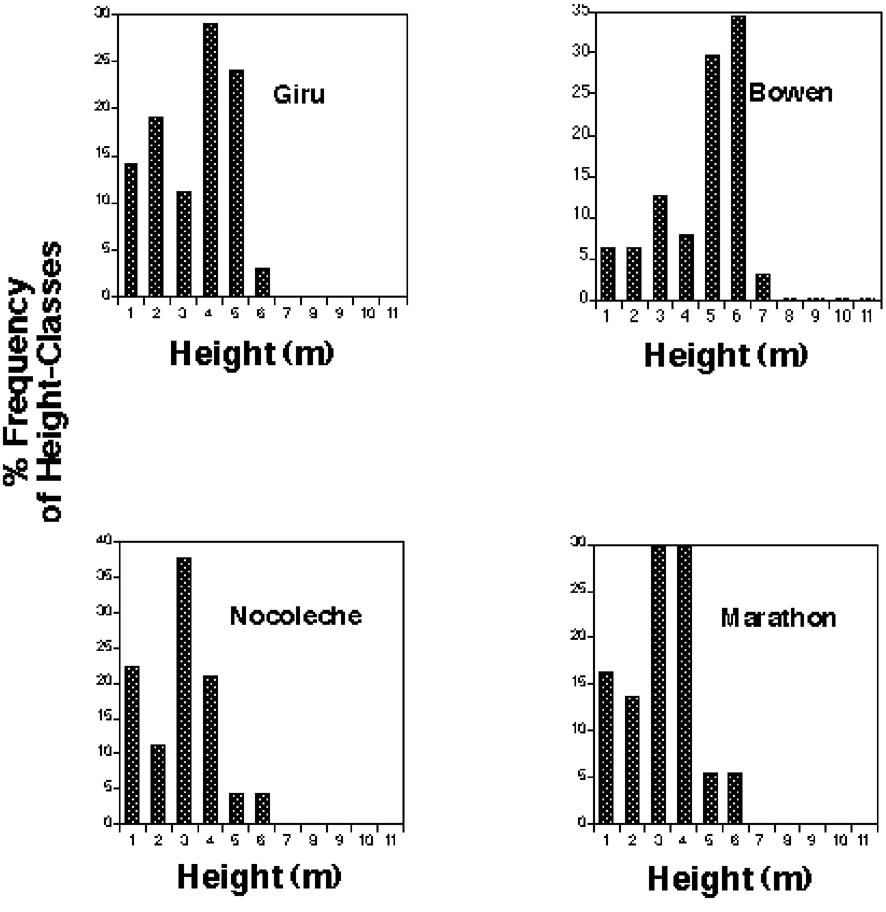

Fig. 2. Height structure profiles of prickly acacia (*Acacia nilotica*) populations at 4 cattle-grazed sites in central Queensland. Data are frequency percentages, height classes are as follows: 1 = 0 - 100 cm; 2 = 101 - 200 cm etc) Rainfall and grazing histories are: Giru (high rainfall, cattle), Bowen (high rainfall, cattle), Nocoleche (low rainfall, cattle), Marathon (low rainfall, cattle).

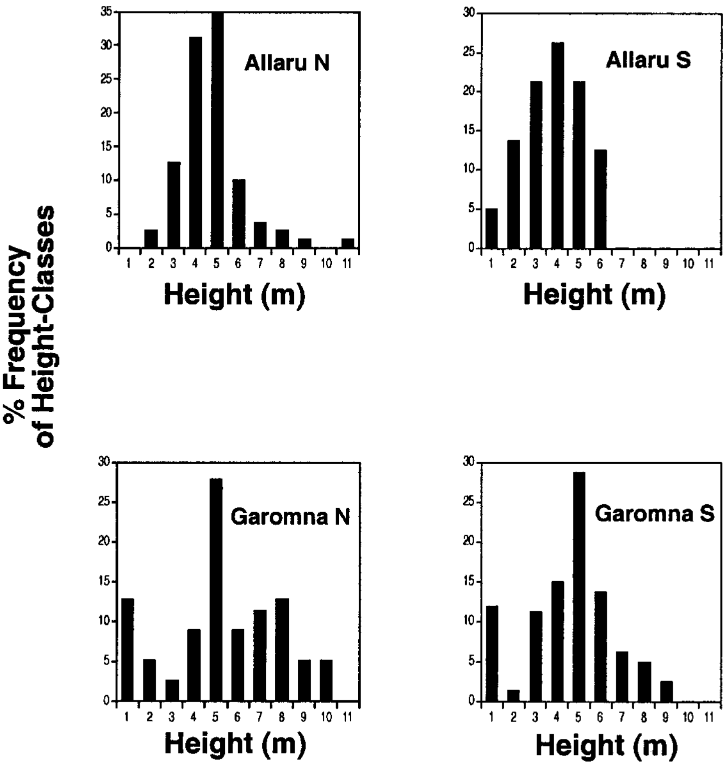

Fig. 3. Height structure profiles of prickly acacia (*Acacia nilotica*) populations at 4 low rainfall sheep-grazed sites in central western Queensland. Data are frequency percentages, height classes are in metres. Rainfall and grazing histories are: Allaru North (sheep, some cattle), Allaru South (sheep, some cattle), Garomna North (sheep only), Garomna South (sheep only).

from high rainfall areas. However, the high percentages of individuals in the lowest size classes on cattle-grazed properties at low annual rainfall indicate a rapid rate of regeneration in recent years, so we predict increases in both density and area infested by prickly acacia on cattle properties in central western Queensland unless appropriate management procedures are undertaken.

Prickly acacia seedlings and juveniles have lower survival on sites where sheep are present, whether by consumption or trampling of young seedlings, or by repeated browsing of older juveniles. We saw no evidence that cattle graze prickly acacia seedlings, in accordance with Barker (1996) who found no evidence for herbivore suppression of recruitment in prickly acacia, though there were some losses due to trampling in heavily used areas. The cohort of young seedlings in the sheep paddock completely disappeared within the first month, due to a combination of trampling and direct herbivory. The heavily grazed and dwarfed individuals which were observed at 2 of the sheep-grazed sites indicates that sheep will browse prickly acacia beyond the seedling stage, which may eventually lead to death of the plant. Continuous browsing over a number of years would inevitably reduce photosynthetic area, limit growth, and prevent the formation of an extensive root system, presumably making these individuals more drought-susceptible.

This is the first direct evidence of sheep suppressing regeneration of prickly acacia, although suppression of regeneration by sheep has been shown in other woody species (Pressland 1975, Lange and Purdie 1976, Crisp 1978, Miller and Halpern 1998, Tiver and Andrew 1997), and by other herbivores (Myster and McCarthy 1989). As observed in Lange and Purdie's (1976) *A. papyrocarpa* Benth. study, sheep-browsed dwarves may survive as stunted, non-reproductive individuals for months or even years before finally succumbing. Previous studies of *Acacia nilotica* have concluded that neither sheep nor goats had any effect on juveniles (Carter and Cowan 1993). Grazing induced mortality may only occur when years of biomass reduction by repeated browsing are combined with drought conditions, a process not detectable in short-term grazing trials. Milton (1994) attributed mortality of populations of 3 species of shrubby Asteraceae to factors other than defoliation, but the study indicated that grazing could have a substantial effect on growth form and reproductive success. Similarly, grazing by prairie dogs (*Cynomys* spp.) limits recruitment of *Prosopis glandulosa* in grasslands of southwestern North America (Weltzin et al. 1997).

It appears that the lower regeneration of prickly acacia at sheep-grazed sites is due to a combination of trampling and grazing of young seedlings, and browsing and stunting of juveniles as long as their canopies remain within browse range. The reintroduction of sheep, either alone or in a grazing rotation with cattle, could be a useful control measure for prickly acacia in western Queensland, at least preventing further increases in density and spread on already infested properties. Unfortunately sheep do not thrive in the wet humid conditions which prevail on the coast, so alternative methods of control will be required there.

Anecdotal evidence that prickly acacia has become much more of a problem in the Mitchell Grass Plains of central western Queensland since many properties

Table 3. Percentage of prickly acacia (Acacia nilotica) juveniles 100 to 300cm height at each of the 8 sites. Differences in mean between cattle-grazed and sheep-grazed sites are significant (t = 2.872, df = 6, p (2-tail) = 0.0284).

Site	*A. nilotica* 100–300cm	Mean	S. D.	S.E.
		(%)		
Grazed by Cattle				
Giru	30.0			
Bowen	32.8			
Nocoleche	48.6			
Marathon	43.25	38.662	8.741	4.37
Grazed by Sheep				
Allaru North	12.82			
Allaru South	35.0			
Garomna North	7.59			
Garomna South	13.16	17.142	12.175	6.087

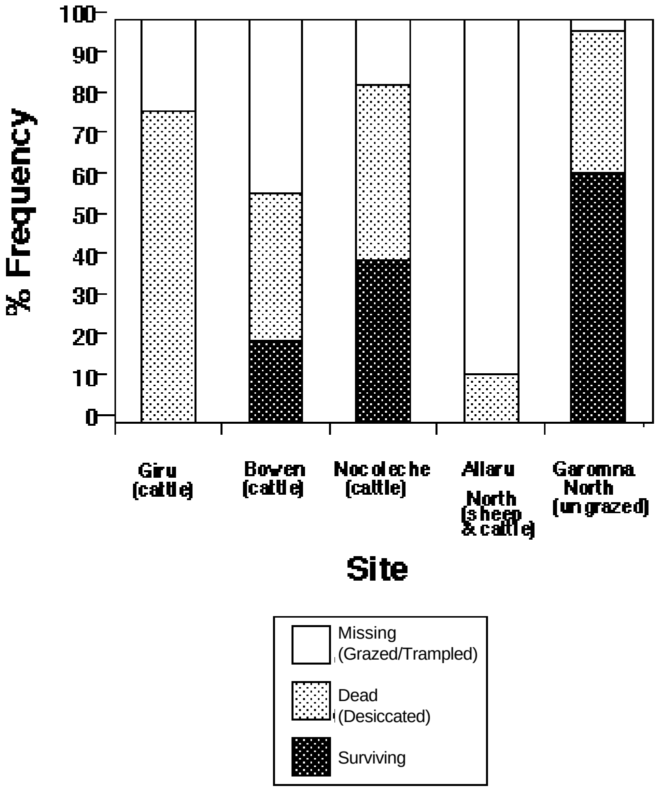

Fig. 4. Percentage losses by desiccation, missing (either trampled or grazed) and survival in cohorts of prickly acacia (*Acacia nilotica*) seedlings at 5 locations in central Queensland. Seedling cohorts germinated during the wet season January 1996 rains and their progress was followed until July 1996.

have been changed from sheep to cattle enterprises is supported. This also explains why landholders who still run sheep are much less concerned than others about the pest potential of prickly acacia (Brown and Carter 1998). Where sheep are still present, prickly acacia seedlings have not survived in large numbers since the major germination event which occurred during 1973/74, and some landholders even expressed concern that older trees were dying off and not being replaced rapidly enough to maintain a good source of drought fodder and shade for their livestock (B. Fells, pers. comm.) Alternatively, on properties without sheep, prickly acacia seedlings have had high survivorship over the last 25 years and density has continued to increase since 1973/74 (Brown and Carter 1998). Landholders on cattle properties were more concerned about the pest potential of prickly acacia, since its value as fodder and shade could be negated by the costs of increased difficulty in management of stock and possible losses of grass fodder by shading and competition.

The episodic La Niña generated mass recruitment in prickly acacia and other woody weeds may present particularly difficult management problems. Harrington (1991) suggested that although competition from grasses was important in limiting the survival of woody plant seedlings in most years, climatic conditions were occasionally adequate for mass establishment and that post-establishment disturbances such as fire would be critical to managing shrub populations. Mortality due to desiccation of prickly acacia seedlings may reach 60% within the first few months post-emergence. Even higher mortality of seedlings is found in other arid zone shrubs including narrow-leaved hopbush (*Dodonaea viscosa* Jacq. ssp. *angustissima* DC., syn. *D. attenuata* Cunn.), a native increaser species of southern Australian rangelands. Harrington (1991) estimated from watered pot trials that in only 6 out of 97 years have soil moisture levels been sufficient to allow widespread recruitment in western New South Wales. *Callitris columellaris* F. Muell. shows high seedling loss to desiccation (100% in 18 months) even during a high rainfall season in South Australia (Read 1995), further indicating that pulses of regeneration in many native shrubs rely on La Niña episodes of heavy prolonged rain and flooding followed by several successive years of high aggregate rainfall which provide follow-up rains for establishment. Similarly high desiccation rates of seedlings of *Acacia ligulata* Cunn. ex Benth. and *Casuarina cristata* Miq. *ssp. pauper* F. Muell. (variable, up to 80%) were shown within the first couple of (dry) years after emergence in western New South Wales (Auld 1995). Prickly acacia is not as prone to desiccation as these species, and given the high seed loads, it seems likely that at least some plants establish in most years, but as with other shrubs in the arid zone there are pulses of recruitment during high rainfall years associated with La Niña events (Brown and Carter 1998). The effects of La Niña generated recruitment flushes of prickly acacia in the Mitchell grasslands have probably been amplified because of the replacement of sheep by cattle as the dominant herbivores.

Control of prickly acacia

We suggest that prickly acacia is more likely to become a management problem on cattle properties than sheep properties in the Mitchell grasslands. At present in these areas it is only at high densities in creeklines and boredrains. Densities are lower on upland sites but populations are continuing to regenerate rapidly, suggesting that further increases in density and spread are likely. Of prime concern are the prickly acacia infestations under higher rainfall regimes such as those on the east coast of Queensland where it is able to form dense unmanageable thickets on most landscape types. As a priority, management strategies should aim to prevent further spread of prickly acacia from property to property in eastern Queensland and to prevent introduction of prickly acacia into other regions in Queensland, Western Australia, the Northern Territory and northern New South Wales where computer modelling predicts that the climate would support severe infestations (Kriticos 1997). The most effective means of preventing spread will be by quarantining cattle from infested properties before transporting them to other properties within Queensland or interstate. An appropriate quarantine period would be 6 days, the time taken for seeds to pass through the digestive tract of cattle (Carter and Cowan 1993). Quarantining livestock for a brief period before moving between paddocks should also be effective in preventing further spread on infested properties.

Control techniques which are attuned to the ecology of the pest species concerned, and to the processes of the ecosystem within which it occurs are more likely to be effective. Relatively minor changes in management such as the use of an alternative species of livestock which can browse the pest plant more effectively may be a very economical means of achieving control. Sheep may be used in inland low-rainfall areas, but do not thrive in very high rainfall areas. In the low-rainfall Mitchell Grasslands of central western Queensland, sheep grazing may be sufficient to control the levels of prickly acacia recruitment experienced in most seasons. However, when mass recruitment occurs associated with prolonged rainfall and flooding it is highly unlikely that even with sheep grazing at moderate to high levels, that there would be adequate grazing pressure to defoliate all seedlings. Some plants would always establish during the periodic La Niña phases which occur about every 20 years in eastern Australia. In addition, the increased availability of palatable herbage in high rainfall years may reduce the relative acceptability of prickly acacia seedlings at precisely the time when suppression by hervivory would be required to control shrub numbers. This phenomenon has been observed with rabbits grazing western myall (*Acacia papyrocarpa*) in enclosures with and without available herbage (Lange and Graham 1983), and may help explain the widespread establishment of prickly acacia on both sheep and cattle properties during 1974/75. During such establishment periods, the stocking rates of sheep required to achieve control would most likely be deleterious to the survival of desirable native shrub species, and also cause soil erosion and compaction. So, although grazing by sheep may prevent increases in population density in most years, there may still be peaks of regeneration during La Niña wet periods.

The recovery of the Giru population to extremely high densities only 15 years after chaining demonstrates the ability of prickly acacia to regenerate following top removal. These results suggest that chaining cannot be recommended as a control measure for prickly acacia in high rainfall areas, unless some form of follow-up treatment is applied. Chaining is very expensive and should only be used in situations and seasons where there is likely to be a successful outcome, such as at lower rainfall sites, especially if carried out during droughts.

Other combinations of ecologially attuned control methods may be appropriate for prickly acacia. Such control practices have already been used with some success in other species, particularly for mesquite (*Prosopis* spp) in North America (Jacoby 1985, 1986), and should be considered for the control of leguminous shrubs in other tropical grasslands, such as prickly acacia in Queensland. After widespread recruitment episodes, fire may be used to control shrubs, an alternative technique which has been found useful with other woody weed species in northern Queensland (Grice 1997) and the USA (Ortmann et al. 1998). Fire is an attractive and cheap treatment considering that fodder availability far exceeds that required for herd use during high rainfall years. The possibilities for cost-effective control of prickly acacia by controlled burning should be investigated. Some (presumably) native insects were observed to cause seedling mortality, although only at low percentages. There may be some value in importing and testing insect species which consume either seeds or, more particularly, seedlings of prickly acacia. A national program to cap free-flowing artesian bores should also reduce the area of key habitat where *Acacia nilotica* can rapidly establish, thus providing a regular source of seed for cattle to spread to upland landscapes.

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Endophytic fungi in Canada wild rye in natural grasslands

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Abstract

Some grasses harbor endophytic fungi living in intercellular spaces in the leaves, stems and reproductive organs. The fungi can dramatically affect the physiology and ecology of plants. For example, fungi may produce toxins that deter herbivores and they may alter the water status of the plant to increase drought tolerance. The distribution of fungal infection in natural plant populations is unknown for many host species. We investigated the occurrence of endophytic fungi in *Elymus canadensis* L. (Canada wild rye) from 13 remnant prairie sites in the midwest and 23 sites in the southern Great Plains. Collections of plant tissue came from Nebraska, Kansas, Minnesota, Iowa, Missouri, Illinois, Oklahoma, and Texas. All midwest plants were grown in a common garden site in eastern Nebraska. Seeds collected from Oklahoma and Texas accessions were planted in the greenhouse. At least 3 tillers from 2 plants of each accession were screened for endophytes, using light microscopy. The endophytic fungus was found in seed of all accessions and in plants from all but 4 accessions. The functional significance of the fungus is unclear, but it may affect plants by enhancing productivity or deterring herbivores. The widespread occurrence of endophytic fungi in natural populations of *E. canadensis* suggests that the plant-fungal association may be long-standing and important in the evolution and success of this native prairie species.

Resumen

Algunos zacates albergan hongos endofiticos que viven en los espacios intracelulares de las hojas, tallos y órganos reproductivos. Los hongos pueden afectar dramáticamente la fisiología y ecología de las plantas. Por ejemplo, el hongo puede producir toxinas que desalientan a los herbívoros y ellos pueden alterar el estado hídrico de la planta para incrementar la tolerancia a sequía. La distribución de la infección fungal en poblaciones de plantas naturales es desconocida para muchas de las especies hospederas. Investigamos la ocurrencia de hongos endofiticos en *Elymus canadensis* L. (Canada wild rye) en 13 sitios de pradera en el medio oeste y en 23 sitios en las Grandes Planicies del Sur. Colecciones de tejidos de plantas arribaron de Nebraska, Kansas, Minnesota, Iowa, Missouri, Illinois, Oklahoma, and Texas. Todas las plantas provenientes del medio oeste se cultivaron en un sitio de jardín común en el este de Nebraska. Las semillas colectadas de las entradas de Oklahoma and Texas se plantaron en invernadero. Al menos 3 hijuelos de dos plantas de cada entrada se inspeccionaron mediante luz microscópica para determinar los endófitos. El hongo endófito se encontró en las semillas de todas las entradas y en plantas de todas menos 4 entradas. El significado funcional del hongo no es claro, pero puede afectar las plantas aumentando su productividad o desalentando a los herbívoros. La ocurrencia tan amplia y dispersa de los hongos endofiticos en las poblaciones naturales de *E. Canadiensis* sugiere que la asociación planta-hongo puede ser importante en la evolución y éxito de esta especie nativa de las pradera

Key Words: *Elymus canadensis*, *Epichlo typhina*, *Neotyphodium*, geographical pattern, mutualism, tallgrass prairie

Many grasses are infected by clavicipitaceous fungal endophytes that grow in the intercellular portions of the stems, leaves and reproductive organs. The fungi are often asymptomatic and are known to occur in all grass subfamilies and in most of the large grass genera (Clay 1990). Much of the research on fungal endophytes concerns the incidence and the effects of the infection in the important forage and turfgrass genera, *Festuca* (fescue) and *Lolium* (ryegrass). Endophytic fungi in agronomic *Festuca* and *Lolium* decrease the palatability of the grass to insect and mammalian herbivores and can cause toxicosis in livestock due to fungal and possibly, plant, production of alkaloids (Bacon et al. 1977, Funk et al. 1983 and Clay et al. 1985). The fungi can also enhance the growth and productivity of the plant (Belesky and Fedders 1995), especially under drought conditions (Arachevaleta et al. 1989). Bacon (1995) and Ball et al. (1993) reviewed the history of the endophyte, *Neotyphodium coenophialum,* (formerly known as *Acremonium coenophialum*) in tall fescue in which the particularly hardy, disease-resistant and (unknown at the time) endophyte-infected cultivar, KY 31, was widely adopted throughout the United States from the 1940's onward. The existence and role of the fungal endophyte in KY 31 was documented in the late 1970's, when reports of livestock disorders began to accumulate (Bacon et al. 1977, Hoveland et al. 1980).

Recently, efforts to characterize the evolution and ecology of the fungal-plant relationship in natural grass endophytes have been undertaken—for example, is the association mutualistic and how might such an arrangement have arisen? White (1988) presented some hypotheses about the origin and evolution of some of the known plant-fungal associations. In some grasses, the

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endophytic fungus forms external fruiting structures (stromata) that prevent the grass from flowering—thus the fungus completes its sexual lifecycle at the expense of the host plant. Since the host incurs some negative impacts, this type of association is pathogenic and White (1988) called this a "Type 1" association. In "Type 3" associations, stromata have never been observed and the fungus appears to spread asexually, by growing into the embryo and dispersing with the seed, and also spreading with clonal growth of the grass. In this type of association, the fungus appears to have positive effects on the plant, by protecting it from herbivores and enhancing growth. However it should be noted that the classification of many endophyte infections as mutualisms has been heavily influenced by results from a few agronomic species. Recent results from native species have emphasized the variety of negative, neutral and positive plant consequences (other than release from herbivory) that can result from endophyte infection (Saikkonen et al. 1998, 1999). White (1988) further defines a Type 2 association, in which only 1–10% of the individual plants within an infected population produce stromata, even though 50–75% of the individuals may harbor the fungus. The fungal-plant association in *Elymus canadensis* is thought to be Type 2 (White 1988) but more field observations are necessary to quantify the frequency and type of fungal infection in this species.

The frequency and type of infection of endophytic fungi throughout the range of a potential host are well-known for only a few host species. These species tend to be forage species tested because of the potential for causing livestock toxicity. The distribution of these species has been extensively influenced by human land management and planting. Studies on the extent of the fungal distribution within and between natural populations may shed light on the origin and evolution of the plant-fungus association. In one of the most complete studies to date on a natural grass population and its endophytes, Schulthess and Faeth (1998) found high seasonal and spatial variability in *Neotyphodium starrii* in the grass *Festuca arizonica*.

Our goal was to describe the extent of endophytic fungal infection in *Elymus canadensis* in the central grassland region of the United States. *E. canadensis* is a native, cool-season bunchgrass, abundant in tall and mixed-grass prairies. This species is known to harbor endophytic fungi, and a previous study of herbarium specimens suggested that fungi are present in about 60% of the *E. canadensis* individuals in North America (White 1987). The fungus is similar to *Epichloë typhina* (Ascomycetes), but because the sexual structures are seldom observed, it has been placed, along with other related grass endophytes into the genus *Neotyphodium* (Glenn et al. 1996). We screened fresh plant tissue collected from 2 sites in Nebraska and Kansas for the presence of *Neotyphodium*. We also screened tissue from a common garden that had been established from seed from 11 remnant tallgrass prairies in Nebraska, Iowa, Minnesota, Missouri, and Illinois, and from greenhouse grown plants derived from seed collected from Oklahoma and Texas.

Materials and Methods

Collections of *E. canadensis* germplasm ranged from Minnesota to Texas, with 8 states represented (Fig. 1). Sites consisted of virgin tallgrass prairie from roadsides, cemeteries, railroad right of ways or preserves, pastures, or farmland which had reverted to rangeland (Table 1). Some of the tissue was collected from a common garden site, which harbored plant accessions from 11 different sites (Sites 1–11 in Table 1) and some of the tissue was collected directly from the sites.

The common garden site near Mead, Nebr. (41.2°N, 96.5°W) was established in the following way. *E. canadensis* seed was

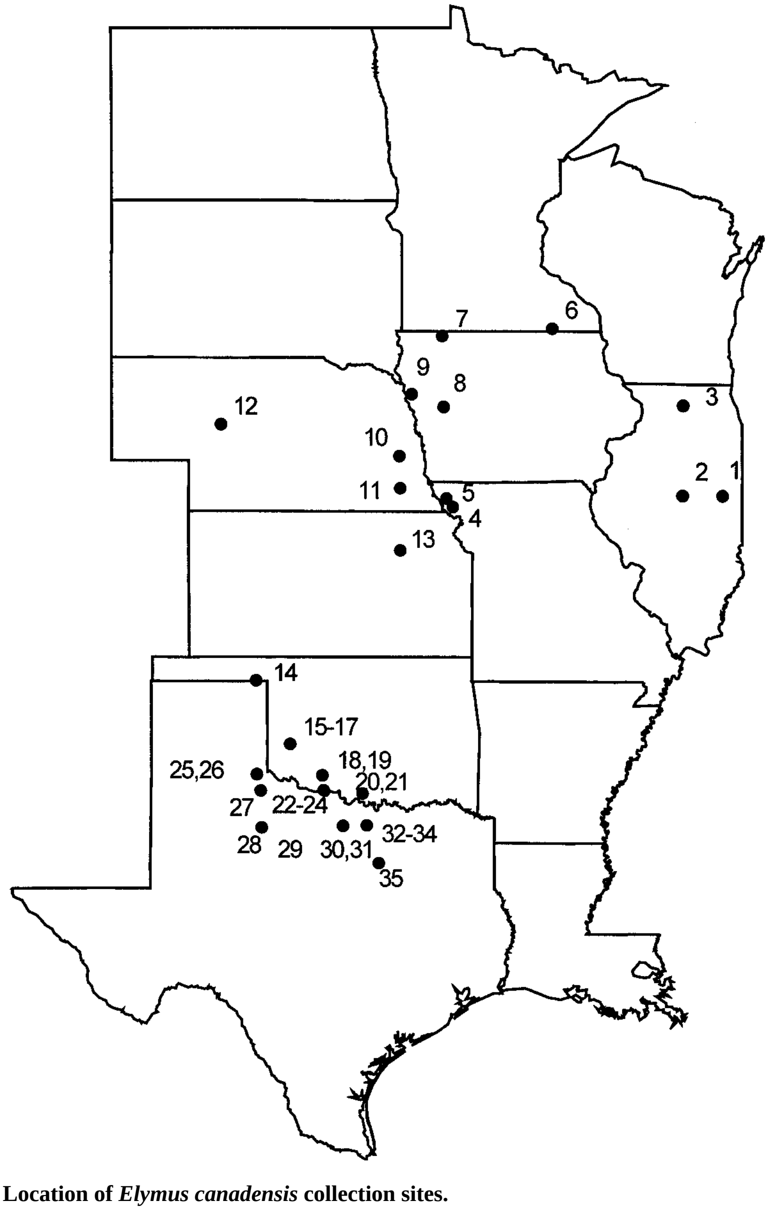

Fig. 1. Location of *Elymus canadensis* collection sites.

Table 1. Sites where germplasm of *Elymus canadensis* was collected and screened for the presence of a fungal endophyte. See Figure 1 for numbered site locations. Plant material from sites 1–11 and 14–35 was propagated in a greenhouse and transplanted into a common garden before endophyte screening took place. Tillers and seeds from sites 12–13 were collected directly from the site and screened for endophyte presence.

Site Number	Location	Nearest Town	Longitude/Latitude	Endophyte In Seed	Endophyte In Plant
1	Loda Cemetery	Loda, Ill	88.05W/40.32N	+	+
2	McLean Right of Way	Danvers, Ill	89.10W/40.32N	+	+
3	Beach Cemetery	Rockford, Ill	89.08W/42.08N	+	+
4	Holt County	Mound City, Mo	95.12W/40.08N	+	+
5	Atchison County Roadside	Rockport, Mo	95.29W/40.25N	+	+
6	Iron Horse	Hayfield, Minn	92.50W/43.55N	+	+
7	Compass	Worthington, Minn	95.40W/43.40N	+	+
8	Willow Township Cemetery	Charter Oak, Ia	95.36W/42.04N	+	+
9	Sioux City	Sioux City, Ia	96.20W/42.28N	+	+
10	Narodni Hrbitior Cemetery	Touhy, Nebr	96.52W/41.08N	+	+
11	Nine Mile Prairie	Lincoln, Nebr	96.50W/40.45N	+	+
12	Vinton Ranch	Mullen, Nebr	101.20W/41.70N	+	+
13	Konza Prairie	Manhattan, Kans	96.50W/39.20N	+	+
14	OKCS-38	Beaver, Okla	100.29W/36.36N	+	+
15	OKCS-30	Elk City, Okla	99.40W/35.15N	+	+
16	OKCS-26	Mangum, Okla	99.46W/35.03N	+	+
17	OKCS-29	Erick, Okla	99.54W/35.05N	+	+
18	OKCS-23	Snyder, Okla	98.55W/34.48N	+	+
19	OKCS-20	Snyder, Okla	98.55W/34.48N	+	+
20	OKCS-16	Waurika, Okla	98.05W/34.09N	+	+
21	OKCS-7	Lone Grove, Okla	97.16W/34.10N	+	+
22	OKCS-19	Lawton, Okla	98.30W/34.27N	+	+
23	OKCS-9, OKCS-40	Frederick, Okla	98.52W/34.16N	+	+
24	TXCS-13	Graham, Tex	98.41W/33.11N	+	-
25	TXCS-28	Wellington, Tex	100.27W/34.50N	+	+
26	TXCS-27	Childress, Tex	100.17W/34.43N	+	+
27	TXCS-17	Paducah, Tex	100.17W/34.15N	+	+
28	TXCS-20	Guthrie, Tex	100.14W/33.34N	+	+
29	TXCS-22	Crowell, Tex	99.35W/33.48N	+	+
30	TXCS-23	Henrietta, Tex	98.01W/33.38N	+	+
31	TXCS-15	Electra, Tex	98.54W/33.58N	+	+
32	TXCS-11	Montague, Tex	97.39W/33.39N	+	+
33	TXCS-30	Montague, Tex	97.37W/33.45N	+	–
34	TXCS-12	Nocona, Tex	97.57W/33.31N	+	–
35	TXCS-24	Dallas, Tex	97.07W/32.56N	+	–

collected in 1989 from remnant prairies in the central United States (Hopkins et al. 1995). At each site, spikes were collected in a haphazard manner from plants located throughout the remnant site. Seed from all the spikes collected at a site were threshed and the seed was bulked. The bulked seed was given an accession number that identified both the accession and the collection site. The accessions represent a sample of the germplasm from each respective prairie. Seed from each accession was wet chilled for 3 weeks at 4.5°C and planted in the greenhouse into plastic seedling tubes or mini-pots in February 1990. After emergence, the seedlings were thinned to 1 seedling per tube. Seedlings of the accessions were transplanted into 3 field evaluation nurseries in the spring of 1990. The evaluation nurseries were located at Mead, Nebr., Ames, Iowa (Lat. 42.0°N, Long. 93.6°W), and West Lafayette, Ind (Lat 40.4°N, Long. 86.9°W). At each location, the seedlings of each accession were transplanted into single row evaluation plots. Rows and plants within rows were spaced 1.1 m apart. There were 10 plants per plot at Mead and Ames and 7 plants per plot at West Lafayette. There were 2 replications of each plot at the 3 locations.

The plots were evaluated for yield and forage quality in 1991 and 1992. In 1993, seed was harvested on a plot basis from the plants at the 3 locations. The seed was threshed, cleaned and bulked by accession. It was possible to maintain the genetic purity of each accession using this process because *E. canadensis* is a self-pollinated species (Jensen et al. 1990). Seed from 11 remnant prairie accessions were used to plant larger nurseries (Table 1, Sites 1–11). The accessions that were planted were those that had the most potential for use in pasture and prairie renovation based on the agronomic evaluations. Seedlings were propagated in the greenhouse using the procedures described above and transplanted into field nurseries at Mead in the spring of 1993. Each nursery consisted of 12 rows of 40 plants with rows and plants within rows spaced 1.1 m apart. The nurseries were managed for seed production. They were cultivated as needed for weed control by roto-tilling between plants and rows. Herbicides were also applied as needed for weed control. The nurseries were fertilized with 112 kg/ha N as NH_4NO_3 each spring. Seed of accessions from Oklahoma and Texas were collected in 1997 in the same manner as seed from the midwestern sites.

Three fresh tillers from at least 3 different plants were collected from each of the 11 established *Elymus canadensis* accessions at Mead and from the 2 prairie sites (Konza Prairie and Vinton Ranch) in Kansas and Nebraska in 1997. Late in the growing season, 3 additional flowering tillers were collected from each of the 2 prairie sites. Two plants and 3 seeds were examined for each Oklahoma and Texas accession. The midwestern plants and seeds were examined in a laboratory at Creighton University and the Oklahoma and Texas material was examined at the Noble Foundation, using similar procedures. The fresh tillers were taken to the laboratory and kept refrigerated in plastic bags until they could be screened for endophyte infection. We followed procedures outlined in Bacon and White (1994) to prepare and stain the tissue. Sectioned leaf sheath tissue from mature plants was placed within a 10% potassium hydroxide (KOH) solution overnight to soften and clear the tissue. Leaf sheath tissue from younger plants was not treated with KOH. An epidermal peel of the tissue was made and aniline blue stain was placed onto the tissue. The tissue was warmed for 1 minute and a light microscope was used to detect fungal hyphae, visible at 100x power and confirmed at 400x. To screen seeds for the presence of the fungi, we placed seeds within a 1N sodium hydroxide (NaOH) solution to soften overnight. Then seeds were deglumed and placed within a warm aniline blue stain for one and a half minutes. The individual seed was then squashed for microscopic examination. Infection was detected through endophytic hyphae found within the aleurone layer of the seed. Seeds and tillers of Oklahoma and Texas accessions were examined at the Noble Foundation in 1998 using the same procedures given above.

We also checked each accession at Mead for the presence of stromata, the sexual form of fungal reproduction. Stromata appear on *E. canadensis* as a white external mat of hyphae, 3–10 cm long, and enveloping the flag leaf and culm (White and Bultman 1987, White and Morgan-Jones 1987). All tillers from one-third of the plants from each accession were manually checked in July-August 1998 for the presence of stromata. Since *E. canadensis* in this region typically forms seed heads in July and August, the presence of stromata on mature tillers should be most evident during this time period.

The identity of the fungus in *E. canadensis* was assumed to be similar to the *Neotyphodium* endophytes in other C_3 grasses, such as *Festuca*, and the same fungi as that previously described in *Elymus* species by White and Morgan-Jones (1987) and White and Bultman (1987). To provide some corroboration of fungal identity, we used a commercially available immunoblot assay to *Neotyphodium* (Agrinostics Ltd. Co.; 1501 Hickory Hill Drive; Watkinsville, Ga. 30677). The immunoblot produced a positive reaction to the *E. canadensis* endophyte in a random sample of tillers. In addition, we plated out the fungi in a random sample of seeds and greenhouse-grown plants. Seeds and 5 mm sections of tillers were surface sterilized with 1.25% Clorox (NaOCl) for 15 min. and rinsed twice in sterile water, as described in Bacon and White (1994). Seed and tillers were placed in potato dextrose agar for 5 weeks and observed every 2–3 days. Seeds tended to be more contaminated with bacteria and other fungi than tillers; a more thorough decontamination protocol (e.g. Marshall et al. 1999) may be necessary for seeds. Two weeks after the initial plating, endophytic fungal hyphae grew out the ends of the tiller sections so that the entire mass was dumbbell-shaped. A swab of the endophytic fungus was placed on a fresh plate and in 2–3 weeks the fungal mass was 2–3 cm in diameter, white and cottony on the top and brown when viewed from the bottom of the plate. Samples of the fungi were examined via light microscopy and we noted the appearance of solitary phialides which appeared to have basal septa. Conidia were produced after 2–3 weeks of growth. These plating observations match those of White and Morgan-Jones (1987), and provide evidence that the *E. candensis* fungal endophyte should be placed in the *Neotyphodium* group described by Glenn et al. (1996).

Results

The fungal endophyte appeared in leaf sheaths as straight and sometimes wavy strands of hyphae that were typically much longer than an individual cell and never appeared to invade the cell (Fig. 2). In seeds, the hyphae appeared as dense mycelial mats. In 36 populations of *Elymus canadensis* from 8 states, the endophyte was found in every seed examined, and in at least 1 plant from all but 4 accessions (TXCS-12, TXCS-13, TXCS-24, TXCS-30). Two accessions (OKCS-26, OKCS-40) contained endophyte in only 1 of the 2 plants examined. In tall fescue, factors such as temperature, moisture, and time influence endophyte viability in seed (Williams et al. 1984). It is possible that viability of the endophyte, but not of the seed, was lost during seed storage in these accessions, resulting in presence of endophyte free plants. Despite thorough field observations, no evidence of stromata were found on the 11 accessions at Mead.

Discussion

Two other studies on the extent of endophyte infections in natural populations of *Elymus* (*canadensis* and *virginicus*) have been done. White (1987) examined herbarium specimens at the University of Texas, Texas A&M, and Sul Ross State University. He found that 38 of 62 individuals (61%) of *E. canadensis* and 21 out of 45 individuals (47%) of *E. virginicus* were infected. He suggested that 1–10% of these individuals bears the stromata stage for potential sexual reproduction, while in the remaining infected individuals, the fungus reproduces asexually by growing into the seed (White and Bultman, 1987).

Clay and Leuchtmann (1989) performed the second study on the extent of endophyte infection in *Elymus*. They examined over 150 seed collections from *E. virginicus* and found that 72% of the seeds were endophyte infected. The seed was collected from the vicinity of Indiana University in south central Indiana. In these samples, both the *Epichloë* (stromata present on culm) and *Neotyphodium* (no stromata development) types of fungal endophyte were detected.

No evidence of stromata was present in our field populations (Mead only). Stromata are most obvious when plants are fairly mature and the flowering culms are elongating to produce seed heads, a

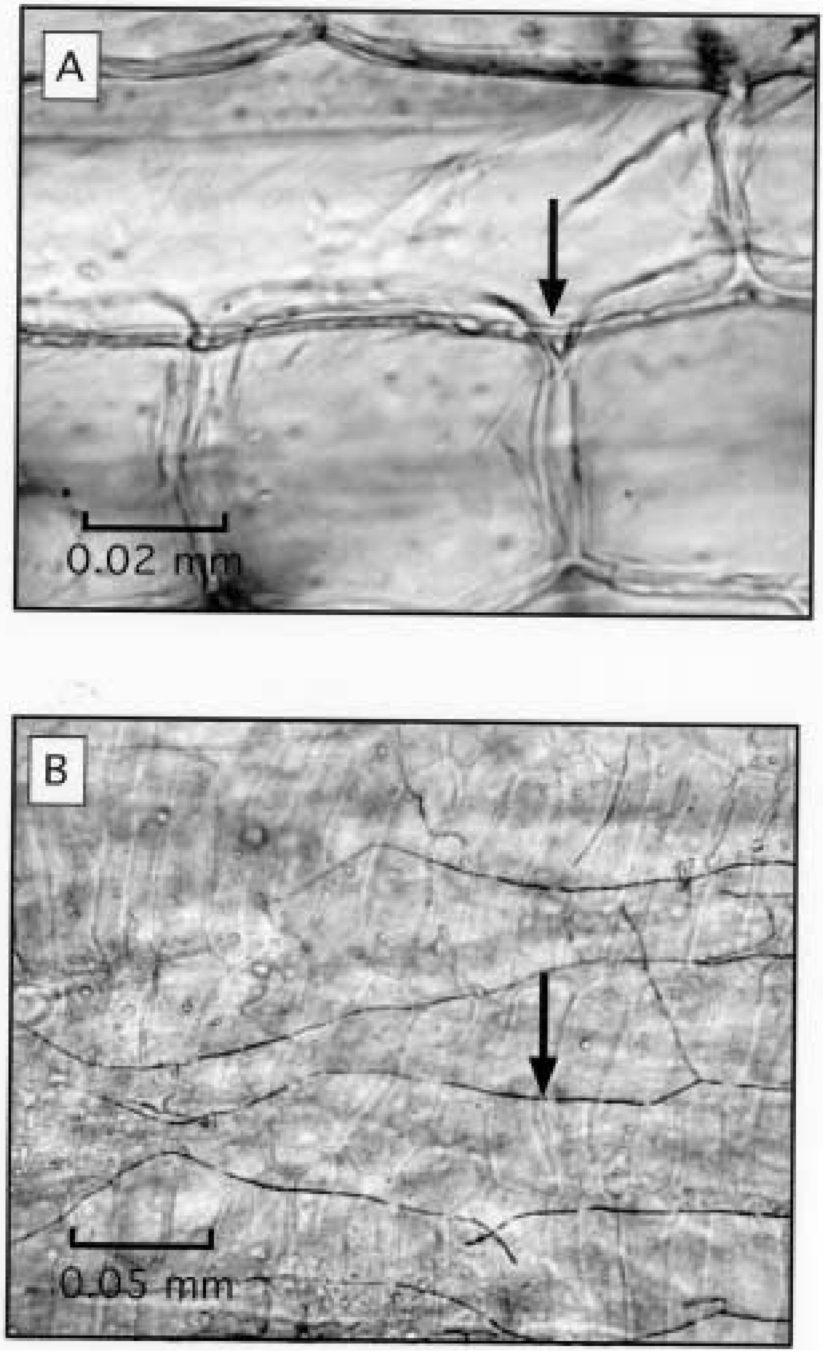

Fig. 2. Slides of endophytic fungal hyphae (arrows) in seed (A) and sheath tissue (B) from *Elymus canadensis*. Slides were cleared and stained with aniline blue solution.

stage that occurred in July–August at the Mead common garden site. In other studies of stromata occurrence, plants growing in wet areas were more likely to have stromata than plants in dry uplands (White, personal communication). Our common garden plants were generally large and vigorous, as they were maintained in cultivated plots with minimal competition. Thus, it is unlikely that these plants were lacking in resources, so the factors promoting stromata development remain unclear. However, these results do clearly demonstrate that fungal transmission in *E. canadensis*, as in tall fescue and ryegrasses**,** occurs primarily via seed. Since the plant materials evaluated at Mead were 2 seed generations removed from the original plants in the remnant prairies, the presence of the endophyte in the plants demonstrates that in *E. canadensis* the endophyte is transmitted across generations via seed.

We found higher incidence of infection than did either White (1987) or Clay and Leuchtmann (1989), as our infection rate approached 100%. Leuchtmann (1992) documented endophyte infection rates of 58 to 80% in native populations of *Lolium perenne, L. multiflorum, Festuca arundinacea* and *F. pratensis* in natural habitats in Europe. A number of studies have shown increases in the frequency of fungal endophytes in plant populations through time (e.g. Thompson et al. 1989, Shelby and Dalrymple, 1993). These increases are likely due to either 1) contagious spread of the fungus or 2) increased growth and fitness of the endophyte-infected plants due to greater herbivore resistance and competitive ability. Our results suggest that contagious spread is unlikely, since we observed no external, spore-producing stromata. Furthermore, our collections came primarily from relatively old habitats (e.g. virgin tallgrass prairie). The Oklahoma and Texas collections came from more disturbed sites than the midwestern accessions, but essentially no commercial varieties of *E. canadensis* are available in this region, so even the tissue from disturbed areas probably represents indigenous plants. Therefore, it seems possible that the fungal endophyte in *Elymus canadensis* increases plant fitness, through enhanced growth or herbivore resistance.

Preliminary tests of a few *E. canadensis* tillers suggest that ergot alkaloid levels are substantially less than the levels in endophyte-infected tall fescue (N. S. Hill, personal communication). The ergot alkaloids are one of the means by which mammalian herbivores are deterred in tall fescue, but at least 3 other alkaloidal compounds may be involved in herbivore deterrence in *Neotyphodium*-infected tissue (Siegel and Bush 1994, 1997) . Other means by which the endophytic fungus could have positive effects on the plant are through increasing the growth and ability of the plant to cope with drought stress, as has been found in tall fescue (Arachevaleta et al. 1989). However, the possibility exists that *Neotyphodium* infection in *E. canadensis*, despite its widespread occurrence, does not confer drought tolerance or herbivore resistance on plants. Saikkonen et al. (1999) found no evidence that endophytes confer grazing resistance in native Arizona fescue populations and suggest endophytes in natural populations may be important in increasing pathogen resistance and competitive ability of adult plants rather than in mediating interactions with herbivores (Saikkonen et al. 1998). More experiments on the alkaloid levels, herbivore preference, pathogen resistance and drought response of endophyte-infected and uninfected plants of *E. canadensis* are necessary to elucidate the ecological significance of this widespread plant-fungal association.

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‘Immigrant’ forage kochia seed viability as impacted by storage methods

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Abstract

‘Immigrant’ forage kochia (*Kochia prostrata* (L.) Schrad.) is a valuable introduced subshrub, often used in reclamation plantings and seedings on western rangelands. Seedling establishment is best from fresh seed; however, many users plant stored seed and experience poor seeding success. One cause for failure is loss of seed viability in storage. Forage kochia seed was harvested on 4 dates in fall 1996 from 2 sites (wildland and irrigated) and tested for viability when fresh and after storage treatments. Storage treatments included low and high seed water contents (2–6% and 12-16%), cold and warm storage temperatures (2° and 25° C), and duration of storage (4, 8, and 12 months). Mature, highly viable forage kochia seed remains viable in storage longer than seed harvested prematurely. Low seed water content (2–6%) is essential to preserving maximum seed viability. Storing seed at a cold temperature (2° C) is also helpful in maintaining viability.

Key Words: *Kochia prostrata*, revegetation, seed care, greenstripping

Resumen

La Kochia forrajera (*Kochia postrata* (L) Schrad) ‘Inmigrant’ es un valioso subarbusto introducido que a menudo es utilizado en plantaciones y siembras para restaurar los pastizales del oeste. El establecimiento de plántulas es mejor a partir de semilla nueva, sin embargo, muchos usuarios plantan semilla almacenada y obtienen un pobre establecimiento de plántulas. Una de las causas del fracaso es la perdida de viabilidad de la semilla durante el almacenaje. Se cosecho semilla de Kochia forrajera en 4 fechas de otoño de 1996 y en 2 sitios (con riego y natural) y se probaron para determinar su viabilidad cuando estaban recién cosechadas y después de tratamientos de almacenamiento. Los tratamientos de almacenamiento incluyeron bajos y altos contenidos de agua de la semilla (2–6% y 12–16%), temperaturas de almacenamiento frías y calientes (2° y 25°C) y duración de almacenamiento (4, 8 y 12 meses). La semilla madura de alta viabilidad permanece viable mas tiempo bajo almacenamiento que la semilla cosechada prematuramente. Un bajo contenido de agua (2-6%) en la semilla es esencial para conservar la máxima viabilidad de la semilla. Almacenado la semilla a temperaturas frías (2°C) también es útil para mantener la viabilidad.

Forage kochia (*Kochia prostrata* (l.) Schrad.) was first introduced to the United States from the Soviet Union during the early 1960’s (Keller and Bleak 1974). It is a semi-evergreen subshrub native to arid and semiarid regions of central Eurasia where it is valuable forage (Balyan 1972). Many assessions of forage kochia have been tested as possible forage and reclamation plants for semi-arid locations since its introduction (Keller and Bleak 1974, Stevens et al. 1985, McArthur et al. 1996). The variety ‘Immigrant’ was released in 1985 for forage and erosion control on greasewood-shadscale (*Sarcobatus vermiculatus* (Hook.) Torr. -*Atriplex confertifolia* (Torr. & Frem.) Wats.), sagebrush-grass (*Artemisia* spp.-grass), and pinyon-juniper (*Pinus* spp.-*Juniperus* spp.) rangelands of the Intermountain West (Stevens et al. 1985). Immigrant forage kochia has been used successfully as a revegetation species on harsh sites (Blauer et al. 1993, Frischknecht and Ferguson 1984, McArthur et al. 1974, Monsen and Turnipseed 1990) and is used extensively for seeding after fires on cheatgrass (*Bromus tectorum* (L.) dominated rangelands (Horton et al. 1994, McArthur et al. 1990). It has the valuable characteristic of sprouting after fires on these sites (McArthur et al. 1990).

Seed demand for Immigrant is generally high because of its range of uses and adaptability. For best establishment, fresh seed should be planted in late fall or early winter (Haferkamp et al. 1990, Monsen and Kitchen 1994). Many users, however, have planted year-old seed and experienced low seeding success. A probable cause of this problem is low seed viability due to short shelf-life of the seed between the time of viability testing and the time of purchase, which creates the potential for undetected losses in viability (Moghaddam 1978, Stevens and Jorgensen 1994). To maximize seeding success and financial return, it is beneficial to understand how viability changes over time in response to storage conditions (Stevens and Jorgensen 1994).

This research examined the effects of storage conditions, harvest date (an index of seed maturity), and maternal growth environment on viability of Immigrant forage kochia seed. These factors undoubtedly influence seeding success on western rangelands.

Methods

Fruits (hereafter referred to as seed) were collected from 2 sites. The first was a USDI Bureau of Land Management seeded (Immigrant) site, located 11 km north of Dugway, Tooele County, Ut. (40° 20' N., 112° 44' 36" W.) where several hundred mature forage kochia plants were present. The Natural Resources Conservation Service has classified the soil as a very deep, well-drained Tooele fine, sandy loam (Coarse-loamy, mixed, superac-

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tive, calcareous, mesic Typic Torriorthent) which receives an average of 17 cm of annual precipitation (Trickler, et al. 2000). The second site was an irrigated field operated by Stevenson Intermountain Seed near Manti, Sanpete County, Ut. (39° 16' 30"N., 111° 38' 8" W.) where certified Immigrant forage kochia seed is grown for commercial use. The crop is irrigated as needed to maximize production, and the soil is a Sigurd gravely loam (Loamy-skeletal, carbonatic, mesic Xeric Torrifluvent) (Soil Conservation Service 1981).

Seed was harvested from both sites in 1996 on 4 October, 18 October, 1 November, and 15 November. Twenty plants were selected at each site to represent the population's variability. Seed was handstripped from each of these plants on each collection date and the phenological stage of seed maturity was recorded to allow application of this data to subsequent years and multiple sites. The seeds were then air-dried for 3 to 10 days. Empty and immature fruits, fruit fragments, leaves, and small stems were removed using 1.0mm, 1.8 mm, and 4.8mm rounds (Seedburo Equipment Company, Chicago, Ill.)

A subsample (3 to 20 g) of each seed lot was dried to 0% moisture in a drying oven at 125° C. This sublot was used as a reference in calculating seed water content for the levels desired in storage. The remaining fresh seed was then divided evenly into 32 sublots for a complete factorial arrangement of the storage treatments [4 harvest dates x 2 growth environments (wildland and irrigated sites) x 3 storage temperatures (fresh seed with no storage, cold storage at 2° C, and warm storage at 25° C) x 3 levels of seed water contents during storage (fresh seed with no storage, low seed water content at 2-6%, and high seed water content at 12-16%) x 4 storage lengths (0, 4, 8, and 12 months)]. Seed was then further air-dried or rehydrated until the desired seed water content levels were achieved. Each of the sublots was weighed and stored in a plastic vial, with each group of vials sealed in a plastic bag and placed in a cardboard box.

Percent seed viability was assessed for each seed lot, when fresh and after each storage period. Each test included 4 replications of 25 seeds from each seedlot. Seed was placed in 100 mm X 15 mm plastic petri dishes on two 1-mm thick blotters (Anchor Paper, St. Paul, Minn.) saturated with tap water. Dishes were randomized, stacked, and placed in plastic bags in order to retain moisture. To ensure even light treatment for all dishes, a blank dish with 2 dampened blotters was placed on the top of each stack. Blotters were resaturated as needed throughout the germination test. Stacks were randomly arranged in a germination chamber and rearranged after weekly counts.

Seed was incubated in a controlled environment chamber with a 12-hour diurnal photoperiod at 10/20° C. Every 7 days, the germinated seed in each dish were counted and removed. Germination was defined as 5+ mm radicle emergence (Young et al. 1981). After 28 days, firmness of ungerminated seed in each dish was determined using a cut test to examine embryonic tissue (Association of Official Seed Analysts 1988). Dormant seed was defined as firm but ungerminated after 28 days. Germinated seed plus dormant seed equaled total viable seed for each dish.

Percent viability was calculated for each replication and was arcsin transformed before analysis to normalize the data. A factorial analysis of variance appropriate to the completely randomized experimental design was used to determine significance of treatments and interactions (SAS 1998).

Results and Discussion

Maternal Growth Environment

Maternal growth environment of the seed may affect ripening rate or other factors of importance to seed quality (Balyan 1972). Effects of seed maturity, growth environment, and storage conditions on seed viability of Immigrant forage kochia seed were highly significant ($p < 0.01$). Seed from the wildland site was more viable (75%) when fresh compared to seed from the irrigated site (65%). Viability after storage was lower for seed from both sites, with the relative difference being similar to that of their original viability, as wildland seed was 45% and irrigated seed was 38% viable overall, after 12-months storage. Causes of these differences would be highly speculative at this point, as further studies over time or involving more sites would be warranted. Thus, in all following discussion, tables, and figures, data shown are means from both sites.

Harvest Date

An important consideration concerning low seed viability of forage kochia is early harvest. Seed growers may feel compelled

Table 1. Means (standard errors) of percent viability for 'Immigrant' forage kochia seed incubated for 28 days in a 12-hour diurnal photoperiod at 10/20° C. Seed was harvested from an irrigated site and a wildland site in central Utah in fall 1996 and tested for viability when fresh and after storage treatments. High seed water content was 12-16% and low was 2–6%. Storage at a cold temperature was 2° C, and the warm temperature was 25° C. For all means, N = 8.

			STORAGE LENGTH					
			4 months		8 months		12 months	
			STORAGE TEMPERATURE					
Harvest Date	Water Content	Fresh Seed	Cold	Warm	Cold	Warm	Cold	Warm
			(%)					
4 Oct.	High	17 (5)	43 (4)	0 (0)	23 (4)	1 (0)	17 (5)	0 (0)
	Low		11 (3)	15 (4)	9 (2)	13 (4)	15 (3)	11 (3)
18 Oct.	High	85 (2)	75 (3)	14 (4)	54 (5)	16 (5)	43 (6)	4 (1)
	Low		77 (5)	78 (4)	66 (4)	75 (3)	72 (4)	64 (4)
1 Nov.	High	92 (2)	81 (2)	0 (0)	65 (3)	1 (0)	41 (4)	0 (0)
	Low		89 (2)	87 (2)	87 (3)	88 (4)	83 (4)	82 (4)
15 Nov.	High	87 (3)	86 (4)	1 (0)	82 (5)	4 (3)	69 (7)	0 (0)
	Low		82 (4)	92 (1)	85 (4)	81 (6)	85 (4)	84 (4)

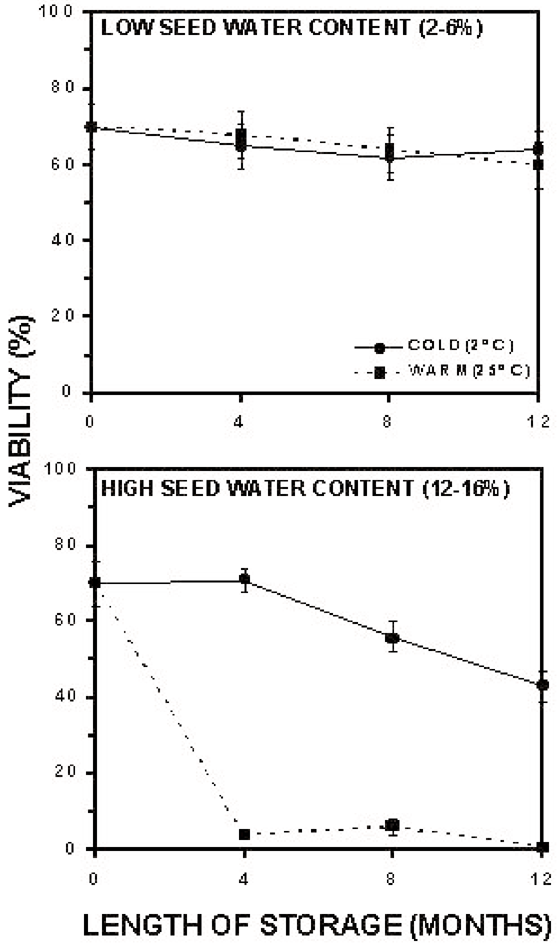

Fig. 1. Percent viability of 'Immigrant' forage kochia seed from all collection dates and both growth environments stored with 2 seed water content levels (low at 2–6% and high at 12–16%) and at 2 temperatures (cold at 2° C and warm at 25° C) shown over increasing length of storage (0, 4, 8, and 12 months). This 3-way interaction was significant at $p < 0.01$. For all means N = 32.

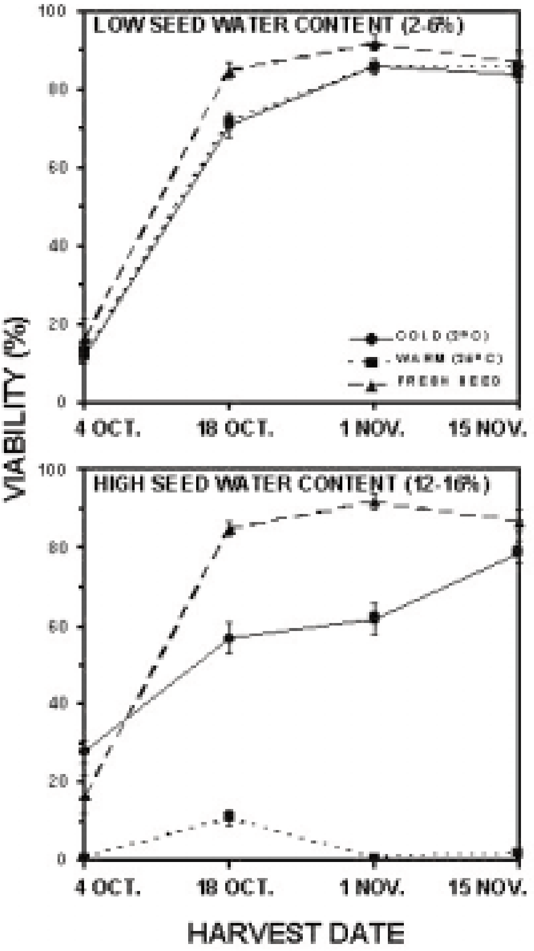

Fig. 2. Percent viability of 'Immigrant' forage kochia seed from both growth environments, meaned across all storage lengths, stored with 2 seed water content levels (low at 2–6% and high at 12–16%) and at 2 temperatures (cold at 2° C and warm at 25° C) shown over successive harvest dates (4 October, 18 October, 1 November, and 15 November). This 3-way interaction was significant at $p < 0.01$. For means of fresh seed N = 8, and for all other means N = 24.

to harvest before the seed ripens fully in October or November to prevent losses associated with fall storms (Moghaddam 1978). However, immature seed may not be capable of surviving storage and/or producing viable seedlings (Waller et al. 1983).

Seed collected from both sites on the first harvest date (4 October) were immature. The seed and stems were still very green, moist, and not easily stripped from the inflorescence. Seed maturity, or the developmental stage for optimum germination, is judged in the field stage when seed can be easily stripped by hand from the inflorescences, after the stems have changed to a reddish color and dry up (Balyan 1972, Waller et al. 1983). By 18 October, approximately half of the seed at the collection sites had started to mature and turn red. By 1 November, the seed was fully ripe, as it was very red, dry, and easily hand-stripped. By the fourth harvest, seed at the wildland site was still very ripe and mostly still on the stalk. At the commercial site, large amounts of seed had already shattered and dropped, signifying it had reached full maturity.

When fresh seed was tested, viability was low (17%) for seed from the first harvest, as expected from its appearance. Viability was high for fresh seed from the second, third, and fourth harvests (88% collectively) because all or most of the seed was mature by then. Seed from the last 3 harvests also retained viability over time (Table 1). Seed viability from the first harvest varied but was typically lower with storage.

Storage Conditions

Forage kochia seed is known to have a short shelf-life, especially under uncontrolled warehouse storage conditions (Balyan 1972, Jorgensen and Davis 1984, Keller and Bleak 1974). Not stored properly, seed can lose 80 to 90% viability in less than a year (Moghaddam 1978, Stevens et al. 1985).

The interaction among seed water content, storage temperature, and length of storage was highly significant ($p < 0.01$). Figure 1 illustrates the effects of seed water content and storage temperature over time on seed viability. Seed stored with a high seed water content at a warm temperature lost 94% viability, while seed stored at a cold temperature with a high seed water content lost only 20% viability. Storing seed with low water content, whether in a cold or warm storage temperature, preserved seed viability for the majority of seed, with only 9% viability lost overall. It is imperative to store forage kochia seed with a low water content to ensure preservation of viability.

Differences among the effects of seed water content, storage temperature, and seed maturity level also led to a highly significant interaction ($p < 0.01$). Seed stored with low water content at a cold or warm temperature was able to retain most of the seed viability after storage (Fig. 2). This was especially true for the most mature seed from the latest harvest. They remained 85% viable after 12 months in storage, compared to 87% viable when fresh. Mature seed appeared to be most resilient to adverse storage conditions. Figure 2 also depicts the dramatic loss of viability in seed from all harvest dates which were stored with a high seed water content at a warm temperature. Seed stored with a high seed water content in a cold temperature retained much more viability than those stored with the same seed water content at a warm temperature. Storing forage kochia seed at a cold temperature aids in retaining seed viability; however, storage with a low seed water content is most effective. Stewart et al. (1999) found that these storage conditions also preserved maximum dormancy and maintained the most delayed and desynchronized germination rate for forage kochia seed.

Conclusions

Recommendations to obtain higher seed viability from stored Immigrant forage kochia seed include delaying harvest until seed is mature, when seed is red and easily hand-stripped from the inflorescence. This is typically sometime from October to November (Balyan 1972). Early collection yields mostly nonviable seed, while later collection yields highly viable seed which are also longer-lived in storage.

To maintain high seed viability in storage, first priority should be given to drying fresh seed to a low seed water content (2–6%) and maintaining that level through the term of storage. A second priority should be to store the low-water content seed at a cold temperature (2° C). As the use of forage kochia increases on western rangelands, these recommendations will aid in obtaining and maintaining the highest possible viability when Immigrant forage kochia seed is stored and planted.

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Carbon and nitrogen dynamics in elk winter ranges

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Abstract

Recent increases in elk (*Cervus elaphus* L.) herbivory and changes in hydrology towards drier conditions have contributed to declines in willow (*Salix* spp. L.) communities in the winter ranges for elk in Rocky Mountain National Park. In 1994, we constructed 12 large elk exclosures in 2 watersheds of the winter range for elk in the park, and conducted field experiments from 1995 to 1999 to investigate the effects of herbivory and proximity to surface water on the dynamics of C and N. Litterfall biomass averaged 65.6 and 33.0 g m^{-2} inside and outside the exclosures, respectively. Elk herbivory increased ($P < 0.05$) N concentration of willow litter from 1.25 to 1.49%, but there were no differences in losses of C and N from litterbags placed in grazed and ungrazed plots in any of the growing seasons. Carbon losses from litterbags were higher in lower landscape positions ($P = 0.001$), in comparison to upper landscape positions. Shoot biomass of willow plants fertilized with N averaged 27.3 g and was higher ($P < 0.05$) than that of unfertilized plants, which averaged 20.2 g, indicating that N availability limits plant growth in our study sites. Elk herbivory had no effect on soil inorganic N availability, even though we estimated that the return of N to the soil in grazed plots could be as much as 265% of the N return in exclosed plots. In the long-term, greater return of N to the soil combined with increased litter quality in the grazed plots could contribute to increases in N cycling rates and availability, and these changes could affect ecosystem structure and function in the winter range for elk in Rocky Mountain National Park.

Key Words: Willow, *Salix*, *Carex*, litterfall, litter decomposition, nitrogen availability.

Resumen

El reciente incremento en la herbivoría del alce (*Cervus elaphus* L.) y los cambios en la hidrología hacia condiciones mas secas han contribuido a la disminución de las comunidades de "Willow" (*Salix* spp. L) en los pastizales de invierno para alces del Parque Nacional de las Montañas Rocallosas. En 1994 construimos 12 grandes exclusiones contra alce en 2 cuencas hidrológicas de pastizales de invierno para alce del parque y de 1995 a 1999 condujimos experimentos de campo para investigar los efectos de la herbivoría y proximidad de la superficie de agua en las dinámicas de C y N. La biomasa de mantillo promedió 65.6 y 33.0 g m^{-2} dentro y fuera de las exclusiones respectivamente. La herbivoría del alce aumentó ($P < 0.05$) la concentración de N del mantillo de "Willow" de 1.25 a 1.49%, pero no hubo diferencias en las pérdidas de C y N de bolsas con mantillo colocadas en parcelas con y sin pastoreo en ninguna de las estaciones de crecimiento. Las pérdidas de carbón de las bolsas con mantillo fueron mayores en las posiciones de terrenos bajos ($P = 0.001$), en comparación con las posiciones de terrenos altos. La biomasa de tallos de plantas de "Willow" fertilizadas con N promedió 27.3 g y fue mayor ($P < 0.05$) que la de las plantas sin fertilizar, la cual promedió 20.2 g, indicando que la disponibilidad de N limita el crecimiento de las plantas en nuestros sitios de estudio. La herbivoría del alce no tuvo efecto en la disponibilidad del N inorgánico del suelo, a pesar de que estimamos que el retorno de N al suelo en las parcelas con pastoreo pudiera ser tanto como el 265% del N retornado en las parcelas excluídas. A largo plazo, el mayor retorno de N al suelo, combinado con un aumento en la calidad del mantillo de las parcelas con pastoreo contribuir a incrementar las tasas de reciclaje de N y su disponibilidad, y estos cambios podrían afectar la estructura y función del ecosistema en los pastizales de invierno para alce del parque Nacional de la Montañas Rocallosas.

Since 1968, elk (*Cervus elaphus* L.) numbers in Rocky Mountain National Park, Color. have been managed under a policy of natural regulation, which rests on the assumption that density-dependent mechanisms would result in an equilibrium between large ungulate herbivores and plant resources. During this period, elk numbers have increased from approximately 1,000 to about 3,300 animals, and park managers are concerned about the effects of these increases on the soils and vegetation of the elk winter range within the park (Singer et al. 1998b).

Willow (*Salix* spp. L.) communities have reportedly been declining in elk winter ranges of the park during the last few decades (Hess 1993, Singer et al. 1998b), and several studies are currently being conducted to investigate the extent of these changes (R. Peinetti, pers. comm., 1999). Similarly, declines in willow populations have also been reported for Yellowstone National Park (Chadde and Kay 1991, Kay and Wagner 1994, Singer et al. 1998a). In addition to increased elk herbivory, 2 other factors have been proposed to explain these apparent

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declines in willow communities of Rocky Mountain National Park: (1) climates are warmer and drier this century, possibly resulting in lowered stream flows and less water availability to plants (Singer et al. 1998b); and (2) beaver populations have declined on the eastern slope of the park (Stevens and Christianson 1980), which may further contribute towards the drying of these ecosystems.

Large herbivores can significantly influence plant community structure and biogeochemical cycles within the soil-plant system (Frank et al. 1994, Frank and Groffman 1998, Hamilton et al. 1998, Schuman et al. 1999, Wijnen et al. 1999). Herbivores can influence nutrient cycling by removing plant biomass and returning more readily available nutrients to the soil (McNaughton et al. 1988, Frank et al. 1994, Hamilton et al. 1998), increasing soil N mineralization rates and plant N uptake (Frank and Groffman 1998, Wijnen et al. 1999), spatially redistributing nutrients within the landscape (McNaughton 1985, Afzal and Adams 1992, Russelle 1992), or decreasing the amount of litterfall and nutrient return to the soil in litter (Pastor et al. 1993).

Beaver (*Castor canadensis* Kuhl) can also influence plant communities and biogeochemical cycles of ecosystems. By building dams, beavers contribute to the entrapment of sediment and organic matter and modify water availability, nutrient cycling, and the dynamics of organic matter decomposition (Naiman et al. 1986, Naiman and Melillo 1984). It has been suggested that the observed declines in beaver populations in the eastern slope of Rocky Mountain National Park have contributed to a decrease in the surface area of water (ponds and streams) within the winter range of elk since the beginning of this century, therefore decreasing water availability for willows. These reductions in water availability could further reduce the ability of willow to respond to elk herbivory (Singer et al. 1998b) and could also alter the biogeochemical cycles of those ecosystems. However, the extent of the influences of these changes over the elk winter ranges of the park is unknown.

Plant-available N is usually a limiting element for plant growth in terrestrial ecosystems (Power 1977, Kiehl et al. 1997, Wijnen et al. 1999) and the cycling of N in these systems is linked to the C cycle by interactions between decomposers, plants, and herbivores (Aber and Melillo 1991, Pastor and Naiman 1992). There is no available information about the effects of elk herbivory or the reduction in surface water on the dynamics of C and N in the winter ranges of elk in Rocky Mountain National Park. This information is necessary for helping park managers formulate policies that will maintain herbivore populations at levels that are adequate for preserving the natural functioning of these ecosystems. Therefore, the objective of this study was to perform experimental field manipulations to investigate the effects of elk herbivory and proximity to surface water on the C and N cycles in the winter ranges of elk in the park.

Methods

Study Sites

The winter range for elk in Rocky Mountain National Park encompasses about 10,000 ha, which includes land within the eastern side of the park and private and national forest lands outside the park in the town of Estes Park and Estes Valley, Colo. (Singer et al. 1998b). Our study sites were located in 2 riparian ecosystems on the northeastern side of Rocky Mountain National Park: 1) Moraine Park, along the Big Thompson River watershed, at an elevation of 2,481 m and 2) Horseshoe Park, along the Fall River watershed, at an elevation of 2,598 m. The latitude and longitude of the area of the watersheds are 105° 36' N and 40° 22' W. The 2 watersheds are within 5 km of each other and have perennial alpine snowfields at their headwaters. Mean annual precipitation for the sites is 41 cm (Singer et al. 1998b) and peak stream flow usually occurs in early to mid-June (USDA 1995, 1996, 1997). The 30-year average temperature for the adjacent Estes Valley ranges from 9 to 17°C during the 5-month growing season of May through September (Alstad et al. 1999). The study area consists of wet meadows dominated by willow (mainly *Salix monticola* L., *S. geyeriana* Anderss., and *S. planifolia* Pursh), other shrubs such as birch (*Betula* spp. L.), sedges (*Carex* spp. L.), rushes (*Juncus balticus* Willd.), and grasses (*Phleum* spp. L., *Calamagrostis* spp. Adans., *Bromus* spp. L., *Poa* spp. L.). The elk population of Estes Valley numbers about 3,300 animals, of which about one third generally spends the winter within the park (Larkins 1997, Singer et al. 1998b).

Experimental Treatments

In the wet meadows of both parks, 12 exclosures (30 m x 46 m each) were erected within willow communities along the rivers between August and November of 1994. Next to each exclosure, 30 m x 46 m plots were chosen and marked off as paired plots open to grazing (grazed plots). The area within each exclosure was subdivided into 15 m x 23 m sub-plots and 2 treatments were imposed throughout the period of the study: (1) 75% current annual growth removal (clipped plots), and (2) no clipping at all (ungrazed plots). The 75% current annual growth removal treatment was applied between January and April of 1995, 1996, 1997, and 1998, and consisted of clipping all forage shrubs and herbaceous plants in each sub-plot. All clipped plant biomass was removed from the exclosures. Therefore, each site consisted of: (1) grazed plot (outside the exclosure); (2) ungrazed plot; and (3) clipped plot (both inside the exclosure).

Eight sites (4 in Moraine Park and 4 in Horseshoe Park) were placed in areas with little or no beaver activity, and contained heavily browsed willow plants, which had their height suppressed by elk browsing (short willow). The other 4 sites (2 in each park) were located in nearby (about 1 to 2 km) wetter areas, generally containing taller willow plants subjected to less browsing by elk (tall willow). The difference between the willow plants in the 2 areas (tall willow and short willow) was strictly morphological since the willow species composition of the communities in the 2 areas was the same. In half of the short willow sites (2 in each park), hydromanipulation treatments were imposed by placing sheet metal check dams on ephemeral stream channels both inside the exclosures and in the grazed plots. We expected these check dams to catch snowmelt and rain runoff through the spring and raise the water table at the sites. Twenty-five dams were installed in April and May 1995 and were relatively successful in holding additional water at these sites. The dams were intended to add water, but in no way was the treatment able to simulate water additions in the amounts accomplished by beaver dams on larger, permanent streams (Singer et al. 1997). In each exclosure and associated grazed plot, an average of 5 shallow (0.5 to 2 m) wells were installed in the spring of 1995 for the purpose of monitoring groundwater levels. During early 1996 and 1997, 3 beaver dams were constructed near 2 sites within the wetter area of Moraine Park, but these dams were washed out during the spring flood of 1996 and 1997.

Litterfall

Litter was collected in each experimental plot during the fall of 1995, 1996, and

1997, through the use of 15 greenhouse trays (totaling ~ 2.3 m^2) arranged in a 5 x 3 regularly spaced grid (9.1 m x 15.9 m). The grids were established randomly within each sub-plot before willow senescence began, and each tray was anchored to the ground using 2 or more large spikes. Litter was collected weekly from early September to late October until litterfall was complete. The litter was then composited within each experimental replication, sorted by genus and litter type, air dried, and weighed. Oven-dry corrections were applied within each category by drying a subsample at 60°C. Litterfall biomass was calculated as oven dry mass per unit area. Total N and C content of litter was determined using a LECO CHN-1000 analyzer.

Litter Decomposition

During September and October of 1994, before the establishment of the exclosures, we collected litter material throughout the study area to generate a standard litter that was used in the decomposition experiments. Willow leaf litter was obtained by locating greenhouse trays directly under willow canopies throughout the study area (dominated by *S. monticola*, *S. geyeriana*, and *S. planifolia*) and collecting the leaves periodically. C*arex* litter was collected by clipping and collecting standing dead biomass. We dried all litter in a 35°C forced air oven, and subsamples (2 g) from the 2 standard litter types (willow leaves and *Carex* tissue) were enclosed in 1 mm nylon mesh bags. These bags containing the standard litter were used in litter decomposition experiments to investigate the effects of herbivory, landscape position, and plant cover on the decomposition rates of willow and *Carex* litter during the growing seasons of 1995, 1996, and 1997. During the growing season of 1995, we investigated the effect of herbivory on litter decomposition by randomly placing 4 bags of each litter type (willow leaves and *Carex* tissue) in the ungrazed plots within the exclosures and in the grazed plots outside the exclosures (no bags were placed in the clipped plots) for all of the 12 sites. The results from the 4 bags of each litter type within each treatment replicate were combined to reduce microsite variability within each of the 12 treatment replicates. In 1996 and 1997, we investigated the effect of herbivory, landscape position, and plant cover on litter decomposition. For this, we selected, in each of the ungrazed and grazed plots within the 12 sites, 2 willow shrubs located at 2 different landscape positions: (1) lower landscape positions, next to a stream or a pond, and (2) upper landscape positions, at least 10 m away from a stream or a pond and 0.5 m higher in the landscape than lower landscape positions. Bags of both willow and *Carex* litter were placed under the canopies of the selected shrubs ('willow canopies') and in open grass areas ('*Carex* plots') located within 2 m of the shrubs. Two bags of each litter type were placed within each treatment replicate and their results pooled in order to reduce microsite variability.

In all experiments, the litterbags were placed on the soil surface and left in the field during the entire length of the growing season (from late May until mid-September). At the end of the season, they were collected, air-dried, weighed, ground to a fine powder to pass a 40 mesh sieve, and stored until analysis. Carbon and N in the decomposed litter were analyzed using a LECO CHN-1000 analyzer, and C and N losses were calculated in an ash-free dry weight basis by subtracting the amounts in the post-decomposition from the pre-decomposition litter.

Elk Dung Quantification

We estimated the amount of C and N returned to the soil in elk dung by counting the number of scat piles along 30 m transects within our experimental grazed plots, and measuring the concentrations of C and N in the dung. The survey was conducted after the elk herds left the winter range for the summer range during late spring 1997. We selected 8 grazed plots (4 in each park) and established 4 randomly placed transects per plot. In each transect, we measured the distance from the scat piles to the transect, and calculated the density of piles per area. Only scat piles that were visually identified as from the previous fall and winter were counted. To estimate dry matter and C and N content in each dung pile we obtained 51 samples (26 from Horseshoe Park and 25 from Moraine Park) by collecting all dung from fresh piles during late Fall of 1997. After collection, the samples were oven-dried at 50°C, weighed, ground to a fine powder, and sub-sampled for determination of moisture (oven-dried at 105°C) and ash content (500 °C). The concentrations of C and N in the dung were determined using a LECO CHN-1000 analyzer and expressed on an ash-free dry weight basis.

Soil Characteristics and N Availability

Soil samples (0–15 cm) were collected in July 1997 from the grazed, ungrazed, and clipped plots. Within each treatment replication, a total of 25 to 30 cores were randomly collected with a soil core sampler 2 cm in diameter and combined in a paper bag. After collection, the samples were taken to the laboratory, air-dried, and passed through a 2 mm sieve. Soil particle distribution was measured in each sample using the hydrometer method (Gee and Bauder 1986). Subsamples (10 g) of each sample were ground to a fine powder with a ball mill. The sand fraction (> 53 µm) of each sample was ground to a fine powder with a ball mill, for determination of particulate organic matter (POM) C and N (Cambardella and Elliott 1992). Total C and N in the total soil and sand fraction were determined with a LECO CHN-1000 analyzer.

In addition, during the summer of 1996 we collected soil samples (0 to 20 cm) under willow trees and in associated open grass areas next (within 2 m) to the trees. A total of 33 pairs of samples (shrub canopy plus open grass) were taken from the 12 ungrazed plots within the exclosures of Moraine Park and Horseshoe Park. The samples were air-dried and sieved through a 2 mm screen. Sub-samples (10 g) of each sample were ground to a fine powder with a ball mill, and total soil C and N were determined using a LECO CHN-1000 analyzer.

Soil moisture (0 to 14 cm) measurements were performed weekly in 8 sites in Moraine Park and Horseshoe Park (4 in each watershed) by Time Domain Reflectometry (TDR) (Ledieu et al. 1986) with a Trase System model 6050x1 during the growing season of 1997. The TDR rods were vertically placed in each measurement position and left there for the whole season. Within each site and grazing treatment, soil moisture was measured under willow canopies and in associated *Carex* plots next to the willow shrubs in both upper and lower landscape positions. Within 3 ungrazed plots in each park, soil temperature was measured using HOBO® temperature data loggers during the growing season of 1997. The loggers were wrapped with a thin plastic film to avoid damage by soil moisture, and were buried in a vertical position from 1 to 6 cm of depth. In each of the sites, we performed comparisons of soil temperature between (1) willow canopies and *Carex* plots and (2) streamside and upper landscape positions. The temperature measurements were performed every 15 minutes for periods of 7 to 14 days.

In 1995, 1996, and 1998 in situ soil N availability in the experimental plots was assessed using ion-exchange resin bags. Paired cation and anion resin bags made from nylon stockings and containing about 15 cm^3 of exchange resins were placed 5 cm beneath the soil surface (Binkley 1984). In 1995 and 1996, fifteen pairs of resin bags were placed in a regularly spaced grid (9.1 x 15.9 m) within each treatment (grazed, ungrazed, clipped) in the 12 sites. To analyze the temporal variability of N availability, 2 sets of bags were placed in each of the 3 treatments during each of the growing seasons of 1995 and 1996. The first set was left in place from mid-June to mid-July, and the second set from mid-July to mid-August. A different experimental procedure was utilized in 1998, in which 6 pairs of resin bags were randomly placed within each of the 12 ungrazed and grazed plots (no bags were placed in the clipped plots), and left in the field from May to October. For all 3 years, after removal of the bags, the N adsorbed in the resins was extracted with 50 ml of 2 M KCl, and the extracts were frozen until analysis for NO_3^--N and NH_4^+-N on an Alpkem automated spectrometer.

In 1997 and 1998, in situ measurements of net N mineralization were performed by conducting field soil incubations as described in Kolberg et al. (1997) using aluminum cores 15 cm long and 5 cm in diameter. During the 1997 growing season, cores were placed in upper and lower landscape positions within the 12 ungrazed and grazed plots of the 2 watersheds. Within each landscape position and grazing treatment, cores were placed under willow shrubs and in associated *Carex* patches within 2 m of the willow plants. Four cores were placed inside each treatment replicate to reduce micro-site variability. Cation and anion resin bags were placed in the bottom of each core to capture the inorganic N leached from the core. During the 1998 growing season, 6 open-top field soil incubation cores were placed within the ungrazed and grazed plots in 3 different 6-week incubation periods (June to July, July to August, and August to October). Net soil N mineralized during the incubation periods was calculated by subtracting the initial amount of inorganic N in the soil from the final amount of inorganic N after the incubations, and the results were expressed in g N m^{-2}.

Nitrogen Fertilization

In each ungrazed and grazed plot in the 12 sites, we placed 2 paired circular subplots (each with 2 m radius) around willow plants at the end of the growing season of 1998. Within each pair of circular subplots, we applied 2 fertilization treatments: (1) no fertilization, and (2) 10 g N m^{-2} as ammonium nitrate. During late July 1999, before the elk returned from the summer range at higher elevations, willow shoots (current year growth) were collected from the plants inside the subplots, dried at 60°C, weighed, and ground to a fine powder to pass a 40 mesh sieve. Concentrations of C and N in shoots were determined using a LECO CHN-1000 analyzer.

Table 1. Litterfall biomass in ungrazed, clipped, and grazed plots of Moraine Park and Horseshoe Park during 1995, 1996, and 1997. Values represent means (n = 12) with standard errors in parentheses. Means within the same group followed by different letters are significantly different at P < 0.05.

Treatment	Willow (*Salix* spp.) leaves	Other shrub leaves[1]	Herbs[2]	Wood	Unidentified material	All litter
			(g m^{-2})			
1995						
Ungrazed	32.9 (9.8) a	5.9 (2.7) ab	10.1 (2.4)	3.0 (1.0)	0.6 (0.2)	52.5 (10.2) a
Clipped	34.1 (8.5) a	13.2 (6.3) a	8.0 (1.0)	4.4 (1.4)	0.3 (0.1)	60.0 (8.9) a
Grazed	19.1 (7.1) b	1.7 (0.6) b	6.4 (0.9)	3.1 (1.4)	0.5 (0.2)	30.9 (8.5) b
1996						
Ungrazed	55.0 (13.6) a	9.1 (3.9) ab	3.1 (0.6)	3.1 (1.1)	1.4 (0.4)	71.6 (12.6) a
Clipped	47.1 (10.6) ab	18.3 (8.6) a	2.6 90.5)	1.6 (0.4)	0.8 (0.2)	70.2 (9.7) a
Grazed	26.6 (8.1) b	3.7 (0.8) b	3.4 (0.5)	5.1 (2.2)	0.7 (0.3)	39.4 (9.1) b
1997						
Ungrazed	45.3 (12.3) a	8.7 (4.0) ab	14.3 (3.3)	3.1 (1.0)	-	71.5 (11.1) a
Clipped	41.6 (10.4) a	15.5 (6.3) a	7.2 (0.7)	2.2 (0.7)	-	66.4 (10.1) a
Grazed	15.9 (6.0) b	3.0 (0.9) b	7.5 (1.0)	2.4 (1.1)	-	28.8 (7.1) b

[1] Mostly birch (*Betula* spp.) leaves.
[2] Litter material from forbs and *Carex* spp. combined.

Statistical Analyses

Statistical analyses were performed using the SAS Statistical Package (SAS, Version 6.12, SAS Institute Inc., Cary, N.C., 1995). The data on litterfall, litter nutrient content, litter decomposition, soil characteristics, N availability, and N fertilization were analyzed using a split-plot factorial design where watershed was considered a random effect. Watersheds and height of willow plants were not significantly different ($P < 0.05$) for any of the variables analyzed, therefore the data values from tall and short willow sites in both Moraine Park and Horseshoe Park were pooled (12 replications) in the analyses to determine the effect of browsing on litterfall and N availability, and the effects of browsing, proximity to surface water, and canopy position on litter decomposition. The data on soil nutrient content between willow canopies and open grass areas was analyzed using paired t-tests.

Results and Discussion

Litterfall

Litterfall biomass in the ungrazed and clipped plots was greater than in the grazed plots for the 3 growing seasons (Table 1). Across all growing seasons, litterfall biomass averaged 65.6 and 33.0 g m^{-2} inside and outside the exclosures, respectively. On average, willow leaves accounted for 58% of the litterfall biomass followed by herbs (20%), other shrub leaves (16%), wood (5%), and unidentified material (1%). However, the use of trays for collecting litterfall may underestimate the amount of grass litterfall, since a significant portion of the senescent tillers still remain attached to the plant and were not collected and counted as litter. Willow leaf litterfall in the ungrazed and clipped plots was greater than in the grazed plots during the 1995 and 1997 seasons, but in 1996 there were no significant differences between clipped and grazed plots (Table 1). Leaf litter from other shrubs, mostly birch (*Betula* spp.), was significantly lower in the grazed plots when compared to the clipping treatment inside the exclosures, but there were no differences between grazed and ungrazed plots. No treatment differences were observed for the amounts of herb or wood litter during the three growing seasons.

Inside the exclosures, even the removal of 75% of current annual growth in the clipped plots did not result in significant differences between the ungrazed and clipped plots during the growing seasons. We suggest this lack of difference between clipped and ungrazed plots occurred in part because the artificial clipping of willow did not satisfactorily simulate elk browsing. Other studies have demonstrated the limitations of clipping experiments to reflect accurately the natural patterns of herbivory (Paige 1999). Visual observations in our field plots suggested that clipped plants inside the exclosures were morphologically similar to the

Table 2. Nitrogen content and carbon to nitrogen ratio of different litter types in ungrazed, clipped, and grazed plots of Moraine Park and Horseshoe Park in 1997. Values represent means (n = 12) with standard errors in parentheses. Means within the same group followed by different letters are significantly different at P < 0.05.

Treatment	Willow (*Salix* spp.) leaves	Other shrub leaves[1]	Carex	Forbs
Nitrogen (%)				
Ungrazed	1.25 (0.10) b	1.23 (0.15)	1.40 (0.11)	1.79 (0.13)
Clipped	1.27 (0.09) b	1.11 (0.13)	1.22 (0.08)	1.71 (0.15)
Grazed	1.49 (0.08) a	1.09 (0.11)	1.23 (0.09)	1.82 (0.12)
Carbon to nitrogen ratio				
Ungrazed	45.8 (3.2) a	48.5 (12.0)	37.2 (2.9)	31.0 (3.0)
Clipped	43.0 (4.2) a	53.4 (11.6)	42.1 (2.8)	32.6 (2.9)
Grazed	37.7 (3.1) b	49.9 (14.3)	43.5 (3.1)	31.4 (2.6)

plants in the ungrazed treatment, regarding height and canopy structure, while the grazed plants were apparently more suppressed and shorter than the plants in the 2 treatments inside the exclosures. These patterns probably result from the additional damage to willow leaders caused by elk when striping off leaves from the plants, as compared to artificial clipping. On average, elk may browse on more than 70% of the leaders in each plant in our study sites, and may remove nearly 40% of the length of each leader (Singer et al. 1998b). Additional field observations from our experiments demonstrate that an average of 20% of the length of browsed willow leaders may die after elk browsing due to bark damage, while only 2% of the length of the leader may die in the case of artificially clipped plants (R. Peinetti, pers. comm., 1999). We suggest that the differences in litterfall observed between grazed and clipped treatments in our study may result from: (1) greater leader damage during elk browsing, in comparison to artificial clipping, and/or (2) greater increases in plant height in clipped plants, in comparison to grazed plants, due to differences in the patterns of tissue removal during elk browsing or artificial clipping, which may influence canopy architecture.

Willow leaf litter in the ungrazed and clipped plots had lower N content and higher C to N ratio than willow leaf litter in the grazed plots, but no significant treatment differences were found in litter from other shrubs, *Carex*, or forbs (Table 2). Similar to our findings, Alstad et al. (1999) reported that early season willow tissue N concentration in plants under elk herbivory in our sites was significantly higher than in plants protected from herbivory. Often, grazing leads to increases in plant tissue N (McNaughton 1985, Holland and Dettling 1990, Coughenour 1991, Hamilton et al. 1998) due to faster nutrient cycling and uptake by plants or a reduction in tissue biomass for allocation of N. Higher N concentration and lower C to N ratios in litter may lead to faster litter decomposition and greater nutrient availability (Ritchie et al. 1998, Irons et al. 1991). In our study site, the effects of elk herbivory on willow litter N concentration could lead to increases in the rate of litter decomposition and nutrient cycling, which could lead to changes in species composition and ecosystem functioning (Aber and Melillo 1991, Holland et al. 1992, Ritchie et al. 1998, Stohlgren et al. 1999).

Litter Decomposition

Losses of C and N from willow and *Carex* litter bags was not affected by grazing treatments in any of our experiments. However, in the 3 growing seasons, C losses from willow litter bags were higher than from *Carex* litter bags and, interestingly, N losses from willow litter were lower than from *Carex* litter (Table 3).

In 1996, C losses from litter bags were higher in streamside positions than in upper landscape positions, but no significant differences were observed for N losses during 1996 or C and N losses during 1997 (Table 4). Soil moisture is usually an important factor contributing to decomposition and, in general, litter decomposition increases with increasing soil moisture in semi-arid ecosystems (Schlesinger 1997). Higher C losses observed in streamside positions in our study are likely due to higher soil water availability (Fig. 1), suggesting that eventual reductions in surface water may lead to reductions in litter decomposition rates in our sites. However, no significant differences in willow or *Carex* litter decomposition were observed between streamside and upper landscape positions around the 2 beaver ponds in 1996. Average C and N losses from litter bags of the 2 litter types placed in streamside and upper landscape positions around the ponds were 36.4 and 2.9%, respectively.

Table 3. Carbon and nitrogen losses from willow (*Salix* spp.) and *Carex* leaf litter bags in Moraine Park and Horseshoe Park during the growing seasons of 1995, 1996, and 1997. Values represent means (n = 12) with standard errors in parentheses.

Litter type	C loss	N loss
	(%)	(%)
1995		
Willow	30.2 (2.7)	6.3 (2.0)
Carex	22.9 (2.6)	10.3 (2.1)
P-value	N.S. [1]	0.026
1996		
Willow	29.0 (1.9)	3.4 (5.1)
Carex	22.9 (2.4)	15.2 (4.7)
P-value	0.046	0.005
1997		
Willow	22.1 (1.4)	2.7 (2.4)
Carex	16.4 (1.8)	16.7 (4.3)
P-value	0.013	0.005

[1] Not significantly different at P < 0.05.

Table 4. Carbon and nitrogen losses from litter bags placed in upper and lower landscape positions of Moraine Park and Horseshoe Park during the growing seasons of 1996 and 1997. Values represent means (n = 12) with standard errors in parentheses.

Landscape position	C loss	N loss
	(%)	(%)
1996		
Streamside	31.7 (2.3)	5.7 (6.1)
Upper landscape	20.3 (1.9)	12.8 (6.0)
P-value	0.001	N.S.[1]
1997		
Streamside	18.1 (1.9)	6.5 (4.2)
Upper landscape	20.4 (1.3)	12.9 (2.7)
P-value	N.S	N.S.

[1] Not significantly different at P < 0.05.

Litter bags placed under willow canopies lost significantly more C and N than bags placed in *Carex* plots (Table 5), even though soil moisture levels were slightly lower under willow canopies, compared to *Carex* plots, especially in Horseshoe park (Fig. 1). Average maxi-

Table 5. Carbon and nitrogen losses from litter bags placed under willow (*Salix* spp.) canopies and in *Carex* spp. plots in Moraine Park and Horseshoe Park during the growing seasons of 1996 and 1997. Values represent means (n = 8) with standard errors in parentheses.

Position	C loss	N loss
	(%)	(%)
1996		
Willow canopies	35.7 (1.7)	24.2 (1.8)
Carex plots	7.7 (2.9)	-1.6 (2.4)
P-value	0.001	0.022
1997		
Willow canopies	23.1 (1.5)	15.5 (1.7)
Carex plots	16.0 (3.5)	3.4 (3.5)
P-value	0.001	0.012

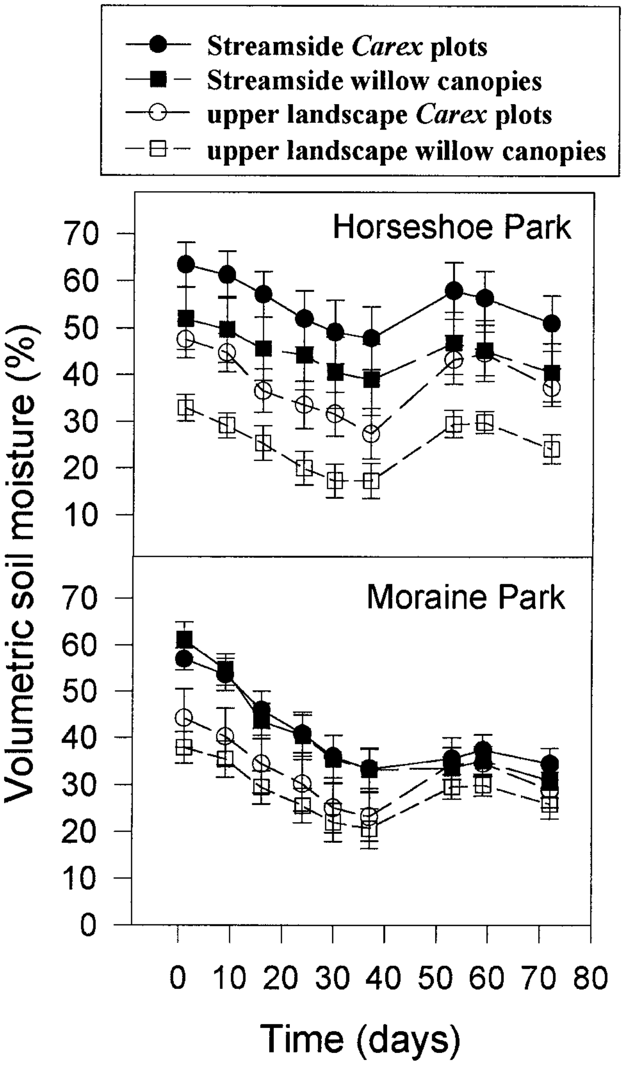

Fig. 1. Soil moisture (0 to 14 cm) under willow canopies and in *Carex* plots in upper and lower landscape positions of Horseshoe Park and Moraine Park from early June to late August of 1997. Error bars represent standard errors of the means (n = 8).

mum soil temperatures from 1 to 6 cm in depth during the 1997 growing season were significantly lower under willow canopies than in *Carex* plots in both Moraine and Horseshoe parks (Fig. 2). These results indicate that the presence of willow shrubs has a significant influence on microclimatic conditions in our sites, contributing to reductions in soil temperature and soil moisture. We suggest that the rate of nutrient loss from litter bags was higher under willow canopies because: (1) shading by willow canopies may decrease soil temperature and help preserve moisture at the top few centimeters of the litter layer and soil, and this may enhance litter decomposition and/or (2) *Carex* plants may have held litter bags off the soil, which may have let them dry out more and decompose less than bags placed under willow canopies.

Return of N to the Soil

Based on the biomass and N content of aboveground litter in our sites (Tables 2 and 3), we calculated that the N return to the soil in aboveground litter during the 1997 growing season was greater in the ungrazed and clipped plots (0.83 and 0.82 g N m^{-2}, respectively) than in the grazed plots (0.42 g N m^{-2}), excluding the contribution of N in wood litter in all treatments. Litter from willow, other shrubs, and herbs contributed to 62, 17, and 21% of the N returned to the soil in litter inside the exclosures, and 51, 16, and 33 % of the N returned to the soil in litter within the grazed plots, respectively. Elk dung biomass deposited on the soil during the 1997-98 season averaged 42.2 ± 6.2 g m^{-2} across all sites. This value is similar to those reported by Frank and McNaughton (1992), who found that average herbivore dung deposition during the 5 month season in the winter range of Yellowstone National Park was 76.9 ± 30.1 g m^{-2}. In our sites, average elk dung N concentration in the samples collected in late fall of 1997 was 2.0 %. Based on our results, we estimated that approximately 0.87 ± 0.12 g N m^{-2} returned to the soil in elk dung during the 1997–98 winter season in our study site. Therefore, the amount of N returned to the soil as elk dung plus aboveground plant litter averaged 1.3 g m^{-2} in the grazed plots. The estimated amount of N returned to the soil in elk urine in our sites, based on the diet and specific characteristics of the herd, could be approximately 98% of the N returned to the soil in dung (K. Schoenecker, pers. comm., 1999). Based on these estimates, after including the potential N inputs from urine, the total amount of N returned to the soil in the grazed plots could be as high as 2.2 g N m^{-2}, which corresponds to 265%

Table 6. Soil characteristics (0–15 cm) of ungrazed, clipped, and grazed plots of Moraine Park and Horseshoe Park in July 1997. Values represent means (n = 12) with standard errors within parentheses.

Treatment	Total C	Total N	POM[1] C	POM N	Sand	Silt	Clay	pH[2]
	(g kg $soil^{-1}$)							
Ungrazed	50.3 (9.0)	3.38 (0.63)	15.9 (3.5)	0.81 (0.19)	523 (59)	209 (40)	152 (19)	4.64 (0.10)
Clipped	47.7 (7.1)	3.27 (0.54)	13.3 (2.0)	0.63 (0.09)	494 (55)	235 (47)	161 (25)	4.67 (0.12)
Grazed	42.7 (6.2)	2.82 (0.44)	11.3 (2.0)	0.53 (0.12)	549 (37)	234 (29)	118 (19)	4.60 (0.11)

[1] Particulate Organic Matter
[2] Measured in water (2:1, water:soil)

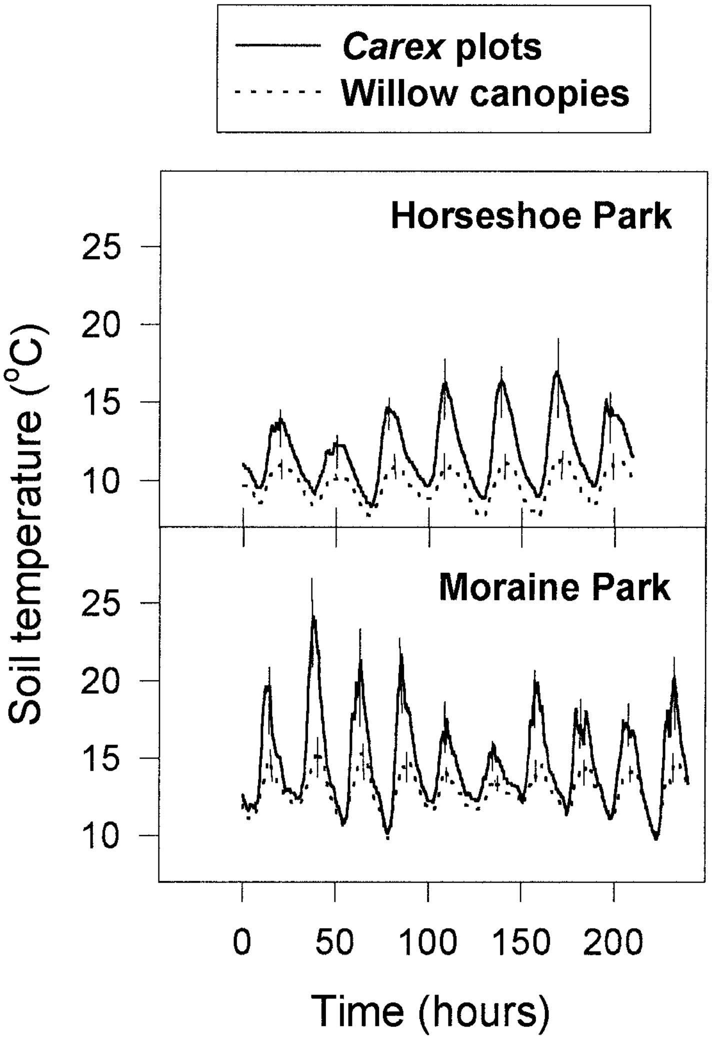

Fig. 2. Soil temperature (1 to 6 cm) under willow canopies and in Carex plots in Horseshoe Park and Moraine Park during July 1997. Vertical lines represent the range of the 95% confidence interval for the means of maximum temperatures (n = 3).

of the N returned as aboveground litter in the exclosed plots. Our results are consistent with the findings of Frank and McNaughton (1992), who found that elk and bison populations in Yellowstone National Park excreted 0.81 to 4.60 g N m^{-2} year^{-1}, an amount that corresponded to roughly 4 times the amount of N returned in litterfall in their study site.

Soil Characteristics and N Availability

There were no significant differences in total soil C and N, POM C and N, soil texture, and soil pH between grazing treatments in our sites 4 years after the establishment of the exclosures (Table 6). Similar to our findings, Frank and Groffman (1998) found no differences in in soil total C and N between grazed plots and exclosed plots that had been protected from herbivory for 33 to 37 years in Yellowstone National Park. In addition, we found no differences in total soil C and N (0 to 30 cm) between soil samples taken in *Carex* plots or under willow canopies. Total soil C and N averaged 62 and 4.4 g kg^{-1} in *Carex* plots and 58 and 4.0 g kg^{-1} under willow canopies, respectively.

In all experiments with both ion-exchange resin bags and field soil core incubations, there were no significant differences in soil N availability between grazing treatments during the years of the study. Several studies have reported increases in the rates of soil N mineralization with herbivory (McNaughton et al. 1988, Holland and Detling 1990, Frank and Evans 1997). Frank and Groffman (1998), reported that N availability in plots grazed by elk was 100% higher than exclosed plots. It is possible that the short time (4 years) since the establishment of the exclosures in our study did not allow for the development of detectable differences in soil N mineralization and availability between grazing treatments. Alternatively, since the explanations for the influences of herbivores on N availability are not quite well understood, other mechanisms may have contributed to the lack of differences in N availability between grazing treatments.

The assessment of N availability with ion-exchange resin bags during 1995 and 1996 indicated that, in general, both NH_4^+-N and NO_3^--N availability were higher during early to mid-season and declined afterwards (Table 7). In 1998, there was only 1 resin bag incubation period, and the total amount of N adsorbed to the bags was slightly higher than the sum of both periods of either 1995 or 1996, probably because the incubation period in 1998 was a few weeks longer. On average, the amount of NH_4^+-N adsorbed to the resin bags was 137 to 412% higher than NO_3^--N during the 3 growing seasons.

Table 7. Inorganic nitrogen adsorbed to ion exchange resin bags during different incubation periods during 1995 and 1996, and from 1 incubation period during 1998. Values represent means (n = 12) with standard errors within parentheses.

Incubation period	NO_3^--N	NH_4^+-N	NO_3^--N + NH_4^+-N
	----------	(mg bag^{-1})	----------
1995			
June to July	1.08 (0.23)	4.45 (0.63)	5.53 (1.45)
July to August	0.64 (0.32)	2.12 (0.44)	2.78 (1.29)
P-value	0.0151	0.001	0.001
1996			
June to July	0.95 (0.52)	3.39 (0.81)	4.34 (1.14)
July to August	1.05 (0.55)	1.44 (0.53)	2.49 (0.87)
P-value	N.S.2	0.001	0.001
1998			
July to October	3.01 (0.55)		
	7.29 (1.98)	10.30 (2.43)	

[1] P-value of comparisons between means of incubation periods.
[2] Not significantly different at P < 0.05.

Table 8. Inorganic nitrogen mineralized during field soil incubations (0 to 15 cm) using aluminum cores during 1997 and 1998. Values represent means for all treatments (n = 12) with standard errors within parentheses.

Incubation period[1]	NO_3^--N	NH_4^+-N	NO_3^--N + NH_4^+-N
	- - - - - - - - - - - - - - - - - - - -	($g\ N\ m^{-2}$)	- - - - - - - - - - - - - - - - - -
1997			
June to July	0.11 (0.04)	0.55 (0.15)	0.66 (0.16)
1998			
June to July	0.71 (0.44)	0.81 (0.80)	1.51 (0.77)
July to August	1.13 (0.38)	1.33 (0.95)	2.46 (1.17)
August to October	0.51 (0.23)	0.34 (0.52)	0.85 (0.59)

[1] Length of incubation period: 1997 = 4 weeks; 1998 = 6 weeks each period.

Table 9. Inorganic nitrogen adsorbed to ion exchange resin bags under willow (*Salix* spp.) canopies and in *Carex* spp. plots during different incubation periods of the 1995 and 1996 growing seasons. Values represent means (n = 12) with standard errors within parentheses.

Position	June to July	July to August
1995	- - - - - - ($g\ N\ m^{-2}$)	- - - - - -
Willow canopies	5.69 (2.13)	2.87 (1.20)
Carex plots	5.80 (1.92)	2.87 (1.11)
P-value	N.S.[1]	N.S.
1996		
Willow canopies	4.98 (0.77)	3.07 (0.55)
Carex plots	4.01 (0.68)	2.42 (0.37)
P-value	0.018	N.S.

[1] Not significantly different at P < 0.05.

The higher proportions of soil NH_4^+-N could benefit plant productivity in our sites, since plants with an evolutionary history of grazing show elevated growth responses to ammonium relative to other inorganic forms of N, particularly when subject to defoliation (Ruess 1984, Ruess and McNaughton 1987, Hobbs 1996). Similarly to the results from the experiments with ion-exchange resin bags, the amounts of net NH_4^+-N mineralized in the soil cores were usually higher than NO_3^--N (Table 8). In addition, total inorganic N in the soil was higher during early to mid-season during the 1998 growing season (Table 8). If plant uptake is higher during early to mid-season when plant growth and nutrient requirements are probably greater, the higher availability of nutrients during that period may contribute to the synchronization of nutrient supply and demand and enhance primary production and nutrient retention within the system (Myers et al. 1994).

Interestingly, the presence of willow had a significant effect on N availability in our experiments with ion-exchange resin bags. During both incubation periods of 1996, the amounts of inorganic N adsorbed to resin bags located under willow canopies was higher ($P < 0.05$) than in bags placed in *Carex* plots (Table 9), but no significant differences were observed during 1995. The higher N availability may be a consequence of higher amounts of litter N inputs and higher rates of N loss from litter under willow canopies, as indicated by our findings in 1996.

The data from the N fertilization experiment demonstrated that willow growth in the winter ranges for elk is limited by N availability, independently of grazing treatment. Both inside and outside the exclosures, N fertilizer additions increased willow shoot length, shoot biomass, and the amount of N in the shoots (Table 10).

Based on our findings, we conclude that proximity to surface water had little effect on the dynamics of C and N in the winter ranges for elk during the period of our studies. In addition, we suggest that elk herbivory could lead to long-term increases in N availability in our sites, because of induced increases in both litter quality and return of N to the soil. Stohlgren et al. (1999) reported that exotic species were more likely to invade landscape patches higher soil N and moisture, which could lead to a decline in native plant species and ecosystem diversity (Billings 1990, D'Antonio and Vitousek 1992). Therefore, eventual increases in N availability in our sites due to elk herbivory could lead to changes in plant species composition and alter ecosystem functioning, because of shifts in the competitive interactions between plant species (Tilman 1982, 1988, Holland et al. 1992, Sterner 1994, Ritchie et al. 1998).

Table 10. Effects of nitrogen fertilization on willow (*Salix* spp.) growth and N assimilation during the growing season of 1999. Values represent means (n = 12) followed by standard errors between parentheses.

Treatment	Shoot length	Shoot biomass	Shoot concentration	Amount of N per shoot
	(cm)	(g)	(%)	(g)
N fertilizer (10 $g\ N\ m^{-2}$)	28.6 (1.4) a[1]	27.3 (2.5) a	2.25 (0.05)	0.62 (0.06) a
No fertilization	22.5 (1.1) b	20.2 (2.4) b	2.14 (0.06)	0.43 (0.05) b

[1] Means followed by different letters are significantly different at P < 0.05.

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Anti-quality components in forage: Overview, significance, and economic impact[1]

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Abstract

Although recognized in importance from the dawn of history, forages have too often been underestimated and undervalued perhaps in part because animal performance has frequently failed to reflect apparent forage quality. Anti-quality components, diverse impediments to quality, have evolved as structural components and as secondary metabolites. They include mineral imbalances or can be related to the presence of insects and diseases. Animal behavior and adaptation are increasingly recognized as important aspects of anti-quality factors. An anti-quality component may reduce dry matter intake, dry matter digestibility, or result in nutritional imbalances in animals. They can act as a direct poison compromising vital systems, result in abnormal reproduction, endocrine function, and genetic aberrations, trigger undesirable behavior responses, or suppress immune function leading to increased morbidity and mortality. The economic impact of anti-quality factors on individual herds can be devastating but definable. Broadscale economic impacts of anti-quality factors are far more difficult to estimate. A loss of 0.22 kg/day in potential gain of stocker cattle due to antiquality factors during a 166-day grazing season translates into a loss of about $55/steer at $1.45/kg or over $2 billion annually when applied to the U.S stocker cattle. Economic losses to tall fescue (*Festuca arundinacea* Schreb.) toxicosis in the U.S. beef industry are probably underestimated at $600 million annually. Reproductive and death losses of livestock due to poisonous plants have been estimated at $340 million in the 17 western states alone. These examples of economic losses due to anti-quality factors may be upper bounds of actual losses but even if a small proportion of the expected losses were eliminated through research, the potential payoff would be extremely high.

Key Words: nutrition, animal health, performance, forage quality, toxins

Resumen

Aunque su importancia se reconoce desde las épocas tempranas de la historia, los forrajes también frecuentemente han sido subestimados y subvaluados, en parte porque a menudo el comportamiento productivo del animal ha fallado en reflejar la calidad aparente del forraje. Los compuestos anti-calidad, obstáculos variados de la calidad, han evolucionado como componentes estructurales y metabolitos secundarios. Ellos incluyen desbalances minerales o pueden ser relacionados a la presencia de insectos o enfermedades. El comportamiento animal y la adaptación se reconocen mas y mas como aspectos importantes de los factores anti-calidad. Un componentes anti-calidad puede reducir el consumo de materia seca, la digestibilidad de la materia seca o producir en los animales desbalances nutricionales. Ellos pueden actuar directamente como veneno dañando sistemas vitales, producir una reproducción anormal, problemas endocrinológicos, aberraciones genéticas desencadenar respuestas de comportamiento indeseable o suprimir la función inmune incrementando la morbilidad y mortalidad. El impacto económico de los factores anti-calidad en los hatos individuales puede ser devastador pero definible. Los impactos a amplia escala de los factores anti-calidad son mas difíciles de estimar. Una perdida de 0.22 kg/día de la ganancia potencial del ganadero debido a factores anti-calidad durante una época de apacentamiento de 166 días se traduce en una perdida de aproximadamente $55 dolares/novillo, a un precio de $ 1.45/kg, o de mas de 2 billones anuales si se aplica al total de la ganadería de E.U.A. Las perdidas económicas de la industria del ganado de carne de los E.U.A. por la toxicosis del Alta fescue (*Festuca arundinacea* Schreb.) son probablemente subestimadas en $600 millones anuales. Solo en los 17 estados del oeste, las perdidas por muerte y reproducción del ganado debido a plantas tóxicas han sido estimadas en $ 340 millones. Estos ejemplos de perdidas económicas debido a los factores anti-calidad pueden ser los limites superiores de las perdidas actuales, pero aun si una pequeña proporción de las perdidas esperadas fuera eliminada a través de investigación, el pago por estas perdidas sería extremadamente alto.

Overview and Significance

The importance of forages has echoed through the ages. The value of forages was recognized from the early dawn of history as animals became domesticated and were moved from place to place in search of forage (Combs 1936). Alfalfa is thought to have been cultivated before the development of the written lan-

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guage (Bolton et al. 1972). During the settlement years in the U.S., the value of forages went largely unrecognized with forages frequently relegated to lands of marginal arable value (Edwards 1948). Often, there was little recognition of differences in value among forage species. This sentiment began to change as P. V. Cardon stated in the 1948 Yearbook of Agriculture, "..., in the wake of war and in the glow of our unprecedented production, this country looks to the future and considers again the land and its management - this time, as never before, in terms of grass." (Cardon 1948). In his preface to Forages: Resouces for the Future, Burton (1986) states "Forages, particularly the grasses, are the most important plants on the face of the earth". Occupying more than half the land area in the U.S. and world wide, forages provide about three fourths of the energy and more than half of the protein in human diets (Burton 1986). Because ruminants and equine obtain 60 to 100% of their feed nutrients from forages and because of the economic importance of forage consuming livestock and wildlife, the value of forage rivals that of the most important field crops. For too long the nutritional and economic value of forages has been underestimated and under-recognized.

As the human population increases, land areas suitable for intensive crop production decrease, and issues of renewable resource conservation become more compelling. As Cardon (1948) stated over a half century ago, "... around grass, farmers can organize general crop production so as to promote efficient practices that lead to permanency in agriculture."

Quality of forage is paramount in obtaining optimum animal performance. Any factor or 'anti-quality component' that prevents forage from contributing its nutritional potential takes on added importance with increased recognition of forage as a feed resource. During recent years, much progress has been made in several areas perhaps most dramatically in elucidating the etiology of tall fescue (*Festuca arundinacea* Schreb.) toxicosis and its relationship to the endophyte fungus *Neotyphodium coenphialum* [(Morgan-Jones and Gams) Glenn, Bacon, and Hanlin; Glenn et al. 1996]. Advances have also been made in identifying specific toxins, and physical and chemical factors that affect intake and digestibility. The role of animal behavior in avoidance of anti-quality factors has great potential and is the subject of a paper presented in this symposium.

There has always been concern that anti-quality components in forages have the potential to compromise food safety and human health. Ergotism in humans consuming wheat (*Triticum aestivum* L.), rye (*Secale cereale* L.), pearlmillet *[Pennisetum americanum* (L.) Leeke], and other small grains contaminated with *Claviceps* species has been documented both historically and during modern times (Krishnamachari and Bhat 1976, Lewis 1977) Humans can potentially be exposed to several mycotoxins by direct consumption of grains contaminated with products of fungal growth although strict control of food quality on the U.S. market makes this unlikely to occur (CAST 1989, Wood 1992). However, possible long-term exposure to low levels of mycotoxins in the food supply is of potential concern. Human consumption of animal products affected by anti-quality factors is also of concern. Ammoniation of hay has been related to hyperexcitability in cattle (i.e. Crazy Cow Syndrome) and high death losses of calves either at birth or within a few days of birth (Essig et al. 1986). A case study in Mississippi suggested that milk from a cow fed ammoniated hay could produce symptoms of hyperexcitability in a non-related calf fed the milk (Essig et al. 1986) raising concerns about milk safety for humans. In the U.S., it is unlikely that lactating dairy cows would be fed ammoniated hay but this could occur in other parts of the world.

The subject of anti-quality factors is far reaching and includes pastures and harvested forages as well as rangelands and grazeable forestlands. The following papers in this volume were part of a symposium held in 1999 on 'Anti-quality Components in Forages' at the joint meeting of the Society for Range Management and the American Forage and Grassland Council. It is hoped that this symposium helped to synthesize the current state of knowledge and to present the information in written format that will serve as a reference for the industry. The subject of anti-quality factors will continue to evolve as new information is generated and this is indeed a topic that will need to be revisited in the future.

What is Forage Quality and Anti-quality ?

It is necessary to clearly understand what forage quality is before we can begin to address its' antithesis, antiquality. In his review of 'Milestones in Forage Research,' Reid (1994) concluded that forage quality was definable as "some product of digestibility and intake of the diet." Mott and Moore (1969) described forage quality as composed of both 'forage nutritive value' (chemical composition, digestibility, and nature of digested products) and 'forage consumed' (acceptability, rate of passage, and availability). Raymond (1968) suggested that quality is defined by the equation 'Nutrient intake = intake of feed dry matter x digestibility of feed dry matter x efficiency of utilization of digested nutrients'. More general definitions of forage quality include "Characteristics that make forage valuable to animals as a source of nutrients; the combination of chemical and biocharacteristics of forage that determines its potential to produce meat, milk, wool, or work" (Barnes and Beard 1992, Barnes et al. 1995). Ball et al. (1991) suggest that forage quality is best defined in terms of animal performance and that it is ultimately the animal rather than the human that determines forage quality.

Although each of these definitions provides useful mathematical and philosophical concepts regarding forage quality, each one appears to fall short of a succinct definition. Dictionary definitions of 'quality' generally refer to the 'degree of excellence'. Thus, we propose that forage quality is best described as *the degree to which a forage meets the nutritional requirements of a specific kind and class of animal*. An 'anti-quality component' would, therefore, be defined as *any factor that diminishes the degree to which a forage meets the nutritional requirements of a specific kind and class of animal*. The word 'animal' is necessary in these definitions to include both 'livestock' and 'wildlife'. Furthermore, it is necessary to specify the kind and class of animal because animal nutritional needs and detoxification abilities vary. A forage that meets the nutritional needs for dry cows would, thus, be a high quality dry cow feed, but may not meet the requirements for finishing steers and would, therefore, be a low quality finishing diet. Likewise, a chemical toxin or a physical inhibitor to intake for 1 species or class of animal may not affect another species or class of animal in a similar manner. Animal behavior and adaptation are increasingly being recognized as important aspects of anti-quality factors. For example, ability of the pregastric fermentor to detoxify many of the potentially harmful plant metabolites has long been recognized. Palatability, rate of passage, digestibility, nutrient density and balance, and intake are all factors determining the degree to which the forage is able to meet the nutritional demands of the animal. Therefore, as suggested by Mott and Moore (1969), quality of the forage is going to be driven by the combination of chemical and physical characteristics that determine 'forage nutritive value' and 'intake' and these are terms that should be defined as a subset under the definition of forage quality.

Classes and Kinds of Anti-quality Components

Anti-quality components encompass a diverse array of unrelated causative agents. These may have evolved as structural components of the plant or as secondary metabolites resulting in plant defense mechanisms. Anti-quality components can be revealed as mineral deficiencies, toxicities, and nutritional imbalances. The origin of anti-quality attributes can be phytochemicals in plant tissues or structural inhibitors in leaf and stem arrangement. Specific chemical inhibitors of quality can result from plant metabolism or from microbial origin. Anti-quality factors in forages can furthermore be related to the presence of insects and diseases.

An anti-quality component may simply act as a reducer of dry matter intake (DMI), may reduce dry matter digestibility, or result in nutritional imbalances. The anti-quality factor may act as a direct toxin that shuts down vital systems in animals, it may result in abnormal reproduction, disturb endocrine or neurological function, cause genetic aberrations, or may suppress immune function leading to increased morbidity and mortality. Because of the many and disrelated syndromes and yet the potential for many interactions and subtle interrelationships, the field of anti-quality factors is both complex and compelling.

Economic Impact of Anti-quality Components

The economic impact of anti-quality factors on individual flocks and herds can be devastating when the result is a large loss in production, reproduction, morbidity, or mortality. Economic consequences can also be severe if the loss is but a single animal with high economic value. The economic effect is much less obvious when the result is a subtle decrease in potential performance. The economic impact of anti-quality components on animal health and production are often difficult to estimate. Nevertheless, broadscale estimates are needed to provide perspective and to help focus research efforts into areas of high potential economic improvement. Estimates of the impact of diminished forage quality with lowered potential for gain highlight the magnitude of economic impact. An example of this can be derived from calculations using the current beef cattle herd in the U.S. and estimates of expected daily gains based on National Research Council data (NRC 1984).

As of 29 January 1999, there were 16.8 million steers and 19.6 million heifers weighing 227 kg or more in the U.S. (Agricultural Statistics 1999). The stocker phase of cattle production into which these cattle could be placed, can make efficient use of forage for economical gains. Ball et al. (1991) summerized beef steer performance on 15 forage systems or specific forages in the Southern U.S. and found that daily gains ranged from 0.43 to 1.08 kg/day during an average 146-day grazing season. Stocker systems in Virginia demonstrated that steers gained 0.90 kg/day during a 166-day grazing season from April to October in an all forage system (Allen et al. 1994). Estimates based on NRC (1984) requirements for a 227 kg steer fed to gain 0.90 kg/day indicate that a dry matter intake (DMI) of 6.26 kg/day at a given nutritive value is required. If nutritive value is diminished and related DMI declines to 6.08 kg/day, a decline in intake of 0.18 kg/day, daily gains would be expected to drop to 0.68 kg/day. This translates into over 8 million kg/day loss of potential gain. If a value of $1.54/kg is assumed, this results in an approximate cost of $12.33 million per day for all stocker cattle in the U.S. or $0.34/stocker per day. This level of loss of potential gain, represents a total economic loss for the 166-day period of over $2 billion. Calculated another way, and again using the Virginia example for steer performance, over the 166-day grazing period, steers gained 151 kg vs 113 kg that were gained under the lower quality diet. The 38 kg difference would be worth about $55/steer at $1.45/kg. These levels of economic losses due to the degradation of forage quality could be considered to be an upper bound of the actual level of loss. That is, it would be expected that if stocker producers were to be aware of the potential weight gain losses due to the lower quality of the diet, they might internalize this into their operations to minimize potential losses. However, this strategy would result into higher associated cost of production. If the impediments to quality or anti-quality factors were identified and eliminated, it might be more cost effective.

The economic impact of mineral imbalances in forages is often poorly understood. However, hypomagnesic grass tetany has been widely researched. This metabolic deficiency of Mg has been estimated to result in the loss of 1 to 3% of the beef cows in the U.S. annually. If the loss is 1% of the 42.6 million cows and heifers that had calved by 1 January 1999 (Agricultural Statistics 1999), the estimated financial loss to producers would be about $150 million assuming a 500 kg cow worth about $0.77/kg. Fortunately, Mg supplementation strategies are available that can largely prevent grass tetany but represent an increase in the cost of production both in terms of added inputs and labor requirements.

Tall fescue (*Festuca arundinacea* Schreb.) is one of the most important cool-season grasses grown in the U.S. occupying over 14 million ha (Sleper and Buckner 1995). Widely adapted, this long-lived perennial forms the basis of many forage-livestock systems. However, much of this fescue is infected with the endophyte-fungus *Neotyphodium coenophialum* (Shelby and Dalrymple 1987). Presence of the fungus confers stress tolerance to the plant (see review by Latch 1997) but production of alkaloids by both the plant and the fungus result in a myrid of animal disorders (Steudemann and Hoveland 1988). It has been estimated that the endophyte in tall fescue results in loss of over $600 million annually to the beef cattle industry alone (Fribourg et al. 1991). Recent evidence suggests that this may be an underestimate. It has been widely accepted that removal of livestock from infected tall fescue pastures resulted in a fairly rapid dissipation of symptoms of tall fescue toxicosis but this now appears not to be the case. Research has shown that one effect of the toxicity is a decline in specific immune function (Saker et al. 1998) during the grazing period. It has now been demonstrated that this loss in immune function is long-lasting, and was measurable throughout the stress of cross country transportation and a following 150-day feedlot finishing period (Saker et al. 2001; Allen et al. 2001). The lowered immunity is likely to contribute to added costs of medications and labor in treating animals that are less-tolerant to stress and disease (Purdy et al. 1989).

Poisonous plants occur in all types of grazing lands including both range and intensively managed pastureland and are one of the most important economic impediments to profitable livestock production (James et al. 1992). Based on an estimated 1% death loss in cattle, a 3.5% death loss in sheep, and a 1% decrease in calf and lamb crops due to poisonous plants, the economic impact within the 17 western states was estimated at $340 million annually (Nielsen and James 1991, James et al. 1992). In their review of the impact of poisonous plants on the livestock industry, James et al. (1992) divide economic losses into direct and indirect losses. Direct losses were described to include death, emaciation, slow growth, decreased reproductive efficiency, abortion, and birth defects. Indirect losses included costs incurred to prevent losses or poisoning, medical costs incident to poisoning, losses of forage quality due to need to alter harvesting schedules, stress effects on management, risk, and effects on land values and grazing permits. In addition to their application to poisonous plants, these types of losses should be accounted for in accessing economic consequences of many types of anti-quality factors.

The potential economic losses discussed above, represent only a few of the areas/issues on which anti-quality components have an impact. Even if these areas were to be the only ones affected by anti-quality components in forage, the potential associated total economic damage would be over $3 billion. At the same time, however, this level of damage provides an estimate of the potential payoff of research addressing the anti-quality components in forage issue. Even if a very small proportion of the expected losses were to be eliminated through research dedicated to minimize the negative impacts of anti-quality components in forage, a relatively large research program could be afforded. That is, the potential payoff, i.e. benefit-cost ratio, of such a research program would be extremely high. It is hoped that the information presented in this symposium will highlight the need and provide the impetus for further research and the dedication of funding sources to support this research for forages are the key to economical production of ruminants and equine and are central to the protection of our natural resources. Forages ARE the most important plants on earth and impediments to their potential as a feed source take on parallel importance.

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Structural anti-quality characteristics of range and pasture plants

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Abstract

Structural anti-quality characteristics are physical plant traits that reduce the performance and productivity of herbivores and quality of their agricultural products. Most structural anti-quality characteristics of plants affect the rate at which herbivores gather and ingest forages, reducing the total amount of food obtained or increasing the time necessary to obtain food. Structural anti-quality can substantially influence searching time (e.g., plant crypticity, distribution), cropping time (e.g., plant fibrousness, tensile and shear strength), and bite size (e.g., plant canopy structure, spinescence). Plant structural characteristics can also reduce digestion (e.g., silica), cause injury (e.g., spines, awns, burrs, calluses), or reduce the quality of animal products, such as wool (e.g., propagules). The effects of structural anti-quality characteristics depend on the morphology of the herbivore, especially its size, the morphology of the focal plant, and their context within the habitat. Integrated grazing management plans should consider options to reduce the negative effects of structural anti-quality. Carefully selecting appropriate livestock species with previous experience, and the appropriate season of grazing can minimize anti-quality on rangelands. Because structural anti-quality may actually promote sustainability of grazing systems by preventing severe defoliation, or by providing refuges for highly desirable forages, it may not be desirable to completely counteract their effects.

Key Words: bite size, chewing, canopy structure, intake rate, physical plant defenses, spines

Resumen

Las características estructurales anti-calidad son características físicas que reducen el comportamiento productivo de los herbívoros y la calidad de sus productos agropecuarios. La mayoría de las características estructurales anti-calidad afectan la tasa a la cual los herbívoros recolectan e ingieren el forraje, reduciendo la cantidad de alimento obtenido o incrementando el tiempo necesario para obtener el alimento. Las características estructurales anti-calidad pueden influir substancialmente el tiempo de búsqueda (por ejemplo, plantas encriptadas y su distribución), tiempo de cosecha (por ejemplo, la fibrocidad de la planta, y la resistencia tensil y de corte) y el tamaño de la mordida (por ejemplo, estructura de la copa de la planta, cantidad de espinas). Las características estructurales de la planta también pueden reducir la digestión (por ejemplo, sílice), causar daño (por ejemplo, espinas, aristas, callos, pelos) o reducir la calidad de los productos animal, tales como la lana (por ejemplo propágulos). Los efectos de las características estructurales anti-calidad dependen de la morfología del herbívoro, especialmente su tamaño, la morfología de la planta focal y su contexto dentro del hábitat. Los planes de manejo integral del apacentamiento deben considerar opciones para reducir los efectos negativos de las características estructurales anti-calidad. Seleccionando cuidadosamente la especie animal apropiada, basados en experiencias previas, y la estación de apacentamiento apropiada se puede minimizar la anti-calidad en los pastizales. Debido a que las características estructurales anti-calidad puede promover la sustentabilidad de los sistemas de apacentamiento al evitar la defoliación severa o preveer refugios para las plantas forrajeras altamente deseables, puede ser no del todo deseable contraatacar sus efectos

The performance and production of wild and domestic herbivores depends on receiving adequate quality and quantity of forage over many time scales. Biochemical and physical characteristics of plants that reduce the performance of herbivores feeding on them compared to a similar plant without the trait are defined as ‘anti-quality’. Structural anti-quality characteristics include all physical plant traits that cause grazing avoidance that do not directly depend on the chemical composition of plant tissues (Briske 1996). Plants may have individual structural anti-quality traits such as canopy architecture, growth form, and mechanical deterrents to grazing, as well as spatial and temporal characteristics of groups of plants that potentially reduce the value of a plant as food. Here we review the modes of action and effects on herbivores of different structural anti-quality characteristics of plants, including crypticity and spatial distribution, canopy structure, plant fibrousness and resistance to chewing, tensile and shearing strength, stems and pseudostems, spinescence, awns, burrs, and calluses, and silica. In addition, we offer suggestions for management techniques that will reduce the negative affects of structural characteristics in herbaceous and woody range and pasture plants that will yield improved animal productivity and wool or hide quality.

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Modes of Action and Effects of Structural Anti-quality Characteristics of Plants

Overview

Structural anti-quality traits of both herbaceous and woody range plants primarily serve to reduce the rate at which herbivores can gather and ingest (harvest) forages (Fig. 1). Herbivores invest up to half of their day harvesting food (Bunnell and Gillingham 1985, Belovsky and Slade 1986, Owen-Smith 1988). Therefore, structural characteristics of plants that increase the time needed to find, crop, and/or chew food of sufficient quality and quantity reduce the time available for other life requisites (e.g., parental care, thermoregulation, rumination, and rest) and thus reduce production and survival. Therefore, forage intake has the potential to limit herbivore production in most rangeland and pasture ecosystems. In fact, the effects of structural anti-quality may exceed that of the more well-known biochemical anti-quality characteristics of plants (Shipley et al. 1999, Van der wal et al. 2000). Structural plant characteristics such as spines, burrs, calluses, and awns can also injure animals, affecting their survival (Cooper and Owen-Smith 1986, Crampton 1974), reduce the quality of products such as hides and wool (Stubbendieck et al. 1992), or reduce digestibility of forage (e.g., silica, Van Soest 1982, Fig. 1). Many aspects of plant structure have multiple negative effects on the ingestion-digestion process and animal performance. Therefore, for each structural plant characteristic, it is important to understand its main mode of action, level of experimental support for its anti-quality properties, field context in which the trait is most detrimental to animals, body size of most susceptible herbivores, and characteristics of the target plant (Table 1). For example, short plants are more detrimental to large animals when forage availability is low and grazing time is limited (Table 1). Short plants may be used more efficiently by small ruminants with low requirements than by larger animals (females vs. males, sheep vs. cattle, Illius and Gordon 1987, 1991). This knowledge can be used by scientists and managers to foresee and reduce the negative effects of each of the following plant anti-quality characteristics.

Crypticity and spatial distribution

Cryptic plants are difficult to find and thus reduce foraging efficiency of herbivores (Feeny 1976). Apparent plants allow animals to walk directly from one preferred plant to the next, whereas a cryptic plant requires that foragers search blindly until plants are randomly encountered. Foraging efficiency and intake rate are affected by the time it takes herbivores to find desirable forages. In any given rangeland, intake rate declines and energy expenditure for locomotion increases as animals become more selective in their food choices (Murray 1991, Laca and Demment 1996). These effects are more pronounced when desirable plants are cryptic.

Quantitative experimental information about the effects of crypticity and spatial distribution of forages on herbivore nutrition is scarce. Models and experiments in controlled conditions clearly indicate that intake rate increases when desirable forages are easy to detect and encounter. Animals learn to associate forages with visual cues forage more efficiently than without cues (Bazely and Ensor 1989, Edwards et al. 1997, Howery et al. 1999a,1999b, Kidunda and Rittenhouse 1992, Ortega and Laca 1997, Renken et al. 1998). A simple model of grazing behavior showed that when herbivores can detect desirable plants or patches from a distance, harvesting is greater than when plants are cryptic (Demment and Laca 1993). Crypticity reduces an animal's harvesting rate the most when bites are small and little forage is available. Model predictions were qualitatively corroborated in experiments with cattle in artificial foraging arenas where food patches were marked using flags or other visual cues (Laca and Ortega 1996). Cattle exhibited greater foraging efficiency (intake/distance walked) when feed pellets were marked with flags, a visual cue immediately recognized by cattle. Likewise, Howery et al. (1999a) found that steers searching for fixed or variable forage locations in a 0.64 ha arena with artificial visual cues spent more time feeding and less time in non-foraging activities than without cues. Animals exposed to fixed and variable forage arrangements with cues also located feed more efficiently and had higher intakes than without cues.

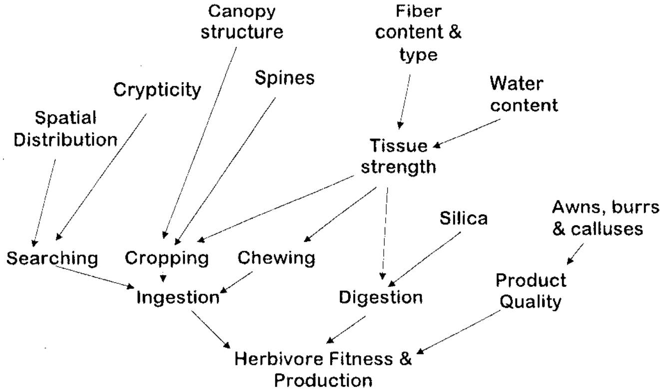

Fig. 1. The modes of action by which structural antiquality characteristics of plants influence animal fitness and production.

Like crypticity, certain spatial distributions of forage plants may serve as an anti-quality trait by affecting herbivore preference and efficiency (Vivås and Sæther 1987, Danell et al. 1991). When a preferred food is distributed randomly or uniformly, herbivores have lower intake rates than when distributions are patchy (Laca and Ortega 1996). Cattle had a higher intake rate on feed pellets with flags than those without flags only when spatial distribution was uniform or random, but not when feed was patchy (Laca and Ortega 1996). The fact that intake rate in patchy distributions is less affected by crypticity indicates that cattle use mechanisms other than visual cues to detect patches of desirable forage. Cattle and sheep can overcome the effects of crypticity when food locations are predictable based on spatial memory (Edwards et al. 1997, Laca 1998). However, spatial memory is expected to be effective only in selecting feeding sites or larger areas (Bailey et al. 1996).

Whether plant dispersion and patchiness serves an anti-quality function depends on the spatial scale considered. Foraging intensity per shrub, tree, small patch, or feeding station increases with decreasing patch density (Vivås and Sæther 1987, Danell et al. 1991, Shipley and Spalinger 1995). More specifically, herbivores take larger bites and more bites per stem in

Table 1. Structural antiquality characteristics of plants, including their effects on animal performance, the level of experimental proof

Anti–quality trait	Effects	Proof	Context	Animal	Plant
Crypticity	Lower bite and intake rate	Limited	Low herbage mass	Large	Rare
Random distribution	Lower bite and intake rate	Limited	Low herbage mass	Large	Low density
Short stature	Reduced bite mass and intake	Plenty	Low herbage mass	Large	Low bulk density
Low bulk density	Reduced bite mass and intake rate	Some	Low herbage mass	Large	Short
Pseudostems	Reduced bite mass and intake rate	Some	Low herbage mass	Large and small	Short
Stems, (hedging, wolf plant)	Reduced bite mass, bite rate and intake rate; barrier; injury	Good	Early stages of bunchgrass	Medium	Bunchgrass, Shrub
Tensile and shearing strength	Reduced bite area, bite mass and bite rate, fatigue	Limited	Late phenological stages; tropical grasses	Small	Grass
Fibrousness, resistance to chewing	Reduced bite and intake rate; lower passage rate	Plenty	High herbage mass; tropical pastures	All	C4, mature or dormant plants
Twig thickness	Restricted relation between bite mass and quality; reduced bite rate	Good		Small, Medium	Dormant shrubs
Spinescence	Reduced bite mass and rate; injury; disease;	Plenty	Low primary productivity	Medium	Woody plants
Awns, calluses, burs	Reduce bite and intake rate injury; disease; damage product	Good		All, particularly sheep, goats	Mature; *Stipa, Bromus, Hordeum*
Silica	Injury; promotes tooth wear; urinary calculi	Good	High primary productivity	Grazers	Grass

patches that contain fewer stems and are scattered further apart, presumably to maximize intake rate at the expense of forage quality. The proportion of a small patch (i.e., feeding station) removed by a herbivore increases with decreasing density. Therefore animals may have a higher harvesting rate at the patch when patches are further apart. However, this trend is reversed at the scale of a large patch or habitat (i.e., large groups of shrubs/trees). More animals spend more time in habitats that provide more food, and thus relatively more biomass is removed and daily intake is increased in more productive habitat patches (Vivås and Sæther 1987, Danell et al. 1991, Edenius 1991).

Canopy structure

Canopy structure determines the size and arrangement of bites of vegetation in space. Bite mass is one of the main determinants of short-term intake rate by herbivores (Black and Kenney 1984, Spalinger and Hobbs 1992, Gross et al. 1993). The mechanisms of cropping (i.e., severing or prehending a bite) and chewing are such that, for a wide range of bite mass, intake rate increases up to 10 fold with increasing bite mass (Gross et al. 1993, Shipley et al. 1994). This range certainly brackets bite mass values that normally can be obtained by livestock and wildlife in rangelands and most pastures. Thus, under most rangeland conditions, herbivores are at least partially limited by bite mass they can obtain.

In grasslands, bite mass is often constrained by the structure, especially height and bulk density, of the canopy of grasses and forbs (Black and Kenney 1984). In an experiment using controlled canopy structures, bite mass of cattle was 0.26 g in 8-cm tall swards, but only 0.12 g in 4-cm swards, despite a constant forage mass kept at 500 kg/ha by varying bulk density (Ungar et al. 1991). Moreover, livestock seem to select patches that yield greater intake rate (Arnold 1987, Laca et al. 1993). Thus, sward structure has a pronounced effect on selective defoliation patterns of vegetation. Herbaceous plants that yield small bites tend to be avoided, and plants that offer large bites of good quality forage tend to be preferred. Depending on the relative and absolute abundance of tall and short plants in the grassland, short plants may become unprofitable to the herbivore (Laca et al. 1994a).

Similarly, browsing herbivores tend to prefer woody plant species and portions of plants that provide larger leaves and thicker and longer annual growth twigs (Danell et al. 1994, Shipley et al. 1998). The arrangement of leaves and stems on some plants, such as willow (*Salix spp*.), allow herbivores to strip many leaves in 1 bite, which substantially increases intake (Stapley 1998). Larger herbivores can obtain a larger bite when branching architecture allows them to take multiple stems in one bite (Vivås et al. 1991). However, small, thin stems branching at wide angles may serve to deter herbivory by separating bites (Myers and Bazely 1991, Vivås et al. 1991). In some plant species, herbivory increases branching and produces a hedge effect that reduces bite size and accessibility. However, in other plant species such as birch (*Betula spp*), moose browsing increased length, diameter and leaf size of re-grown stems, which were in turn used more heavily than unbrowsed trees (Danell et al. 1985).

Canopy structure and its effect on intake rate changes with plant phenology and plant fibrousness. Because nutritional quality is often inversely related to bite mass, bite mass is a trade-off between harvesting rate and nutritional quality (Shipley et al. 1999, Vivås et al. 1991). For example, as grasses mature from vegetative to reproductive stages, overall nutritional value declines (Van Soest 1982, Nelson and Moser 1994**)**. During the vegetative stage of grass phenology, the nutritional quality differs little among plant parts. As grasses mature, the proportion of more fibrous stems and older leaves increases, resulting in large variation in nutritional quality within a plant or sward (Hacker and Minson 1981). To compensate for the decline in quality as grasses mature, herbivores select higher quality parts. However, increased selectivity reduces harvesting rates by slowing cropping rate and reducing bite size to the point that adjacent plants that allow higher intake become preferred. How well herbivores can compensate for changes in nutritional quality depends upon the animal's size and mouth morphology. Because of large mouth parts, larger herbivores are generally less able to select small, more nutritious parts of plants than smaller herbivores. Likewise in woody range plants, the amount of lignin and cell wall generally increases with twig diameter (Vivås and Sæther 1987), but intake rate also increases. Because large herbivores require a greater intake rate than do smaller herbivores to meet their nutritional requirements, plants with smaller leaves and twigs are less profitable and provide a greater defense against large herbivores (Spalinger and Hobbs 1992).

Plant fibrousness and resistance to chewing

Resistance to ingestive chewing, measured as the number of chews per unit mass of particles comminuted to pass a 1.18 mm sieve, is positively related to fiber content (McLeod et al. 1990, Balch 1971). Therefore, intake rate can decline with increasing fiber content in forages because of the associated increase in chewing time necessary to adequately process the forage. In herbaceous plants, resistance to ingestive chewing can be considerably greater for stems than for leaves (McLeod et al. 1990). Stems also are more resistant than leaves to chewing during rumination. Chewing during ingestion accounts for much of the variation in intake rate within feeding stations, and thus fibrousness directly reduces intake rate (Laca et al. 1994b). For example, short-term intake rate of moose (*Alces alces*), deer (*Odocoileus virginianus*), and snowshoe hares (*Lepus americanus*) was lower on red maple stems (*Acer rubrum*, 64% neutral detergent fiber, NDF) than on red maple leaves (32% NDF) for a wide range of bite sizes (Shipley and Spalinger 1992). Likewise, intake rate of cattle was greater for the less fibrous legume-leaf fractions than for grass leaf and stem fractions (McLeod and Smith 1989). Sheep eating perennial ryegrass (*Lolium perenne* L.) with high shear strength had a significantly lower intake rate (6.5 g/min) than did those eating ryegrass with low leaf shear strength (7.6 g/min; MacKinnon et al. 1988). Although ryegrass progenies that differed in shearing strength by 50% differed in harvesting rate, there was no discernible difference in their digestion rate or potential degradability. Thus, effects of fibrousness on eating rate are beyond the effects of fiber on forage digestibility and retention time.

Tensile and shearing strength

Increasing tensile strength of foliage tends to reduce bite size by reducing the bite area that may be cropped (Demment et al. 1992). Bite area declined more steeply with increasing bulk density in dallisgrass (*Paspalum dilatatum* Poir.) than in wild oats (*Avena fatua* L.). This difference was attributed to the greater tensile strength of dallisgrass, with leaf blades 14% lighter (4.3 vs. 4.9 mg) and 89% stronger (11.5 vs. 6.1 Newtons/blade) than wild oats (Demment et al. 1992). At equal bulk density, dallisgrass foliage was expected to be 2.2 times stronger than oat foliage. Although tensile strength is not an absolute limitation to biting (Hughes et al. 1991), it may reduce intake rate by imposing a cost in terms of effort, energy, and time. When grazing swards of high tensile strength, steers sometimes failed to sever the bites of grass apprehended, and had to release some of the forage before being able to complete the biting motion (E. A. Laca, University of California, Davis, personal observation).

Bite mass on woody plants is also controlled by the force required to sever forage. Obtaining a larger bite usually requires that the animal "prune" a thicker twig or multiple twigs (Vivås et al. 1991). Because the force required to crop a twig increases curvilinearly with twig diameter (Shipley et al. 1999), thick or multiple twigs may restrict bite mass or at least slow cropping rate, particularly for small browsing herbivores. As twig diameter increases, herbivores must switch from using incisors to molars to crop bites, which slows intake (Cooper and Owen-Smith 1986).

Stems and pseudostems

Cured reproductive stems can effectively deter grazing by cattle, particularly when plants are in an early phenological stage (Ganskopp 1993, Ganskopp et al. 1992). Plants with stems were less likely to be grazed and severely defoliated than those without stems. In experiments with hand-constructed swards, Flores et al., (1993) found that a bottom layer of dallisgrass stems acted as a barrier to grazing, but pseudostems had no detrimental effect. The effects of the layer of stems were evident only if the stems were higher than the biting depth animals would select in a similar sward made only of leaf laminae.

Spinescence

Herbivores generally have lower intake rates on plants with spines, thorns, prickles, and hairs than the same plants with these structures removed (Cooper and Owen-Smith 1986, Dunham 1980, Gowda 1996). When intake rate is reduced, herbivores spend more time foraging, but often not enough to compensate completely (Cooper and Owen-Smith 1986). Spines influence harvesting rate by reducing bite mass and/or decreasing cropping rate (Belovsky et al. 1991).

Spines reduce bite mass by impeding stripping motions and separating leaves, which forces animals to crop leaves individually (Milewski et al. 1991, Pellew 1984, Stapley 1998). Large herbivores that require large bites, such as kudus (*Tragelaphus strepsiceros*)and giraffes (*Giraffa camelopardalis*), may be particularly affected by spinescence. Thorns and spines also reduce the fraction of a twig that may be pruned and the diameter at which the twig is clipped (Cooper and Owen-Smith 1986). Therefore, small leaves combined with thorns have the greatest anti-quality effects on medium to large herbivores (Belovsky et al. 1991, Gowda 1996, Milewski et al. 1991) because their bite size is more severely restricted.

Spines also slow cropping rate by requiring herbivores to carefully manipulate plants in their mouths to avoid pain and injury (Belovsky et al. 1991, Cooper and Owen-Smith 1986, Dunham 1980). Hooked thorns especially catch on lips, tongues, and ears (Cooper and Owen-Smith 1986). The influence of thorns on ingestion depends on the size of the foraging animal. Smaller animals can maneuver mouthparts more easily among thorns to pluck small leaves, and therefore, thorns may be less effective in reducing cropping rates. Pointed muzzles and mobile lips on larger animals may be adaptations for feeding on thorny vegetation (Myers and Bazely 1991). However, large animals with larger mouths, like giraffes and rhinos (*Diceros bicornis*), often can bite off and chew thorns that impede smaller animals (Owen-Smith 1988, Pellew 1984). In fact, spines may also reduce harvesting rates of very small herbivores, such as plains woodrats (*Neotoma micropus*), by physically impeding or injuring them as they climb up to harvest berries, seeds, and foliage (Cooper and Ginnett 1998).

Spinescence also can injure and physically block animals from feeding on the plant or cause so much pain that the animal refuses to feed on it. For example, prickles on species such as blackberry (*Rubus idaeus*) can interlock, holding stems together and making the patch difficult or impossible to penetrate (Myers and Bazely 1991). Some injuries from spines cause chronic, rather than immediate pain and injury. Scratches and scar tissue can be found in the digestive tract of kudus and domestic goats inhabiting *Acacia* spp. woodlands, suggesting that thorns may injure and scar buccal or esophageal mucosa, and may make these animals more susceptible to disease (Cooper and Owen-Smith 1986).

Because spinescence slows harvesting rate of herbivores, the anti-quality effects of spines varies with habitat productivity, accessibility, proportion of the landscape covered, nutrient concentration and seasonal dynamics in relation to its neighbors (Grubb 1992). The consequences of reduced intake rate to a herbivore are more pronounced where intake rate is more limiting, such as in arid environments that have a low primary productivity, where, not surprisingly, spines are more common (Belovsky and Schmitz 1991).

Awns, burrs and calluses

Many plant species have evolved mechanisms of propagule dispersal that are detrimental to herbivores. Awns, calluses and spikelets such as in *Avena*, *Stipa*, *Bromus*, *Sitanion* and *Hordeum spp.*, are noxious to livestock because they are bristly or scabrous, bearing stiff hairs arranged like harpoons, or sharp calluses. These structures can bury into soft tissues (eyes, mouth, nostrils, and ears), causing distress and infections (Crampton 1974). Sheep and other fiber-producing livestock are also susceptible to injury in any area of the skin, because their hide is more delicate than that of bovines (American Sheep Industry Association 1996). Such lesions cause distress, reduce productivity, contaminate the carcass, and reduce the quality of the hides. Fruiting structures with thorns and hooks, such as those produced by burr clover (*Medicago polymorpha* L.), as well as propagules from several grasses, contaminate and reduce the value of the fleece (American Sheep Industry Association 1996, Stubbendieck et al. 1992).

Silica

Several studies have examined how silica affects herbivores, most notably its effect on digestion (Van Soest 1982), tooth wear (Riet-Correa et al. 1986), and as a cause of urinary calculi (Emerick 1987, 1988). Silica is an indigestible structural component of most grasses (Van Soest and Jones 1968). Silica in grasses reduced in vitro digestibility 3 units per unit of silica (Van Soest and Jones 1968). Furthermore, silica may affect intake rates in a similar fashion as other structural compounds. Grasses with higher silica generally have more rigid and sharper edges that can affect harvesting rates by reducing relative bite mass (Reid 2000). For example, sheep presented with similar sized plants of indiangrass (*Sorghastrum nutans* (L.) Nash) and big bluestem (*Andropogon gerardii* Vitman) strongly prefer big bluestem despite no noticeable differences in nutritional quality between the grasses. Indiangrass, which has higher silica content than big bluestem, has stiffer and sharper-edged blades, which limited bite mass (Reid 2000). Small herbivores, such as voles (*Microtus ochrogaster*), also prefer grasses with lower silica content (Gali-Muhtasib et al. 1992). However, the effects of silica on preference do not seem to be universal. Shewmaker et al. (1989) found no relationship between silicon content and forage preference in sheep.

High silica content of plant tissues can also be detrimental to herbivores by promoting rapid tooth wear (Baker et al. 1959, Riet-Correa et al. 1986). The productive life span of cattle, particularly reproductive beef and dairy cows, can extend beyond 7-8 years. Yet, where forages have high silica content, and when animals are chronically forced to graze close to the soil in excessively short swards, tooth wear may cause culling of otherwise productive animals because they cannot bite and chew enough forage to realize their production potential. Silicon content in forages may further reduce animal health by causing urolithiasis (Baker et al. 1961a,1961b, Bailey 1976).

Conclusions and Management Implications

Any plant trait that affects herbivore diet choice serves an anti-quality function (Belovsky and Schmitz 1991). Therefore, the efficacy of any structural anti-quality characteristic of plants depends on the characteristics of other plants in the environment, the nutritional status of the herbivore, and herbivore species. Because of the relationship between body size and a variety of morphological and physiological characteristics of ruminants (Demment and Van Soest 1985, Illius and Gordon 1987, Shipley et al. 1994), body size has an overriding influence on the effects of any particular anti-quality trait (Table 1).

A number of anti-quality traits affect herbivores by making it hard for them to bite, handle, and chew forages. However, the ability of herbivores to deal with different canopy structures, stems, and spines improves with experience and learning (Flores et al. 1989a, 1989b, Ortega-Reyes and Provenza 1993a, 1993b). Therefore, grazing experience can be used by managers to reduce the effects of structural anti-quality of plants on herbivores.

This review of structural anti-quality factors leads to the following conclusions:

1. Structural anti-quality can have multiple modes of action, from reducing short-term intake rate by increasing search and locomotion costs, to lowering passage rate by increasing resistance to chewing, to directly injuring herbivores.
2. Reduction of intake rate by limitation of bite mass and bite rate is widespread. These limitations are more severe for large herbivores with high physiological demand in environments with low primary productivity.
3. Effects of anti-quality factors depend on herbivore characteristics, notably body size, characteristics of the focal plant, and its context within the habitat. The influence of a given anti-quality trait depends on the characteristics of other plants available to the herbivore. Thus, because quality, diversity and quantity of potential forages vary with season and successional stage, so does the effects of a particular anti-quality factor.
4. Structural and chemical anti-quality factors are interdependent. Forage fibrousness, spines, and stems are structural barriers based on lignin and cellulose, which are quantitative chemical defenses.

As a direct consequence of the fact that structural anti-quality factors tend to limit forage intake over the long term by constraining ingestion constraints, management recommendations follow general grazing management guidelines to ensure that herbivores achieve sufficient quality and quantity of intake. The following management recommendations should be considered in the context of a general grazing management plan developed for the enterprise as a whole.

1. Carefully select livestock species and type to match the forage characteristics of specific zones and paddocks.
2. Ensure pastures have forage that optimizes grazing efficiency for specific herbivores. For example, small ruminants are better suited for grasses with shorter swards.
3. Periodically "clean" grasslands to remove old stems and standing dead forage by grazing with very high animal densities for short times or by mowing. When using animals as the cleaning tool, use animals with low physiological demands and good teeth, like horses, wethers and mature dry cows.

4. Determine the abundance of plants with high silica in different paddocks and assess their impact on tooth wear. Those paddocks should be used by livestock with good teeth whose longevity in the herd is not an issue.
5. Determine which paddocks and seasons have an abundance of plants with awns, calluses, burs and other structures that cause injuries and reduce the quality of fiber, hides, and carcasses. Plan grazing management such that susceptible livestock are not in these paddocks when noxious plant structures are abundant.
6. In areas with challenging forage structure, use animals that have experience with the forages, or gradually introduce livestock to the new forages. This is best accomplished by placing naïve animals with experienced ones at times when their productivity and survival does not depend on structurally defended forages.

These management guidelines are proposed to prepare herbivores for the structural challenges presented by forage plants. It is, however, important to acknowledge positive aspects of anti-quality factors on grazed ecosystems. By preventing complete defoliation, or by providing refuges for highly desirable forages, structural anti-quality traits may promote the sustainability of the system. Thus, these management guidelines must be considered as potential components of integrated grazing management plans that incorporate effects on animal productivity and plant communities.

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Lignin and fiber digestion

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Abstract

Lignin is a polymer formed from monolignols derived from the phenylpropanoid pathway in vascular plants. It is deposited in the cell walls of plants as part of the process of cell maturation. Lignin is considered an anti-quality component in forages because of its negative impact on the nutritional availability of plant fiber. Lignin interferes with the digestion of cell-wall polysaccharides by acting as a physical barrier to microbial enzymes. Lignification therefore has a direct and often important impact on the digestible energy (DE) value of the forage. There are a number of plant-related factors that affect lignification in individual plants and plant communities. Lignification is under genetic control and there are considerable differences in lignin concentration and composition among species and even genotypes within species. Genetic differences in lignification are first expressed at the cellular level and are affected by biochemical and physiological activities of the cell. As cells differentiate, differences in lignification occur depending on the tissues and organs being developed. Lignification tends to be most intense in structural tissues such as xylem and sclerenchyma. Plant organs containing high concentrations of these tissues, such as stems, are less digestible than those containing lower concentrations. The relative proportion of lignified tissues and organs typically increases as plants mature so there is often a negative relationship between digestibility and maturity. All of these plant processes respond to environmental factors that can affect the extent and impact of lignification. Temperature, soil moisture, light, and soil fertility can have either direct or indirect effects on lignification. The most useful management practices for minimizing the negative effects of lignification are manipulation of the plant community such that it contains more desirable species and harvest management to maintain plants in a vegetative stage of development.

Key Words: Anti-quality, digestibility, forage quality, forage utilization

Resumen

La lignina es un polímero formado de monolignoles derivados de la vía fenilpropanoide de las plantas vasculares. Se deposita en las paredes celulares de las plantas como parte del proceso de maduración de la célula. En los forrajes, la lignina se considera como un componente anti-calidad por su impacto negativo en la disponibilidad nutricional de la fibra de la planta. La lignina interfiere con la digestión de los polisacáridos de la pared celular al actuar como barrera física para las enzimas microbianas. Por lo tanto, la lignificación tiene un impacto directo, y a menudo importante, en el valor de la energía digestible (ED) del forraje. Hay un número de factores relacionados con la planta que afectan la lignificación de las plantas individuales y de las comunidades vegetales. La lignificación esta bajo control genético y hay considerables diferencias entre especies, y aun entre genotipos de la misma especie, respecto a la concentración y composición de la lignina. Las diferencias genéticas de lignificación se expresan primeramente a nivel celular y son afectadas por las actividades bioquímicas y fisiológicas de la célula. Conforme la célula se diferencia ocurren diferencias en la lignificación, dependiendo de los tejidos y orgános que se estén desarrollando. La lignificación tiende a ser mas intensa en tejidos estructurales como el xilema y esclerénquima. Los órganos de la planta que contienen altas proporciones de estos tejidos, tales como los tallos, son menos digestibles que aquellos que contienen bajas concentraciones. La proporción de tejidos y órganos lignificados típicamente aumenta conforme la planta madura, por lo que a menudo hay una relación negativa entre la digestibilidad y madurez. Todos estos procesos de la planta responden a factores ambientales que pueden afectar la cantidad e impacto de la lignificación. La temperatura, humedad del suelo, luz y fertilidad del suelo pueden tener también efectos directos o indirectos en la lignificación. Las practicas de manejo mas útiles para minimizar los efectos negativos de la lignificación son la manipulación de las comunidades vegetales para que contengan mas especies deseables y el manejo de la cosecha para mantener las plantas en estado vegetativo.

Lignin is considered an anti-quality component in forages because of its negative impact on the nutritional availability of plant fiber. It differs from most other classes of antiquality components in forages in that it is a structural compound rather than a secondary metabolite. Its evolution in plants is primarily related to plant structure and function and not as a defense mechanism against other organisms. As a component of the cell wall, lignin plays an important role in morphogenesis. Cell walls form the structural framework of the plant architecture that provides mechanical support for plant organs (Varner and Lin 1989). Cell walls also are involved in water balance, ion exchange, cell

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recognition, and protection from biotic stresses (Boudet 1998, Varner and Lin 1989, Vian 1982).

Lignin is an integral component of plant cell walls. It is the last major biopolymer to have evolved within the plant kingdom and is generally regarded as the second most abundant compound, after cellulose, in the biosphere (Boudet 1998, Monties 1991). The most important function of lignin in plants is as a structural component to lend strength and rigidity to the cell wall. It is also important in limiting water loss by reducing permeability of the cell wall, and in impeding disease organisms (Dean and Eriksson 1992, Zeikus 1980). All of these attributes are desirable from the perspective of plant function and survival, but limit the nutritional value of the plant for herbivores.

Fiber is a nutritional entity which is defined as much by its biological properties as its chemical composition (Van Soest et al. 1991). With regard to forages, it has been traditionally defined as the complex of dietary nutrients that are relatively resistant to digestion and are slowly and only partially degraded by herbivores (Chesson and Forsberg 1988, Van Soest 1982). By this definition, fiber is composed of structural polysaccharides, wall proteins, and lignin. The main antiquality role of lignin in forages is in limiting digestion of the structural polysaccharides cellulose and hemicellulose (Hatfield et al. 1999, Moore and Hatfield 1994). Lignification controls the amount of fiber that can be digested and, therefore, has a direct and often important impact on the digestible energy (DE) value of the forage (Jung and Allen 1995). Lignification also influences the amount of dry matter that can be consumed by an animal (Mertens 1994). The undigested portion of the forage passes slowly through the digestive system and contributes to the fill effect of the diet. The greater the concentration of undegradable fiber in the diet the less dry matter an animal can consume. Therefore, lignification impacts forage nutritive value by both decreasing DE concentration and limiting dry matter intake (Moore et al. 1993).

In this paper we discuss the biochemistry of lignin and how it affects the digestibility of forage fiber. We also consider factors that affect lignification and therefore the quality of forages. Finally, we discuss management implications of lignin and suggest strategies for improving forage quality.

Lignin Biochemistry

While lignin has been recognized as a distinct chemical entity of plant cell walls for over 100 years (Sjostrom 1981), there is still considerable scientific argument concerning its structure, biosynthesis, and measurement. These uncertainties arise from the complexity of lignin synthesis and the resultant complexity of lignin molecules. While generalized structures for lignin have been drawn, it is not yet possible to definitely determine the complete structure of any isolated lignin molecule, let alone the structure of lignin in the plant cell wall. Because there is no standard lignin structure for reference, measurement of lignin concentration is empirical and very dependent on methodology. All of these ambiguities have made it very difficult to clarify the roles of lignin in plant growth and development, and the mechanism by which lignin limits cell wall digestibility.

Lignin can be characterized as a polymer formed from monolignols derived from the phenylpropanoid pathway in vascular plants. Recent reviews provide excellent coverage of the process and biochemistry of lignification (Baucher et al. 1998, Boudet 1998). Lignin is deposited in the cell walls of plants as part of the process of cell maturation after cell elongation has ceased. Based on difficulty of lignin extraction from the cell wall, it has been concluded that lignin is chemically linked to carbohydrates and possibly proteins in the cell wall to form large macromolecules. The only cross-linking structure of lignin to other cell-wall components that has been definitively characterized is the linkage of lignin to arabinoxylans in grasses via ferulic acid molecules (Ralph et al. 1995), although chemical extraction data does point toward ∝-ether linkages of lignin directly to polysaccharides (Watanabe 1989). Undoubtedly there are other lignin cross-linking structures involving both polysaccharides and proteins.

The basic pathway of lignin biosynthesis in plants is illustrated in Fig. 1. Guaiacyl-type lignin typically comprises 95+% of the lignin found in gymnosperms, whereas angiosperms generally deposit significant amounts of both guaiacyl- and syringyl-type lignins. Small amounts of *p*-hydroxyphenol lignin are present in most plants. The 5-hydroxyguaiacyl-type lignin is only known to accumulate in the *bm*$_3$ (brown midrib) mutant of corn (*Zea mays* L.) (Lapierre et al. 1988). This particular lignin product accumulates in *bm*$_3$ corn because the gene that converts 5-hydroxyferulic acid to sinapic acid is reduced in activity. As more lignin mutants and transgenic plants involving the lignin pathway have been characterized, it has become apparent that this pathway is actually more of a web than linear (Sewalt et al. 1997b). Because of this web structure and the ability of plants to incorporate non-typical phenylpropanoid precursor molecules, the results of biotechnological manipulation of the pathway have yielded unexpected results and unique lignin structures (Boudet 1998, Ralph et al. 1998). Apparently lignin plays such an important role in plant development that alternative routes and precursors can be used to provide the amount of lignin necessary for normal development. When lignin concentration has been significantly reduced through biotechnology, nonviable plants result (Jung and Ni 1998).

Deposition of lignin in the cell wall of grasses appears to involve ferulate esters of arabinoxylans as nucleation sites. In annual ryegrass (*Lolium multiflorum* Lam.), lignin cross-links to ferulates consisted only of structures that would form if monolignols reacted with the ferulates directly rather than polymeric lignin reacting with ferulate esters (Ralph et al. 1995). This ferulate mediated cross-linking structure is illustrated in Fig. 2. Unlike ferulic acid, *p*-coumarate (the other major cell-wall hydroxycinnamic acid) in grasses does not have a lignin/polysaccharide cross-linking function and most *p*-coumarate is esterified to lignin rather than polysaccharide (Ralph et al. 1994).

Because of complex lignin structure and linkage to other cell-wall polymers, analysis of lignin concentration in forages is difficult. The standard method used in animal and agronomic sciences is the acid detergent lignin (ADL) method, of which there are sulfuric acid hydrolysis and permanganate oxidation versions of the method (Van Soest 1967, Goering and Van Soest 1970). The traditional lignin method used in wood chemistry, Klason lignin, was long believed to give inaccurate results with forages because of perceived contamination (Van Soest 1967, Lai and Sarkanen 1971). It has now been shown that the Klason lignin method does not suffer from contamination when applied to forages and that the ADL method under-estimates lignin concentration (Kondo et al. 1987, Hatfield et al. 1994, Lowry et al. 1994). This under-estimation is especially severe for grasses. The problem with the ADL method appears to be solubilization of lignin at the acid detergent fiber step of the procedure

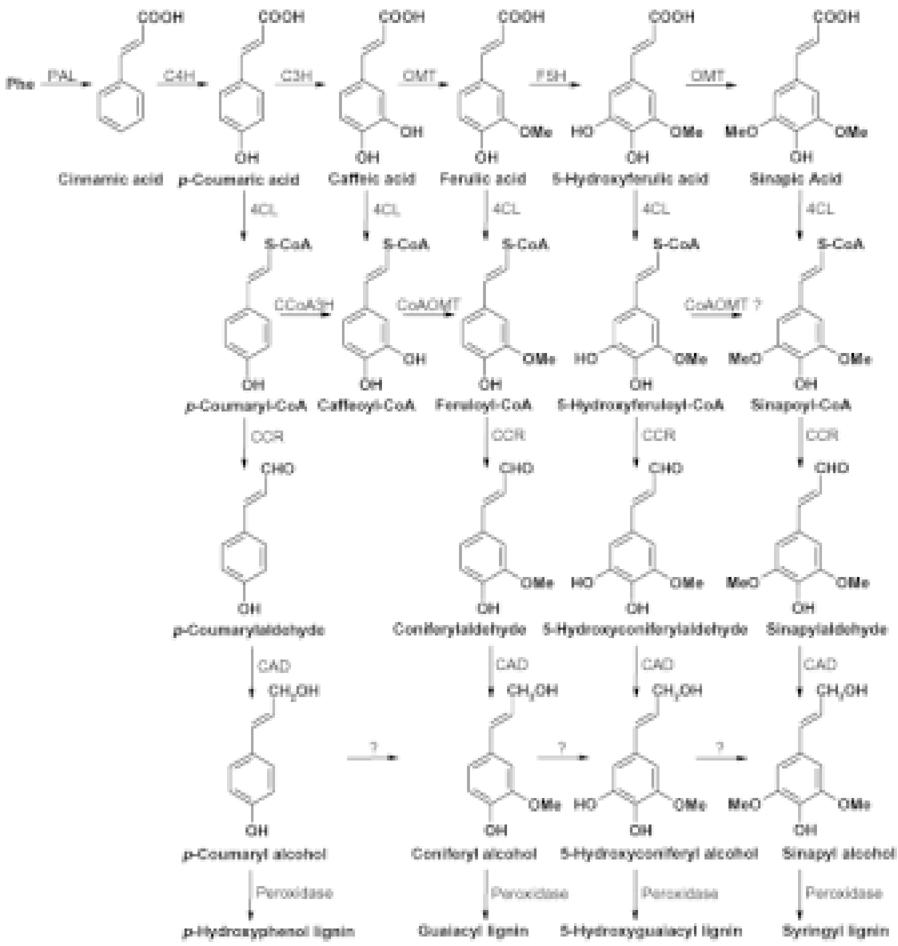

Fig. 1. A schematic representation of the lignin biosynthetic pathway starting from phenylalanine (Phe). Tyrosine is the second precursor to this pathway via tyrosine ammonia lyase to form *p*-coumaric acid. The enzymes involved in lignin synthesis include: PAL, phenylalanine ammonia lyase; C4H, cinnamate 4-hydroxylase; C3H, 4-coumaroyl hydroxylase; OMT, *O*-methyltransferase; F5H, ferulate 5-hydroxylase; 4CL, 4-coumarate-CoA ligase; CCoA3H, 4-coumaroyl-CoA hydroxylase; CoAOMT, caffeoyl-CoA *O*-methyltransferase; CCR, cinnamoyl-CoA reductase; CAD, cinnamyl alcohol dehydrogenase, and peroxidase.

(Kondo et al. 1987, Lowry et al. 1994). Recent work indicates that Klason lignin is a much more accurate method for determining lignin concentration of forages than ADL (Jung et al. 1999). However, lignin concentration estimates from these 2 methods are positively correlated.

Analysis of the hydroxycinnamic acids in cell walls and their cross-linking to lignin involves 2 steps because these compounds are present in more than 1 structural form in the cell wall. Ferulates and *p*-coumarates that are only ester-linked to polysaccharide or lignin are extracted with alkali at room temperature (Hartley 1972, Jung and Shalita-Jones 1990). Extraction with stronger alkali at 170°C cleaves both ester- and ether-linked hydroxycinnamic acids (Iiyama et al. 1990). A combination of these extractions can be used to partition the hydroxycinnamic acids into their 2 linkage forms. Ether-linked hydroxycinnamic acids can also be measured by dioxane-HCl hydrolysis (Scalbert et al. 1985). Unfortunately, the other 5 cross-linking structures of ferulic acid in lignin/polysaccharide bridges cannot currently be quantified (Ralph et al. 1992).

Lignin and Forage Quality

It is a well established fact that lignin concentration of forages is negatively correlated with digestibility (Jung and Deetz 1993). While this relationship has been reported for both dry matter (DM) and cell-wall digestibility (Van Soest 1964, Smith et al. 1972), it only has significance for cell-wall digestion as lignin does not directly impact digestibility of plant cell solubles. The reason DM digestibility is negatively correlated with lignin concentration is because the concentration of lignin always increases as cell-wall concentration rises, and forage cell walls are always less digestible than cell solubles. The negative relationship of lignin concentration and cell-wall digestibility is true regardless of the method of lignin analysis employed and has been observed with in vivo and in vitro measures of digestibility (Jung et al. 1997). Generally, the slope of this negative relationship is less for legumes than grasses, suggesting that lignin is more inhibitory of digestion in grasses (Van Soest 1964, Buxton and Russell 1988). This conclusion has been drawn primarily from research where lignin was measured as ADL and it should be considered suspect because the ADL method under-estimates lignin concentration more severely in grasses than legumes. The opposite conclusion may in fact be true. Microscopic studies suggest that lignin may be more inhibitory in legumes than grasses because lignified legume tissues are virtually indigestible whereas thick-walled, lignified grass tissues can be digested to leave only thin-walled indigestible residues (Engels 1989, Engels and Jung 1998).

Several mechanisms have been suggested for how lignin may inhibit cell-wall digestion, however, it is now generally agreed that lignin simply acts as a physical barrier to the microbial enzymes reaching their target polysaccharides (Chesson 1993, Jung and Deetz 1993). Previous hypotheses concerning toxicity, exclusion of water-soluble enzymes due to hydrophobicity, etc. can probably be discounted. Questions still remain as to how lignin structure, cross-linkage to other cell-wall polymers, and deposition and distribution in the wall may modify the impact of lignin as a physical barrier to cell-wall digestion. This is perhaps best illustrated by the fact that while the negative relationship of lignin concentration is always observed when examined across forage samples of different maturities, when plant maturity is similar (i.e. - forages from breeding studies, corn silage, etc.) large differences in lignin concentration and cell-wall digestibility are observed but lignin and digestibility are often not correlated (Jung and Vogel 1992, Jung and Buxton 1994, Jung et al. 1994). Obviously there must be modifying factors which influence the inhibitory effect of lignin on cell-wall digestion.

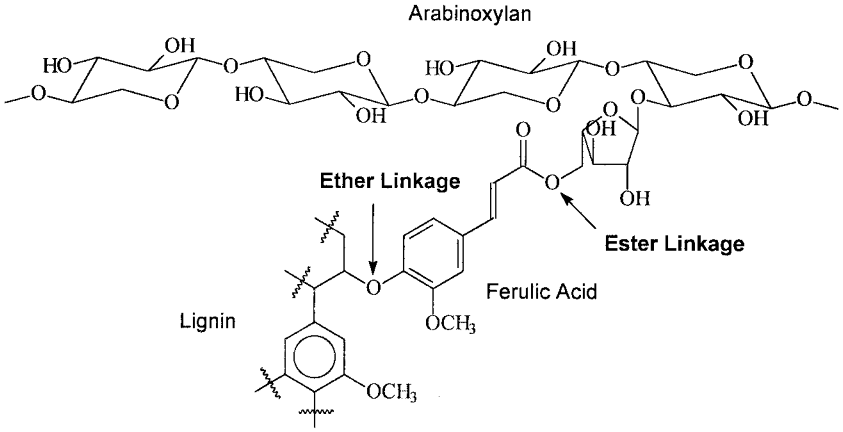

Fig. 2. Illustration of the cross-linking structure in grasses where ferulate esters of arabinoxylan form bridges to lignin. The linkage shown between lignin and ferulic acid is the 4-O-ß structure. The peroxidase/H_2O_2 reaction which catalyzes the cross-links also yields 8-O-4, 5-ß, 8-5, 5-5, and 8-ß structures. The 4-O-ß linkage accounts for only about one quarter of the cross-links between feruloylarabinoxylan and lignin, but it is the only one that can be quantified because it yields intact ferulic acid after high-temperature alkaline hydrolysis (Ralph et al. 1992).

It was proposed by Jung and Deetz (1993) that lignin composition, as measured by the syringyl-to-guaiacyl lignin ratio, would alter the inhibitory impact of lignin on cell-wall digestion because *bm* mutants have more digestible cell walls and a reduced syringyl-type lignin content. However, because *bm* mutants also have less total lignin and generally slightly lower cell-wall concentrations (Cherney 1990), the *bm* mutants are not suited to test the validity of the lignin composition hypothesis. Results from 2 transgenic tobacco (*Nicotiana tabacum* L.) experiments where *O*-methyltransferase and cinnamyl alcohol dehydrogenase activities were down-regulated showed improved cell-wall digestibility when the syringyl-to-guaiacyl lignin ratio was reduced but lignin concentration was not altered (Bernard Vailhe et al. 1996, 1998). However, no change in cell-wall digestibility was observed in an *Arabidopsis thaliana* [(L.) Heynh] mutant that deposits only guaiacyl-type lignin rather than the normal mixture of syringyl- and guaiacyl-type lignins (Jung et al. 1999). Obviously the impact of lignin composition on digestibility is still unresolved.

Jung and Deetz (1993) also proposed that ferulate cross-linking of lignin to polysaccharide in grasses was crucial for lignin to impede cell-wall digestion. Attempts to show negative correlations of ferulate cross-linking (measured as ether-linked ferulic acid) have met with limited success in switchgrass (*Panicum virgatum* L.), big bluestem (*Andropogon gerardii* Vitman), and corn (Jung and Vogel 1992, Jung and Buxton 1994). This may be because ferulate cross-links form early in grass development and subsequent deposition of lignin and cell-wall polysaccharides dilute cross-link concentrations (Morrison et al. 1998). However, using a corn cell culture model system Grabber et al. (1998) have demonstrated that reduced ferulate cross-linking will increase cell-wall degradability. Recently Casler and Jung (1999) found that smooth bromegrass (*Bromus inermis* Leyss) genotypes selected for reduced ferulate cross-linking exhibited improved cell-wall digestibility compared to genotypes with high concentrations of ferulate ether cross-links. It appears likely that ferulate cross-linking of lignin to polysaccharide does influence cell-wall digestibility.

Factors Affecting Lignification

Within the greater context of forage quality there are a large number of factors that can influence the nutritive value of forage. These can be arranged into a hierarchy that indicates the relative dependence of the various levels involved (Fig. 3). It should be realized that all of these processes are dynamic and that there are feedback mechanisms functioning from higher to lower levels. Consequently, there are a large number of interactions that can occur which may confound attempts to sort out the effects of various factors on forage nutritive value. The effects of lignin on forage quality can be altered and, therefore, manipulated at any level in the hierarchy of factors affecting nutritive value.

Ecosystem

The ecosystem level factors that we are concerned with in regard to forage quality are the edaphic, climatic, and biotic factors associated with a given environment that determine the potential plant communities that can be grown. The ecosystems in which forages are grown vary from the very simple to the highly complex and diverse. At one end of this spectrum are highly uniform and inherently productive environments. These can be easily manipulated through management of soil fertility, water, and pests such that the environment can be modified to a large extent to

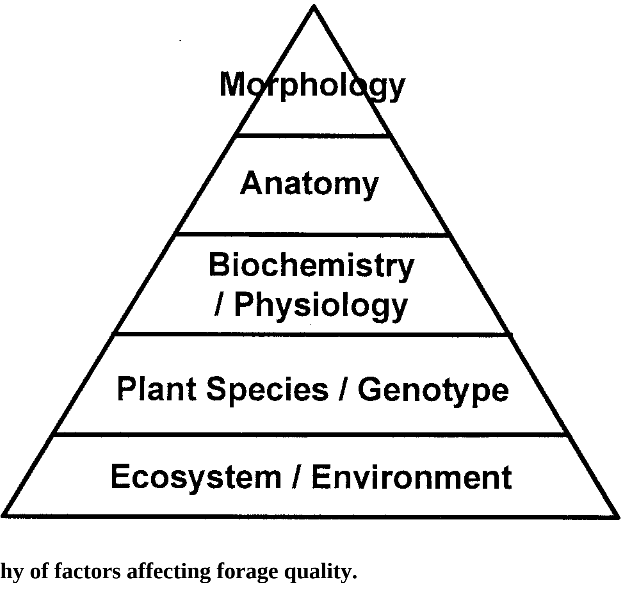

Fig. 3. Hierarchy of factors affecting forage quality.

suit the needs of a specific and generally introduced plant community. In contrast are extremely diverse and inherently less productive environments. These environments are not easily manipulated and consequently have limited potential for modification through management. Forage production within these environments generally involves extensive management of native plant communities. Management of forage quality in these environments is generally accomplished through grazing management and to a lesser extent, other forms of vegetation management.

Plant Species

As described earlier, plant communities utilized for forage vary from simple monocultures of cultivated species to complex and diverse native plant communities. The concentration and composition of lignin varies greatly among genera, species, and, to some extent, within species comprising forage plant communities.

Nearly all important cultivated and many native forages belong to either the grass family (Poaceae) or the legume family (Fabaceae), which are of the subclasses Monocotyledonae and Dicotyledonae, respectively. There are large differences in lignification between grasses and legumes and also differences in the impact of lignin per se on their forage quality (Fig. 4). Lignin concentration of legumes often appears comparable to that of grasses when expressed as a proportion of dry matter. However, when expressed as a proportion of fiber, legumes demonstrate a wider range of lignin concentrations that are generally higher than those of grasses (Buxton and Brasche 1991, Buxton and Russell 1988). As indicated earlier, this difference may be a result of analytical problems regarding lignin measurement. The range in fiber digestibility is similar between legumes and grasses indicating that there are qualitative differences between the 2 families in the way lignin interacts with other fiber components (Buxton et al. 1987, Buxton 1989).

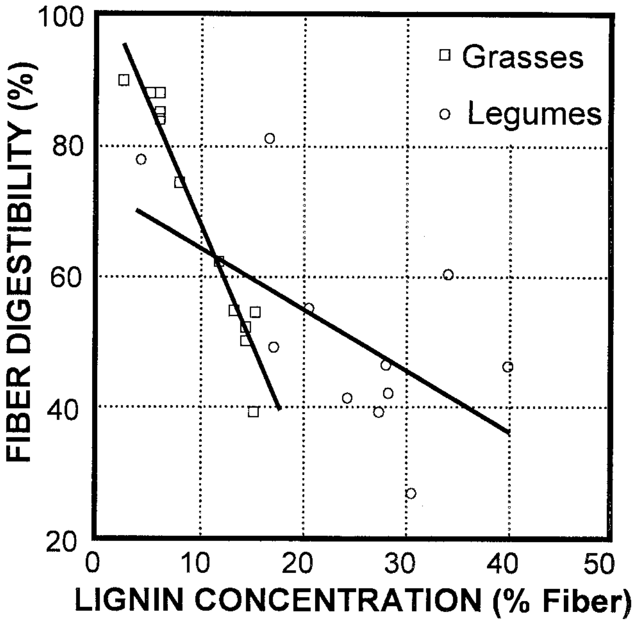

Fig. 4. Relationship between lignin concentration of fiber and fiber digestibility in legumes and grasses (Adapted from Smith et al. 1972).

The most important difference between grasses and legumes is in the concentration of fiber. Grasses have much higher fiber concentrations than legumes and conversely a lower concentration of readily digestible cell contents (Buxton and Russell 1988). So even though lignin has a negative impact on the fiber digestibility of legumes, the fact that they contain much less fiber than grasses lessens its impact on overall digestible energy concentration. For these reasons, lignin concentration is not a good indicator of digestible energy when making comparisons between grasses and legumes.

Other dicotyledonous forbs have lignins that are more similar to those of legumes than of grasses (Higuchi 1990). Most dicotyledonous shrubs and trees have relatively high lignin concentrations and concomitantly low fiber digestibility. This is reflection of the fact that they contain more heavily lignified tissues than do herbaceous species. The foliage of some browse species, however, can often be quite digestible (Chriyaa et al. 1997).

Cool-season and warm-season grasses have similar lignin and fiber composition (Jung and Vogel 1986, 1992). The primary distinction between cool- and warm-season grasses is that warm-season species generally have higher fiber and, therefore, higher lignin concentrations at comparable growth stages. Anatomical differences between cool- and warm-season grasses appear to account for most of the difference in fiber composition between the 2 types of grasses (Akin 1989). Warm-season grasses partition more dry matter into lignified tissues with thickened secondary walls.

Even within a single species or cultivar there may be significant genotypic differences in lignification since many forage cultivars are synthetic populations (Casler and Vogel 1999, Vogel and Pedersen 1993). These differences provide the genetic variability necessary to make improvements in the forage quality of these species through traditional breeding approaches. There are several examples of improvement in forage quality through either direct or indirect modification of lignin by breeding. Selection for decreased lignin in alfalfa (*Medicago sativa* L.) on a whole-plant basis resulted in changes in both fiber concentration and plant morphology (Kephart et al. 1989, 1990). Alfalfa lines selected for low lignin had shorter stems, higher leaf to stem ratios and higher concentrations of fiber in stem bases than high lignin lines. This selection for lower acid detergent lignin in alfalfa resulted in variable and inconsistent effects with respect to improving fiber digestibility (Jung et al. 1994).

Improvements made by selection for high dry matter digestibility in grasses have been related to changes in lignification in some cases. In smooth bromegrass, selection for improved dry matter digestibility was correlated with changes in lignification (Casler and Carpenter 1989, Jung and Casler 1990) and it was concluded that there may be some potential for improving digestibility by selection for low lignin. However, in switchgrass, substantial improvements in dry matter digestibility have been made without changing either the concentration of fiber or lignin (Moore et al. 1993). Selection for high digestibility has resulted in changes in fiber digestibility independent of lignin concentration, but may be related to how lignin interacts with the cell-wall polysaccharides (Gabrielson et al. 1990).

Ploidy level has been demonstrated to have an impact on lignin concentration of forage grasses. In *Brachiaria,* lignin concentration was higher in tetraploid than in diploid accessions (do Valle et al. 1988). However, there were no differences in fiber digestibility among the ploidy levels. In Napiergrass (*Pennisetum purpureum* Schumach.), differences in morphology were observed among triploid, tetraploid, and hexaploid lines, but the chemical compositions of various morphological structures were similar (Schank and Chynoweth 1993).

Biochemistry and Physiology

Genotypic differences among forages are initially expressed at the biochemical level in response to environmental stimuli. The biosynthesis of lignin as described earlier is a complex process involving a number of enzyme-mediated reactions (Boudet 1998). Lignin concentration and composition is regulated by these enzymes and can be altered by attenuating their activities (Dixon et al. 1996).

A well-known example of biochemically altered lignin is the *bm* mutation. The *bm* mutation is characterized by darkened coloration of the leaf mid vein and usually is related to lowered concentrations and altered composition of lignin (Cherney et al. 1991). It occurs naturally in corn and has been induced through mutagenesis in sorghum (*Sorghum bicolor* (L.) Moench.) (Fritz et al. 1981, Porter et al. 1978) and pearlmillet (*Pennisetum americanum* (L.) Leeke)(Cherney et al. 1988). The phenotypic effects of *bm* mutations have been well characterized (Fritz et al. 1990, Gerhardt et al. 1994, Moore et al. 1989) and have been related to altered enzyme activities (Bucholtz et al. 1980, Grand et al. 1985). The *bm* trait is of particular interest in forages because it is usually associated with relatively significant increases in fiber digestibility (Akin et al. 1986, Cherney et al. 1991, Wedig et al. 1987). Commercial varieties of *bm* corn and sorghum have been developed and have been demonstrated to result in improved animal performance (Grant et al. 1995, Lusk et al. 1984, Weller and Phipps 1986).

Only recently, however, have the genetic mechanisms involved in *bm* mutations been studied. In the bm_3 mutant of corn, the trait has been linked to changes in the structure of the O-methyl transeferase (COMT) gene (Vignols et al. 1995). This gene codes for the enzyme that catalyzes the methylation of 5-hydroxyferulate (Boudet 1998). The mutation lowers the activity of the resulting enzyme and results in a lower lignin concentration and an altered lignin composition (Vignols et al. 1995).

Molecular geneticists have recently altered lignin biochemistry of tobacco and alfalfa using anti-sense gene modification techniques (Halpin et al. 1994, Sewalt et al. 1997b, Sewalt and Dixon 1997). Down regulating the activities of phenylalanine ammonia-lyase and cinnamate 4-hydroxylase reduced lignin concentration and resulted in improved fiber digestibility in transgenic tobacco (Sewalt et al. 1997a). In alfalfa, reducing the activities of the methylating enzymes COMT and caffeoyl-CoA O-methlytransferase resulted in only modest changes in lignin concentration and fiber digestibility (Sewalt and Dixon 1997). Molecular approaches such as these offer great promise for developing forage cultivars with improved quality characteristics (Dixon et al. 1996). However, it is unlikely that transgenic forage cultivars will be available to producers any time in the near future.

Physiological responses to several environmental factors may affect the extent of lignification that occurs within a forage plant community. Temperature, soil moisture, light, and soil fertility can have either direct or indirect effects on lignification (Buxton and Casler 1993, Nelson and Moser 1994).

Lignification tends to increase in plants grown under warmer temperatures. This appears to be related mostly to increased activities of lignin synthetic enzymes at higher temperatures (Buxton and Fales 1994), but may also be related in some instances to increased partitioning of plant dry matter to more lignified tissues (Cone and Engels 1990, da Silva et al. 1987). Wilson et al. (1991) reported that growing a number of tropical and temperate forage species under a higher temperature regime did not alter the proportion of various tissues, but rather appeared to increase the intensity of lignification. Similar results were reported for tall fescue *(Festuca arundinacea* Schreb.) grown under 4 temperature regimes (Akin et al. 1987). Increasing temperature did not affect leaf anatomy, but negatively affected the proportion of tissues degraded. Fales (1986) found that growing tall fescue under increasing temperatures did not affect lignification, but increased indigestible fiber concentration. Henderson and Robinson (1982) reported that increasing growth temperatures of subtropical grass species resulted in increased lignification and decreased fiber digestibility. Despite the apparent inconsistencies of the effects of temperature on lignification, the negative effect of increasing temperature on fiber digestibility appears to be consistent (Akin and Chesson 1989, Ford et al. 1979).

Moisture deficit generally decreases lignification, although this effect occurs largely as a function of changes in plant development and morphology (Buxton and Casler 1993). In alfalfa, total-cell wall concentration increased with increasing irrigation levels, but cell-wall composition was unaffected (Halim et al. 1989). Differences in forage digestibility between stressed and non-stressed plants were attributed to delayed plant maturity caused by water stress. Excess moisture can also reduce whole-plant lignin concentration. Growing alfalfa under conditions of excess moisture stunted plant development which resulted in lower concentrations of lignin and other fiber components (Buscaglia et al. 1994).

Light intensity and quality also can affect lignification of forages. Low light decreases lignification on a whole-plant basis (Buxton and Fales 1994). As with most other environmental responses, this decrease is generally related to delayed development of the plant rather than changes in lignification at the cellular level (Buxton and Casler 1993). Shaded plants tend to be less lignified (Buxton 1996). However, the effects of light intensity on lignification and fiber digestion are not always consistent. Henderson and Robinson (1982) reported that increasing light intensity had variable effects on lignification and fiber digestibility of subtropical grass species. Kephart and Buxton (1993) similarly reported that the effects of shading on lignification of a number of temperate and warm-season grasses was inconsistent, however, in their study shading consistently resulted in improved dry matter digestibility.

Light quality apparently does not impact lignification, but may influence fiber digestibility independent of lignification. Jung and Russelle (1991) grew orchardgrass (*Dactylis glomerata* L.) and birdsfoot trefoil (*Lotus corniculatus* L.) under low pressure sodium or flourescent-incandescent lights in a study designed to evaluate the effects of light quality on fiber composition and digestion independent of plant age. They found that fiber digestibility of orchardgrass decreased under sodium lamps. The effect on birdsfoot trefoil fiber digestibility was the opposite. In both cases, changes in fiber digestion were not related to changes in lignification.

Soil nutrients can have both direct and indirect effects on lignification. Deficiencies of many plant nutrients impede growth and development in a manner similar to other plant stresses (Miller and Reetz 1995). Therefore, lignification is generally reduced in plants growing under conditions of low soil fertility. However, there is little evidence to suggest that fertilization affects lignification when nutrient levels are adequate to support normal plant growth or that manipulating soil fertility would be a useful management tool for altering lignification.

Nitrogen fertilization has variable effects on lignification depending on plant species and the environment in which it is grown. Nitrogen fertilization had little or no impact on lignin concentration of pearlmillet stover (Powell and Fussell 1993). In alfalfa, lignin concentration was unaffected by increasing inorganic nitrogen available for plant growth (Cherney et al. 1994). Plant responses to nitrogen may be affected by other environmental factors. Collins et al. (1990) observed an increase in fiber concentration of oat (*Avena sativa* L.) forage with increasing nitrogen fertilizer in 1 environment, but small decreases occurred in response to nitrogen fertilizer in 3 other environments. However, lignin concentration was unaffected by fertilization. Sanderson et al. (1995) reported a significant interaction between plant density and nitrogen fertilization. In their experiment, lignin concentration increased with increasing plant density in corn fertilized with nitrogen. However, lignin concentration was unaffected by plant density in unfertilized corn.

Sulfur fertilization has been reported to decrease lignification and improve fiber digestibility in sorghum (Ahmad et al. 1995), but did not affect either lignin concentration or fiber digestibility in tall fescue or orchardgrass (Chestnut et al. 1986). It has been suggested that fiber concentration in tall fescue may be related to the ratio of nitrogen to sulfur levels available for plant growth (Sweeney and Moyer 1997). However, no such relationship occurred in corn fertilized with varying rates of nitrogen and sulfur (O'Leary and Rehm 1990).

Plant Anatomy

Lignification occurs during the process of cell differentiation and is generally coincident to secondary wall formation (Iiyama et al. 1993). Lignin deposition is initiated in the corners of the cell adjacent to the middle lamella and proceeds inward into the primary and secondary walls. Lignification is always preceded by deposition of structural carbohydrates and lags behind development of the currently developing cell wall layer. Because of this, lignin concentration is usually higher in the primary than the secondary wall. However, in cells with pronounced secondary thickening the actual quantity of lignin may be higher in secondary walls due to their large volume (Terashima et al.1993, Wilson 1993).

The process of lignification occurs relatively rapidly in growing tissues. In sorghum leaf blades, lignin was present in very low concentrations in the leaf intercalary meristem, but increased dramatically to near maximum in cells adjacent to the meristem less than 1 day old (Volenec et al. 1986). Lignification in developing stems is somewhat slower. In elongating corn internodes, lignification was initiated within 2 days after elongation began and by 4 days had proceeded into all elongated tissues (Morrison and Buxton 1993).

Lignin concentration varies greatly from one cell type to another. Consequently, degradability of plant tissues is variable and related to lignin concentration. Tissues with high lignin concentrations include the epidermis (grasses), xylem, and sclerenchyma (Akin et al. 1990, Buxton and Redfearn 1997, Chesson et al. 1986, Twidwell et al. 1991). These tissues are relatively undegradable by rumen microbes (Grabber el al. 1992) and comprise a large proportion of the indigestible fraction of forages (Buxton and Redfearn 1997, Twidwell et al. 1991, Akin and Chesson 1989). Other tissues such as mesophyll and other types of parenchyma are not lignified, contain a large proportion of metabolites, and are highly degradable. Between these extremes are tissues with intermediate and variable degradability such as phloem and collenchyma (Akin 1989, Wilson 1993).

The digestibility of a forage represents the relative contributions of various plant tissues to total herbage dry matter (Magai et al. 1994). The higher the proportion of structural and other lignified tissues, the lower the digestibility of the forage (Akin 1989).

A significant proportion of the differences among species in lignin concentration and fiber digestion reflect differential partitioning among various tissues. Warm-season grasses for example, tend to have a higher proportion of lignified tissues than cool-season grasses (Akin 1989). Differences in fiber digestibility of warm-season and cool-season grasses have been related to anatomical characteristics. Warm-season grasses generally have a higher proportion of structural and other indigestible tissues than cool-season grasses (Wilson and Hattersley 1989, Wilson and Kennedy 1996).

Morphology

Lignification increases as plants mature (Brink and Fairbrother 1994, Cherney et al. 1993, Cuomo et al. 1996, Hockensmith et al. 1997). This is largely a function of changes in the morphology of the plant, and to a lesser degree, the aging of plant tissues (Anderson 1985). Changes in plant morphology are related to ontogeny (Nelson and Moser 1994). In grasses, developmental morphology is characterized by 4 primary growth stages: 1) vegetative, 2) elongation, 3) reproductive, and 4) seed ripening (Moore et al. 1991, Moore and Moser 1995). During vegetative development, the stems remain near the crown and the above ground portion of the plant consists primarily of leaves. During elongation stem internodes lengthen, increasing the proportion of stem tissue in the canopy relative to leaves. During the later 2 growth stages, inflorescences develop, fertilization occurs, and seeds develop. Development of legumes and other herbaceous dicots also occurs in vegetative and reproductive stages (Kalu and Fick 1981). During vegetative development, stem growth occurs simultaneously with leaf development. Continued cambial growth in dicot stems results in accumulation of indigestible xylem tissues. In determinate species, stem growth ceases with the onset of reproductive growth, while in indeterminate species, reproductive and vegetative growth may occur simultaneously.

As plants mature, the ratio of leaves to stems decreases (Albrecht et al. 1987, Nordkvist and Åman 1986, Martiniello et al. 1997). Because stems contain more lignified structural tissues and less metabolically active tissues than leaves, the digestibility of stems is generally much less than that of leaves (Akin 1989, Twidwell et al. 1988). Using a lignin stain and image analysis, Twidwell et al. (1991) characterized the anatomy of switchgrass leaves and stems. They reported that stems contained a greater proportion of structural and other lignified tissues than leaves and that these tissues were more resistant to degradation when incubated in buffered rumen fluid for 24 and 48 hours. Bruckner and Hanna (1990) reported similar findings in a study on the anatomy and digestibility of leaves and stems of small grain species.

Lignin concentration increases with maturity in grasses (Cherney et al. 1993, Foster et al. 1996, McBee and Miller 1993, Titgemeyer et al. 1996) and legumes (Bidlack and Buxton 1992, Kratchunov and Naydenov 1995). Quantitatively, the changes in lignification that occur as plants mature have the largest impact on forage quality of the factors that can be modified by forage management. In grasses, lignin concentrations more than double as plants develop from vegetative to reproductive stages of growth while in legumes, the increase is somewhat less dramatic (Albrecht et al. 1987, Bidlack and Buxton 1992, Brink and Fairbrother 1994).

Management Implications

The goal of managing forage quality is not necessarily to minimize lignin concentration, but rather to minimize its impacts on fiber digestion and intake. To some extent, management can be used to manipulate lignification and its impact on fiber digestion at each of the levels discussed in the previous section (Fig. 3). However, from a practical perspective, the most useful management practices for this purpose are manipulation of the plant community such that it contains more desirable (less lignified and more digestible) plants, harvest management to maintain plants in a vegetative state of development, and when necessary, postharvest treatments to improve the digestibility of low quality harvested forages.

Species and variety selection are extremely useful tools for managing forage quality within the constraints of an ecosystem. Obviously, other factors such as yield, seasonal growth distribution, and establishment and production costs may be as or more important than forage quality. However, altering species composition, either by seeding or vegetation manipulation, can greatly enhance the yield of available nutrients and productivity of the system. The goal is to develop a plant community with inherently high quality characteristics.

Establishment of improved cultivars of adapted species can enhance productivity of forage-livestock systems and increase economic returns. Studies have demonstrated substantial improvements in the performance of beef cattle grazing pastures with improved forage quality characteristics (Anderson et al. 1988, Moore et al. 1995). Estimates in the value of increased production realized from improvements in forage quality range from $50 to $85 per hectare per year (Vogel and Sleper 1994).

Defoliation management is probably the most powerful tool available to producers for managing forage quality. Timing of harvest and grazing events such that forages are maintained in a vegetative state is the most effective and straightforward approach to managing the decline in forage quality associated with plant maturity (Hirschfeld et al. 1996, Norton et al. 1997). Again, decisions with regard to defoliation management need to be weighed against other factors such as yield and effects on plant persistence. In addition to defoliation, maturation of forages can be controlled by burning, clipping, and application of plant growth regulators (Mitchell et al. 1996, Roberts and Moore 1990). However, none of these other treatments has the impact of properly timed defoliation.

There are a number of postharvest treatments that can be used to improve the digestibility of fiber in highly lignified forages. These have been reviewed in some detail by Fahey et al. (1993). There are 4 basic strategies employed in postharvest treatments that have been developed to lessen the impact of lignin on fiber digestion. These include alkaline hydrolysis, enzymatic hydrolysis, oxidation, and microbial treatments. Of these, alkaline hydrolysis is by far the most common and practical.

Alkaline treatments have been demonstrated to improve the digestibility of grasses, but not legumes. The reagents most commonly used for this purpose are ammonia and various hydroxides (Fahey et al. 1993). Ammoniation of forages can be accomplished using anhydrous ammonia applied in gaseous form or by incorporating urea with the forage (Fritz et al. 1991, Moore et al. 1985, Sewalt et al. 1996). Ammoniation increases fiber digestibility and crude protein concentration whereas treatment with sodium hydroxide only increases fiber digestion, however, sodium hydroxide treatment generally results in greater increases in fiber digestibility than ammoniation. Of the alkaline treatments used to improve forage digestibility, ammoniation is the easiest to use. In all cases, chemical treatments used to enhance fiber digestion result in greater improvements when applied to poor quality roughages such as mature grasses and cereal crop residues than when applied to higher quality forages (Klopfenstein 1978).

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Herbivore response to anti-quality factors in forages

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Abstract

Plants possess a wide variety of compounds and growth forms that are termed “anti-quality” factors because they reduce forage value and deter grazing. Anti-quality attributes can reduce a plant’s digestible nutrients and energy or yield toxic effects. Herbivores possess several adaptive mechanisms to lessen the impacts of anti-quality factors. First, herbivores graze selectively to limit consumption of potentially harmful plant compounds. Grazing animals rely on a sophisticated system to detect plant nutritional value or toxicity by relating the flavor of a plant to its positive or negative digestive consequences. Diet selection skills are enhanced by adaptive intake patterns that limit the deleterious effects of plant allelochemicals; these include cautious sampling of sample new foods, consuming a varied diet, and eating plants in a cyclic, intermittent, or carefully regulated fashion. Second, grazing animals possess internal systems that detoxify or tolerate ingested phytotoxins. Animals may eject toxic plant material quickly after ingestion, secrete substances in the mouth or gut to render allelochemicals inert, rely on rumen microbes to detoxify allelochemicals, absorb phytochemicals from the gut and detoxified them in body tissues, or develop a tolerance to the toxic effects of plant allelochemicals. Understanding the behavioral and metabolic abilities of herbivores suggests several livestock management practices to help animals contend with plant anti-quality characteristics. These practices include offering animals proper early life experiences, selecting the appropriate livestock species and individuals, breeding animals with desired attributes, and offering nutritional or pharmaceutical products to aid in digestion and detoxification.

Key Words: anti-quality, conditioned aversions, detoxification, diet selection, forage quality, foraging, grazing behavior, toxic plants

Resumen

Las plantas poseen una amplia variedad de compuestos y formas de crecimiento que son llamadas factores "anti-calidad" porque reducen el valor del forraje y desalienta el apacentamiento de ellas. Los atributos anti-calidad pueden reducir los nutrientes y energía digestibles de la planta o producir efectos tóxicos. Los herbívoros poseen varios mecanismos adaptativos para aminorar los impactos de los factores anti-calidad. Primero, los herbívoro apacientan selectivamente para limitar el consumo de compuestos vegetales potencialmente dañinos. Los animales en apacentamiento dependen de un sistema sofisticado para detectar el valor nutricional o la toxicidad de las plantas relacionando el sabor de la planta con sus consecuencias digestivas positivas o negativas. Las habilidades para seleccionar la dieta aumentan por los patrones adaptativos de consumo que limitan los efectos perjudiciales de los aleloquímicos de la planta, estos incluyen la precaución de probar nuevos alimentos, consumiendo una dieta variada y comiendo plantas de una manera cíclica, intermitente o cuidadosamente regulada. Segundo, los animales en apacentamiento poseen sistemas internos para detoxificar o tolerar la ingestion de fitotoxinas. Los animales pueden expulsar rápidamente el material vegetal toxico después de la ingestión, segregan substancias en la boca o el intestino para hacer inertes a los aleloquímicos, dependen de los microbios ruminales para detoxificar los aleloquímicos, absorber los fitoquímicos del intestino y detoxificarlos en los tejidos corporales o desarrollar una tolerancia a los efectos tóxicos de los aleloquimicos de la planta. El entendimiento de las habilidades de comportamiento y metabólicas de los herbívoros sugiere varias prácticas de manejo del ganado para ayudar a los animales a contender con las características anti-calidad de las plantas. Estas prácticas incluyen el ofrecer a los animales experiencias apropiadas durante las primeras etapas de su vida., seleccionar las especies e individuos de ganado mas apropiados, criar animales con los atributos deseados y ofrecer productos nutricionales o farmacéuticos que auxilian en la digestión y detoxificación.

Forage “quality” is the collective assessment of a plant’s ability to contribute to growth and production of grazing animals. Rangeland forages usually also contain compounds that limit or adversely affect animal production. These attributes are termed “anti-quality” because they restrict “quality” in some way. Implicit in this delineation is the idea that quality and anti-quality parameters are measured by animal response. The grazing value of a specific forage cannot be determined by a few simple laboratory procedures because grazing animals possess a variety of dietary and metabolic mechanisms to exploit plant nutrients and overcome the negative effects of anti-quality attributes. Successful livestock management on rangelands requires an understanding of plant nutritional content and potential effects of anti-quality attributes. However, managers must also be cognizant of the skills herbivores possess to harvest nutrients and avoid toxins. In this paper, we will examine how anti-quality plant attributes affect diet selection and intake. We will also examine the behavioral and digestive strategies that animals

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employ to overcome the anti-quality aspects and gain access to the nutrient and energy resources of plants. Finally, we will suggest management approaches to help animals contend with anti-quality attributes in forages.

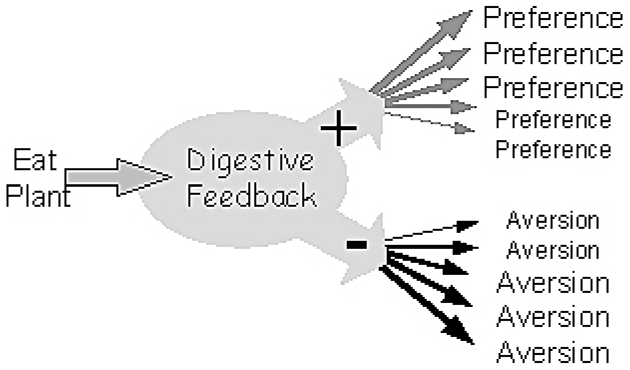

Fig. 2. When an animal eat a plant it receives digestive feedback in the form of energy, nutrients, illness, or toxicosis. If the feedback is positive, preferences are formed to the plant and if the feedback is negative, aversions are formed. The strength of the preference or aversion is determined by the magnitude, nature, and timing of digestive feedback.

Anti-quality Attributes Affect Diet Selection Through Digestive Consequences

Grazing animals are unquestionably sensitive to the quality and anti-quality attributes of plants. For example, animals select diets of higher quality than the average forage available (Arnold 1981, Provenza 1995). Animals also limit their consumption of toxins by selecting plants and plant parts of relatively low toxin concentration (Provenza 1995, Pfister 1999). How animals sense the quality or toxicity of forages has been an active area of research for more than 3 decades. It is now clear that animals ascribe forage value by relating plant flavor to positive or negative digestive consequences (Provenza 1995, 1996). Grazing decisions are based on a series of interrelated and cumulative consequences of consumption.

A plant's chemical and structural attributes dictate its digestive consequences because they set the potential digestible energy, nutrient yield, or toxicity of the plants. The digestion and detoxification abilities of grazing animals, and their microbial symbionts, determine the actual yield of nutrients, energy, or toxins. The results of these plant and animal interactions determine a forage's palatability or hedonic value (i.e., pleasurable and disagreeable sensations experienced through taste and smell). Palatability, in turn, affects the probability that the plant will be eaten in future encounters. The key to how animals respond to anti-quality factors in plants is therefore centered on the consequences of consumption (Fig. 1).

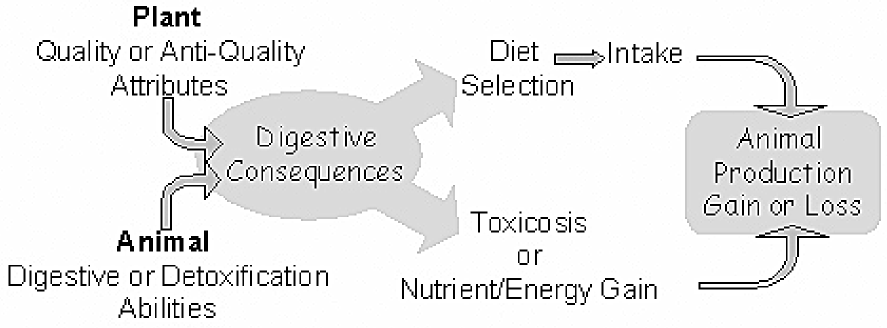

Fig. 1. Digestive consequences are at the center of how animals respond to anti-quality factors in forages. The actual digestive feedback animals receive is determined by plant forage quality and animal digestive and detoxification abilities. The consequences of consumption, in turn, affect diet selection and intake and the nutrients and energy available for animal growth and maintenance.

When a grazing animal smells and tastes a plant, the flavor is either pleasing or distasteful depending on the animal's previous grazing experiences. If the plant is new to the animal, its initial hedonic value depends on its similarity to familiar plants. Grazing animals tend to consume new foods that are similar to preferred foods and avoid new foods that are similar to foods they dislike (Launchbaugh and Provenza 1993, Provenza et al. 1999). When a plant is eaten, it provides feedback during digestion and metabolism. The flavor (i.e., taste and odor) of a plant becomes more or less pleasing to the animal depending on digestive consequences. If consumption of a plant improves the nutrient or energy status of the animal, the plant flavor becomes more desirable or pleasing to the animal. If consumption of the plant yields illness or digestive malaise, the flavor becomes aversive and distasteful (Fig. 2). This is known as a hedonic shift. This "evaluation" system is based on processes occurring at a sub-conscious level that selectively relate gastrointestinal feedback with the flavor, rather than the sight or texture, of a food (Garcia 1989, Provenza 1995). These flavor-consequence relationships form the basis for dietary likes and dislikes.

Once the hedonic value of a plant is established, the animal uses its senses of smell and sight to differentiate between plants and seek foods with high hedonic value and avoid aversive foods. Searching and selective grazing are cognitive processes that can be further reinforced by interactions with other animals (Thorhallsdottir et al. 1990a, 1990b). The resulting behavior patterns lead to increased consumption of foods that are likely to yield nutritional benefit and limited consumption of toxic or low quality plants.

Grazing preference also depends on the animal's nutritional state (Provenza 1995, Provenza et al. 1998). When need for a nutrient is high, preferences for foods containing the nutrient are high. When needs are met, preference declines. For example, lambs fed diets of inadequate sodium, energy, or protein show a strong preference for foods high in sodium, energy, or protein, respectively (Villalba and Provenza 1996, 1999). Thus, an animal's nutritional state influences its incentive to seek and eat particular plants.

How Plant Anti-quality Attributes Drive Diet Selection and Intake

Plants possess a wide variety of chemical and physical properties that reduce forage value and serve as grazing deterrents.

From the animal's perspective, the effects of anti-quality attributes can be expressed along a continuum from those that reduce the forage nutrient or energy yield to those producing toxic or ill effects. How strongly a plant attributes affects diet selection or intake therefore depends on the magnitude, timing, or nature of digestive feedback (Fig. 2).

Reduce Digestive Benefits

Herbivores can quite effectively distinguish between plants that differ in digestible energy or nutrients (Villalba and Provenza 1996, 1997a, 1997b). Lambs formed strong preferences for flavored straw when consumption was followed by ruminal infusions of starch (Villalba and Provenza 1997a, Smith et al. 1999), volatile fatty acids (Villalba and Provenza 1996, 1997b), or protein sources (Villalba and Provenza 1997c). Preference for most rangeland forages is positively correlated with digestive benefits (Arnold and Hill 1972, Arnold 1981). Phytochemicals that reduce the potential digestive yield of a plant can therefore be viewed as anti-quality factors. For example, lignin (Van Soest 1994), tannins (Reese 1979), and resinous compounds (Meyer and Karasov 1991) can reduce forage digestibility by forming insoluble complexes with nutrients. High content of indigestible compounds, such as silica and waxes, can dilute the digestive gain of a plant and reduce preference (Herms and Mattson 1992). Plant digestibility can also be reduced by allelochemicals that inactivate digestive enzymes or harm gut microbes. For example, a wide variety of plants including, potatoes (*Solanum tuberosum* L.), soybeans (*Glycine max* [L.] Merr.) , cottonseeds (*Gossypium* L.) , and tomatoes (*Solanum lycopersicum* L.) contain trypsin and chymotrypsin inhibitors that can interfere with protein digestion, particularly in monogastric animals (Reese 1979, Slansky 1992). Compounds that precipitate proteins, like gossypol (Slansky 1992) and tannins (Reese 1979, Robbins et al. 1991), can also decrease digestibility by binding and inactivating digestive enzymes. Allelochemicals also have anti-microbial effects that inhibit rumen or cecal/colon microbes thereby reducing digestibility (Allison 1978).

The magnitude of digestive feedback can strongly affect intake and preference; however, the rate at which nutrients or energy are liberated may also be important. Sheep prefer foods paired with ruminal energy infusions immediately after consumption to those paired with delayed infusions of energy (Villalba et al. 1999, Smith et al. 1999). A high content of structural carbohydrates, such as cellulose or hemicellulose, in plants may have little effect on the extent of digestion and yet reduce preference and intake by delaying the digestive gain of plant material.

Create Toxic Effects and Food Aversions

Many allelochemicals in rangeland and pastureland plants cause a variety of deleterious neurological, metabolic, and teratogenic effects and are therefore termed toxic. For discussions on the toxic effects of plant compounds refer to other papers in this volume or a recent review by Cheeke (1998). These toxic effects can cause severe production losses and yet not alter diet selection or intake. Strong flavor aversions are observed only when a phytotoxin stimulates the emetic centers of the midbrain and brainstem that control nausea and vomiting (Grant 1987, Garcia 1989, Provenza et al. 1992, 1994a, Provenza 1995). Herbivores can readily form aversions to feeds that stimulate the emetic system, however they may not be able to avoid feeds that do not cause nausea (e.g., cause allergies, bloating, or lower intestinal discomfort; Garcia 1989, Provenza et al. 1992). Further evidence to the important role of the emetic system is that anti-emetic drugs can attenuate lithium chloride-(Provenza et al. 1994a) and alkaloid-induced (Aldrich et al. 1993) aversions in sheep.

Aversive post-ingestive feedback causes cattle, sheep, and goats to decrease intake of foods containing toxins such as alkaloids in larkspur (*Delphinium* spp.; Pfister et al. 1997) and tall fescue (*Festuca arundinaceae* Schreb.; Aldrich et al. 1993), condensed tannins in blackbrush (*Coleogyne ramossisma* Torr.; Provenza et al. 1990), essential oils in big sagebrush (*Artemisia tridentata* Nutt.; Fraker 1999) and juniper (*Juniperus* spp.; Pritz et al. 1997), and allelochemicals in mesquite (*Prosopis glandulosa* Torr.; Baptista and Launchbaugh 2001). Conditioned aversions may be mild (i.e., temporary) or strong (i.e., permanent) depending on the toxin dose and when and how the toxin affects the gut and brain. Doses of allelochemicals that make animals intensely ill form stronger aversions than weak emetic stimulants (Ralphs and Cheney 1993, Launchbaugh and Provenza 1994). To form lasting aversions, consequences must be experienced within 8 hours of consumption (Burritt and Provenza 1991). It is difficult, if not impossible, for animals to learn to avoid a nutritious food that yields toxic effects several days or weeks after consumption. There are several examples in nature where animals prefer less toxic or nontoxic plants apparently because they produce less negative gastro-intestinal consequences upon consumption than alternatives (Provenza 1995, Pfister 1999).

Aversions can also be formed to foods that are not commonly considered "toxic". Soluble carbohydrates or nitrogen content of some feeds or forages can be so dense as to cause gastro-intestinal malaise when eaten in excessive amounts. For example, ruminants often form aversions to fruits and grains because excessive energy consumption can cause illness (Provenza 1995). Aversions have been demonstrated when high doses of energy supplements, such as propionate, were administered to sheep during a meal (Ralphs and Cheney 1993, Villalba and Provenza 1996). Ruminants eating foods high in rumen-degradable protein can also experience high levels of ruminal ammonia, suffer malaise, and decrease intake (Prins and Beekman 1989, Villalba and Provenza 1997c).

How Animals Contend with Anti-quality Factors

To live a healthy life on rangeland, herbivores must consume nutritious plants and avoid toxic or low quality plants. Foraging animals face the challenge of obtaining nutritious diets in environments where nutritional value and toxicity vary greatly from plant to plant, place to place, and time to time. To meet this challenge, herbivores possess several adaptive behavioral mechanisms that limit toxins and increase nutrients ingested, and internal systems that detoxify or tolerate ingested phytotoxins.

Selective Grazing

Selective grazing is the herbivore's first line of defense against the negative effects of plants with toxins or anti-quality attributes (Launchbaugh 1996). To make wise grazing decisions, animals must either be born knowing what to eat or avoid, learn appropriate dietary habits from peers, or learn from individual experiences. Diet selection strategies employed by herbivores have been reviewed in several publications (Provenza et al. 1992, 1998, Launchbaugh 1996, Provenza 1995, 1996, Pfister 1999, Foley et al. 1999). The following discussion provides an overview with reference to animal responses to anti-quality factors in plants.

Instinctive Avoidance

Some researchers contend that animals are instinctively attracted to sweet flavors and repelled by bitter flavors (Rhoades 1979, Owen 1992). Many plant toxins supposedly taste bitter (e.g., saponins and cyanogenic glycosides), have offensive odors (e.g., terpenes), or provoke an astringent sensation when eaten (e.g., tannins); however, these attributes are not universally repellent (Glendinning 1994). Sheep (Arnold and Hill 1972) and cattle (Pfister et al. 1996) do not necessarily avoid bitter tastes nor do sheep form stronger aversions to bitter than to sweet flavors (Launchbaugh et al. 1993). Furthermore, animals acquire preferences for bitter and sour flavors when consumption is followed by calorie enhancement even when these flavors were not initially preferred (Sclafani 1991). There is considerable evidence questioning the existence of an innate recognition system for plant nutritional or toxic qualities based on flavor or any other plant quality.

Learning from Mother and Peers

Livestock live in multi-generational groups in which dietary information can be easily passed from experienced to inexperienced animals. Young livestock therefore do not require perfect and complete dietary information at birth. Learning from mother may even begin before young herbivores, take their first bites. Flavors in uterine fluid can influence food aversions (Smotherman 1982). Mother's milk is also a source of information for young livestock. Nolte and Provenza (1992) found that orphan lambs raised on onion-flavored milk preferred onion-flavored feed later in life. Lambs quickly lean to avoid harmful novel foods their mother was trained to avoid, and to consume novel alternatives consmed by mother (Mirza and Provenza 1990, 1994). Nursing calves began to eat substantial quantities of locoweed (*Oxytropis* spp.; Pfister, unpublished observations) and low larkspur (*Delphinium nuttallianum* Pritz.; Pfister and Gardner 1999) on the same day as their grazing mothers; suggesting that calves mimicked their mother's diet. Young livestock can also learn appropriate food choices from other adult animals and peers (Thorhallsdottir et al. 1990a, 1990b).

Animals are, however, more influenced by their own dietary experiences than by mother or other social models. Lambs consistently avoided a food after experiencing toxicosis even if their mothers readily consumed the food (Provenza et al. 1993, Pfister et al. 1993). Calves that initially ate larkspur with their mothers, sharply curtailed consumption a few days later (Pfister and Gardner 1999), perhaps because of adverse feedback (Pfister et al. 1997). Nonetheless, social facilitation can play a significant role in ameliorating aversions. Ewes and lambs averted to a pelleted ration ingested more of the ration when feeding with non-averted peers than when feeding alone (Thorhallsdottir et al. 1990a). Cattle also consumed more of a toxic plant they had been conditioned to avoid when feeding with non-averted peers (Lane et al. 1990). Likewise, lambs form stronger aversions to a palatable shrub when exposed to the shrub with other lambs that avoid the shrub than when eating with peers that consumed the shrub (Provenza and Burritt 1991).

Individual Learning about Plant Allelochemicals

Conditioned aversions are powerful mechanisms by which animals learn to identify and avoid toxic plants (Garcia 1989, Provenza et al. 1992). Many rangeland plants contain compounds that produce aversions if eaten in sufficient quantities, as discussed above. Aversions can be easily demonstrated by offering an animal a single novel food and inducing gastro-intestinal illness immediately following ingestion; however, generalist herbivores rarely eat 1 plant per feeding bout (Westoby 1978). Several mechanisms enable herbivores to attribute digestive effects to specific plants rather than to all the plants in a meal. One way herbivores apparently accomplish this task is by regarding unfamiliar plants with caution. When consuming mixed meals of familiar and novel foods, herbivores preferentially form aversions (Burritt and Provenza 1989, 1991) or preferences (Provenza et al. 1999, Villalba and Provenza 2000) to novel dietary items. For example, when lambs experience toxicosis after eating a meal of 4 familiar and 1 novel food they subsequently avoided only the novel food (Burritt and Provenza 1991). When foraging bouts include several novel plants, plants that dominate the diet are probably 'weighted' more than less consumed plants, even if the minor foods were responsible for more positive or negative feedback (Provenza et al. 1994b). Furthermore, digestive feedback begins quickly after consumption and flavor-feedback interactions during a feeding bout could help animals attribute digestive benefits or liabilities to specific plants. Finally, grazing livestock on rangelands are usually quite familiar with the forage resource and may seldom encounter truly novel plants. This allows greater opportunity to 'sort out' feedback from individual or similar groups of plant species. Collectively, these mechanisms enable herbivores to discriminate among foods within a meal.

Adaptive Intake Patterns

Sorting out the quality and anti-quality attributes of forages requires keen diet selection skills by the herbivore. Successfully navigating the temporal and spatial variation of forage quality in grazing environments can be accomplished by knowing how much to eat, when to eat, and what else to eat.

Selecting a Varied Diet

Grazing animals have a strong natural propensity to select diets composed of several plant species and sample available plants on a regular basis. This behavior may increase the likelihood of ingesting necessary nutrients (Westoby 1978) and reduce the potential of overingesting toxins (Freeland and Janzen 1974). Plants contain an immense array of allelochemicals, most of which are toxic if consumed in substantial quantities (Cheek 1998). However, plants with toxins also contain varying kinds and amounts of nutrients. Thus, diet selection among toxic plants is a tradeoff between nutrient gain and potential toxicity (Freeland 1991, Provenza 1996). Mammalian herbivores possess many metabolic pathways to detoxify phytotoxins, but each pathway is generally specific to a single or a group of phytotoxins. Some scientists have suggested that by eating a variety of plants, animals spread the ingestion of toxins over several detoxification pathways (Freeland and Janzen 1974, Freeland 1991). Varied diets may also increase the amounts of some toxic foods that can be eaten because of interactions between allelochemicals that reduce toxicity (Freeland et al. 1985, Launchbaugh 1996).

Cyclic and Intermittent Intake

The toxic effects of a plant are determined largely by the amount eaten; but, the ingestion rate may also be important. Grazing animals can avoid toxicoses by limiting their consumption of a specific toxic plant each day to allow sufficient time for detoxification (Foley et al. 1995, 1999). For example, lambs limit intake of the toxin lithium chloride as a function of the amount of lithium chloride infused into their rumen before a meal (Wang and Provenza 1997). Animals might also vary toxic plant consumption daily to limit potential cumulative effects of specific toxins. Field studies with tall larkspur (*Delphinium occidentalis* S. Wats.) revealed that consumption above 25–30% of the diet for 1 or 2 days led to reduced consumption on subsequent days (Pfister et al. 1988). In pen studies, cattle responded to larkspur dosing with distinct cycles of food intake such that 1 to 3 days of higher consumption were followed by 1 to 3 days of reduced consumption (Pfister et al. 1997). Cattle have a dose-response threshold of 14 to 18 mg of toxic alkaloid/kg body weight, so periods of reduced consumption below this threshold probably allowed animals to recover from the larkspur-induced illness.

Regulating Intake of Plant Allelochemicals

Many allelochemicals may impart a distinct flavor to plants. When plant flavor and toxicity are highly correlated, herbivores apparently regulate food intake based on post-ingestive feedback and then adjust intake based on flavor intensity (Launchbaugh et al. 1993). This may explain how animals commonly choose among plant parts, individuals, or populations to select bites with lower than average amounts of phytotoxins. This behavior, summarized by Pfister (1999), has been observed to minimize consumption of cyanide (in sudangrass, *Sorghum bicolor* [L.] Moench ssp. *drummondii* [Nees ex Steud.] de Wet & Harlan*;* and bracken fern, *Pteridium aquilinum* [L.] Kuhn), tannins (in blackbrush), alkaloids (in lupine, *Lupinus spp.*; reed canarygrass, *Phalaris arundinaceae* L.; and, tall fescue), and terpenes (in sagebrush, *Artemisia spp.*). Flavor may not, however, always be a good indicator of toxicity. If toxicity changes without a change in flavor, herbivores are likely to overingest toxic plants because they are not “warned” by a flavor cue. When lambs were offered a feed with a constant flavor and variable toxic feedback, they consumed an amount based on the maximum, rather than the average, dose of the toxin (Launchbaugh et al. 1993). This response reduced the risk of lambs over-ingesting a toxin even when toxicity changes were not accompanied by flavor changes.

Detoxification and Tolerance

Animals possess several mechanisms to negate or restrict the toxic effects of plant allelochemicals once ingested. Animals may eject toxic plant material quickly after ingestion, secrete substances in the mouth or gut to render allelochemicals inert, rely on rumen microbes to detoxify allelochemicals, or absorb phytochemicals from the gut and then detoxify them in body tissues. Additionally, animals can build a tolerance to the toxic effects of some plant allelochemicals. Much has been written about animal abilities to detoxify plant substances. For more detailed reviews, see Freeland and Janzen (1974), Allison (1978), Brattsten (1979), McArthur et al. (1991), Smith (1992), and Cheeke (1998).

Ejection

Once a toxin is eaten, it is in the animals best interest to quickly get rid of it. This can be accomplished through vomition or diarrhea (Kingsbury 1983). Sheep, goats, and cattle can and will vomit in response to eating toxins (Mullenax et al. 1966, Oehme and Barrett 1986). In ruminants, vomition is problematic because animals can aspirate the gut contents into their lungs, which can be fatal. Vomiting in ruminants is apparently sensitive to dose, as some toxic plant doses resulted in vomiting, whereas higher doses produced severe retching (Mullenax et al. 1966). Horses probably do not vomit except when near death, but commonly experience diarrhea (Oehme and Barrett 1986). Diarrhea aids in rapid elimination of toxins from the gut which reduces absorption. In some episodes of diarrhea, there is a decrease in intestinal motility, further reducing the absorption of toxins.

Complex Formation

Chemical reactions during ingestion may provide protection against the effects of some plant toxins. Some browsing herbivores secrete proline-rich proteins (PRPs) in their saliva which bind to ingested tannins reducing absorption and toxic effects (Robbins et al. 1991). Interestingly, salivary proteins from generalist herbivores, like bear and deer, bind several tannins whereas proteins from specialist feeders, like moose and beaver, bind only the tannin most commonly found in their diets (Hagerman and Robbins 1993). Cheeke (1998) speculated that physical forces during ingestion might allow animals to eat more of some plants containing highly volatile chemicals, such as sagebrush. Many terpenes may be lost through volatilization during chewing as when pygmy rabbits eat sagebrush (White et al. 1982). Increased chewing and ruminating has also been weakly associated with increased sagebrush consumption in sheep (Fraker 1999). Further, nasal tissue is capable of detoxifying some toxins through induction of the P450 enzyme system (Brattsten 1979). The inducible presence of a nasal detoxification system may facilitate the consumption of some noxious-smelling plants, like tansy ragwort (*Senecio jacobaea* L.) consumed by goats and sheep (Cheeke 1998).

Some plant toxins are bound or sequestered by other ingested material that prevent toxic actions (Smith 1992). Geophagy (i.e., eating soil) is common among ungulates (Jones and Hanson 1985). Despite the widespread belief that mineral licks are sought by animals for their sodium content, it is more likely that other minerals (e.g., Ca, P, S) are more important (Jakle 1969, Jones and Hanson 1985). Detoxification pathways using sulphur are metabolically expensive and sulphur is usually in short supply (Brattsten 1979, McArthur et al. 1991). Thus, animals might practice geophagy to ingest sulphur. Moreover, mineral licks are often high in various clays (Jones and Hanson 1985) and some clays naturally bind to phytotoxins (Smith 1992). Geophagy may, therefore, deactivate some ingested plant toxins.

Degradation by Microbes

Ruminants often have a significant advantage over nonruminants when dealing with toxic plants because their large forestomach is well adapted to degrade or detoxify plant toxins (Oehme and Barrett 1986, Smith 1992, Pfister 1999). The nearly neutral pH of the rumen environment may modify a plant toxin or the toxin may be quickly diluted in the large volume (e.g., 225 to 265 liters for cattle) of the rumen. Of great significance for ingesting toxic plants is the massive number of rumen microbes which transform allelochemicals. Generally, for a rumen microbe to degrade a toxic plant compound, utilization of the compound must yield energy, and the microbial population must inhabit a particular rumen niche that allows it to survive when the toxin is not present (Weimer 1998). Microbial interactions with most phytotoxins lead to degradation or detoxification rendering the compounds inert or less detrimental. In some cases, however, rumen microbes can convert innocuous substances into toxic compounds such as the conversion of nitrite from the less toxic nitrate and the hydrolysis of cynogenic glycosides to toxic hydrogen cyanide (Allison 1978).

Tissue-level Detoxification

Once plant toxins are absorbed from the gut into the blood, they are often transported to the liver (i.e., hepatic tissue). The liver primarily and secondarily the kidney, intestinal mucosa, lungs, and skin contain enzyme systems that metabolize (or alter) toxic compounds rendering them inert (McArthur et al 1991). This biotransformation involves several enzyme systems that generally yield polar compounds that can be excreted in urine or feces. For more details on detoxification in mammalian tissue see Brattsten (1979), McArthur et al. (1991), Smith (1992), or Launchbaugh (1996).

Tolerance

The last line of defense against the deleterious effects of plant allelochemicals occurs when the tissues vulnerable to damage by an allelochcemial become less sensitive or shielded in a process called physiological tolerance (Provenza et al.1992) or target-site insensitivity (Slansky 1992). Some herbivore species or individuals are more tolerant to specific toxic plants than others. For example, sheep can tolerate and detoxify more pyrrolizidine alkaloids than cattle and it therefore takes 5 times more tall larkspur to poison sheep compared to cattle (Olsen 1978). The superior tolerance of larkspur by sheep was thought to result from differences in ruminal metabolism; however, recent studies indicate that nicotinic acetylcholine (nAch) receptors of sheep bind the larkspur toxins much less avidly than do cattle nAch receptors (Stegelmeier et al. 1999).

Influence of Previous Dietary Experience on Degradation, Detoxification, and Tolerance

The ability of a compound to restrict plant quality or cause toxicosis depends partly on the dietary experience of the herbivore. With continued consumption of a plant containing a specific allelochemical, the animal may gain an ability to overcome its negative effects (Freeland and Janzen 1974). It is well known that enzyme systems in animal tissue can increase their detoxification capacity and efficiency in the repeated presence of a toxic substrate (Freeland and Janzen 1974, Brattsten 1979). In the case of tansy ragwort alkaloids, pretreatment of animals with the alkaloid jacobine results in elevated alkaloid detoxification activity (Miranda et al. 1980). Enhanced secretion and activity of chemical complexing substances has also been observed with the production of proline-rich saliva in response to high-tannin diets (Mehansho et al. 1985, Robbins et al. 1991).

Rumen microbes may also facilitate the ability of animals to adapt to diets high in phytotoxins. Microbial populations can change rapidly depending on the substrates available for degradation (Van Soest 1994). For example, ruminants that have dietary experience with oxalate-containing plants can tolerate levels of oxalates that would be lethal to nonadapted animals (James and Cronin 1974, Allison and Cook 1981). This protection from oxalates is attributed to oxalate-degrading rumen bacteria (Allison and Cook 1981). Likewise, dietary experience with nitrate-containing plants often leads to increased tolerance of nitrates attributed to increased populations of nitrite-degrading rumen microbes (Smith 1992). Exposure to fibrous diets at a young age has also been shown to improve fiber digestibility later in life (Distel et al. 1994). These "inducible defenses" could explain why herbivores often appear less sensitive to toxic or low quality plants with continued exposure. Nonetheless, adaptation does not develop to all toxins. The effects of many toxins are cumulative and animals get progressively more poisoned as they continue to ingest plant material containing these toxins.

Influence of Animal Nutritional Status on Detoxification

Detoxification of plant allelochemicals is a metabolically costly endeavor requiring nutrients and energy to alter toxins and maintain an acid-base equilibrium (Jessop and Illius 1997, Foley et al. 1999). Improving the nutritional state of the animal can often lead to increased rates of detoxification or decreased toxic effects (Freeland and Janzen 1974, Boyd and Campbell 1983), which can lead to increased intake of foods that contain toxins (Wang and Provenza 1996). Nutrient and energy availability can influence plant toxicity by altering rates of gastro-intestinal absorption and enzymatic detoxification, availability of co-substrates for detoxification, environmental conditions in the gastro-intestinal tract or body fluids, and capacity for tolerance (Boyd and Campbell 1983, Slansky 1992, Cheeke 1998). Dietary nutrients and energy are also required to maintain healthy rumen microbial populations (Van Soest 1994) important for detoxification of many plant allelochemicals (Allison 1978).

Management Practices to Help Animals Contend with Anti-quality Attributes

The most common approaches to reducing losses caused by anti-quality factors in forage plants are to change the plant community or grazing management strategy. Poisonous plants have been sprayed and mowed; shrublands with low forage value have been treated with herbicides, mechanically altered, or burned to remove the shrubs in favor of herbaceous forages; and, toxin-free forage varieties (e.g., endophyte-free fescue) have been developed and planted. Grazing periods have also been planned to minimize negative impacts of anti-quality factors. A more contemporary approach is to change the grazing animal, rather than the vegetation, to promote or encourage the animal's natural abilities to combat anti-quality attributes. A first step in creating herds or flocks of animals that can overcome anti-quality attributes is to identify the most significant challenges that specific foraging situations present to herbivores. For example, in sagebrush-dominated communities, selecting or shaping animals with a significant ability to digest and detoxify monoterpene essential oils could greatly increase the amount of available forage. Once a foraging challenge is identified, management plans can be drafted to help animals meet this challenge.

Offer Animals Proper Early Life Experiences

Attempts to fashion animals with specific dietary attributes could begin at birth because early life experiences can strongly affect dietary habits later in life. Previous dietary experiences can influence the flavor preferences of animals (Nolte and Provenza 1992) and their ability to digest (Distel et al. 1994), detoxify (Distel and Provenza 1991, Robbins et al. 1991), and harvest (Ortega-Reyes and Provenza 1993) specific plants. Furthermore, experiences early in life often have a more lasting effect on consumption patterns than experiences later in life (Distel et al. 1994). Exposing animals to potentially troublesome plants in their youth may improve their ability to harvest, digest, and detoxify the plants when they mature.

Select Appropriate Livestock Species and Individuals

It is well known that animal species differ in diet selection and intake. For example, when juniper consumption was compared for several rangeland herbivores in Texas, a clear pattern emerged of juniper intake as follows: deer>goats>sheep>cattle (Launchbaugh et al. 1997). A simple approach to making use of low quality or toxic forages is to select a livestock species that naturally makes good use of the target plant. For example, sheep can more safely graze larkspur-infested rangeland than cattle because they are more able to survive the toxic effects of larkspur (Olsen 1978, Pfister 1999). This simple concept is however often difficult for livestock producers to enact because changing the species being raised generally requires substantial changes in fencing, livestock handling equipment, management skills, knowledge, and philosophy. A more acceptable way to assemble groups of animals with desired dietary and digestive attributes might be to select an adapted breed within a species. Research on cattle (Herbel and Nelson 1966, Winder et al. 1996), sheep (Warren et al. 1984), goats (Warren et al. 1984, Pritz et al. 1997), and horses (Mariner and Alexander 1991) has revealed that breeds differ in dietary characteristics.

Individual variation within a breed may also create a basis for selecting animals to meet specific foraging challenges. Research on the behavioral, metabolic, and production effects of anti-quality factors have consistently revealed that animals vary significantly in their response to toxic or low quality plants. Furthermore, dietary differences between animals appear to be relatively consistent through a grazing season and between years (Launchbaugh et al. 1997). Most toxic plants with acute neurological effects (e.g., larkspurs; lupines; poison hemlock, *Conium maculatum* L.; broom snakeweed, *Gutierrezia sarothrae* [Pursh.] Britton & Rusby; pine needles, *Pinus* spp.) exhibit wide variability in dose response when ingested by livestock (Pfister 1999). In future years, individual animals may be screened for response to anti-quality factors or susceptibility to toxins. For example, susceptibility to larkspur alkaloids could be tested using a muscle biopsy to indicate the binding affinity of the individual to toxic alkaloids. Using this or similar approaches, groups of animals may be assembled to access nutrients and withstand toxins in chemically defended plants.

Breed Animals with Desired Attributes

There is significant and growing evidence that the digestive and detoxification abilities of animals are heritable characteristics (Winder et al. 1995, Launchbaugh et al. 1999, Snowder et al. 2001). These inherited characteristics could influence diet selection and intake in several ways. Animals that have superior abilities to detoxify specific allelochemicals should be able to eat plants containing these phytochemicals and experience less negative feedback. A genetic basis for the detoxification abilities of animals is evidenced by the observation that detoxification of some drugs (e.g., hexobarbitol; Vessell 1968) and phytotoxins (e.g., flauoroacetates; Oliver et al. 1979, Mead et al. 1985) is strongly inherited. Dietary preferences are also influenced by inherited characteristics. Animals that are able to extract above average amounts of energy from specific plants, because of superior digestive abilities, should experience greater positive digestive feedback and form stronger and longer lasting preferences for these plants. The inheritance of enzyme systems involved in digestion is well documented (Velázquez and Bourges 1984). Differences in absorption of minerals (Green et al. 1989) and nutrients (Beaver et al. 1989) during digestion have been traced to animal breed and therefore indicate a genetic basis for digestion. Given the important role of digestive feedback in directing diet selection, it is not surprising that several studies have revealed significant inheritance values for diet patterns. A study of 60 young male Spanish goats in Texas showed dietary similarities between sire groups even though all goats were raised in a similar environment (Warren et al. 1983). A more recent study with Spanish x Boer cross goats revealed that the consumption of juniper by free-ranging goats had a heritability of .28 (C.A. Taylor, unpublished data). In other words, 28% of the variation in juniper consumption could be attributed to goat sire. Winder et al. (1995) reported significant heritability estimates for consumption of several range plants by Brangus cattle in New Mexico. Examination of big sagebrush consumption by more than 400 Rambouillet ewes over 2 years concluded that 25–28% of individual variation in sage consumption was heritable (Snowder et al. 2001). These studies point clearly to the possibility of breeding animals to overcome the challenges of specific anti-quality attributes.

Offer Nutritional or Pharmaceutical Products to Aid in Digestion and Detoxification

The examination of anti-quality factors in plants often focuses on the biological mechanisms by which phytochemicals impact animal production. In several cases, these examinations led to the development of “antidotes” that help herbivores disarm specific allelochemicals or survive their biological assaults. For example, understanding the specific action of fescue alkaloids lead to the development of a compound (i.e., a dopamine antagonist) that blocks metabolic effects of the alkaloid (Aldrich et al. 1993). Supplementation of calcium can improve survival of sheep grazing halogeton (*Halogeton glomeratus* [Bieb.] C.A. May) infested rangeland because rumen microbes detoxify oxalates in halogeton by forming insoluble calcium oxalates that are excreted in the feces (James and Cronin 1974). Increased levels of dietary sulfur (Conn 1979) and vitamin B_{12} (Brattsten 1979) have been shown to decrease the formation of hydrogen cyanide from cyanogenic glycoside containing plants. The toxic effects of larkspur alkaloids can be counteracted by injections of the cholinergic drug, physostigmine (Pfister et al. 1994). The complexing action of some allelochemicals, such as tannins, can be surmounted by supplementing animals with compounds such as polyethylene glycol that bind with the ingested phytochemicals before they can bind dietary and microbial proteins (McNabb et al. 1993). Simply improving the nutritional state of animals can often lead to increased rates of detoxification and decreased toxic effects (Freeland and Janzen 1974, Foley et al. 1995), which can lead to increases in intake of foods that contain toxins (Wang and Provenza 1996).

Development of vaccines to inoculate animals against specific plant toxins is becoming a reality. Recent work in Australia (Edgar et al. 1998) and in the U.S. (Lee and Stegelmeier, personal communication) indicate that commercial vaccines against some plant toxins (e.g., pyrrolizidine alkaloids) are feasible. One ancillary benefit of developing toxin-protein conjugates for vaccines is the concurrent use of such conjugates for immunoassays that will be useful for field-based assessment of toxin concentrations.

Conclusions

Foraging on rangelands and pasture poses several significant challenges to the herbivores. Grazing animals must utilize the nutritional value of plants to evade starvation, gain weight, and produce young while avoiding and negating the anti-quality attributes that are an implicit component of almost all forages. Livestock management in these situations can be significantly challenging. Developing grazing plans to minimize the impacts of plant anti-quality attributes requires an understanding of the behavioral and metabolic mechanisms that herbivores employ to extract nutrients from low quality or chemically-defended plants. New frontiers in forage and grazing management therefore lie in understanding the basics of animal behavior, digestion, and metabolism in relation to anti-quality characteristics. Understanding animal response to anti-quality factors in plants will, by necessity, focus on the consequences of consumption; a simple idea with immensely complex implications.

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Animal health problems caused by silicon and other mineral imbalances

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Abstract

Plant growth depends upon C, H, O, and at least 13 mineral elements. Six of these (N, K, Ca, Mg, P, and S) macro-elements normally occur in plants at concentrations greater than 1,000 mg kg^{-1} level. The remaining micro-elements (B, Cl, Cu, Fe, Mn, Mo, and Zn) normally occur in plants at concentrations less than 50 mg kg^{-1}. Trace amounts of other elements (e.g., Co, Na, Ni, and Si) may be beneficial for plants. Silicon concentrations may range upwards to 50,000 mg kg^{-1} in some forage grasses. Mineral elements required by animals include the macro-elements Ca, Cl, K, Mg, N, Na, P, and S; the trace or micro-elements Co, Cu, Fe, I, Mn, Mo, Se, and Zn; and the ultra-trace elements Cr, Li, and Ni. When concentrations of these elements in forages get 'out of whack' their bioavailability to animals may be jeopardized. Interactions of K x Mg x Ca, Ca x P, Se x S, and Cu x Mo x S are briefly mentioned here because more detail will be found in the literature. Limited published information is available on Si, so we have provided more detail. Silicon provides physical support to plants and may reduce susceptibility to pests. However, Si may have negative effects on digestibility and contribute to urinary calculi in animals.

Key Words: Forage, mineral interaction, mineral requirements, mineral nutrition, ruminant diets.

Resumen

El crecimiento vegetal depende del C,H,O y al menos de 13 elementos minerales mas. Seis de estos macroelementos (N, K, Ca, Mg, P y S) normalmente ocurren en las plantas en concentraciones mayores a 1000 mg kg^{-1}. El resto de los elementos (B, Cl, Cu, Fe, Mn, Mo, y Zn) normalmente se encuentran en las plantas en concentraciones menores a 50 mg kg^{-1}. Cantidades traza de otros elementos (por ejemplo, Co, Na, Ni y Si) pueden ser benéficas para las plantas. En algunos zacates forrajeros las concentraciones de silicio pueden variar hasta 50,000 mg kg^{-1}. Los elementos minerales requeridos por los animales incluyen los macroelementos Ca, Cl, K, Mg, N, Na, P y S, los elementos traza o microelementos Co, Cu, Fe, I, Mn, Mo, Se y Zn y los elementos ultra-traza Cr, Li y Ni. Cuando las concentraciones de estos elementos en los forrajes alcanzan proporciones altas su biodisponibilidad puede estar en peligro. Las interacciones de K x Mg x Ca, Ca x P, Se x S, y Cu x Mo x S se mencionan brevemente aquí porque en la literatura seran encontrados mas detalles. La información publicada disponible sobre Si es limitada por lo que nosotros damos mas detalle de ello. El silicio provee un soporte físico a las plantas y puede reducir la susceptibilidad a las plagas. Sin embargo, el Si puede tener efectos negativos en la digestibilidad y contribuir a formar cálculos urinarios en los animales.

Simple deficiency or excess of dietary mineral elements may cause animal health concerns. In addition there are known imbalances among elements that directly or indirectly affect bioavailability of other elements (Grace and Clark 1991, Grace 1994). Through out the review, reference will be made to ruminant mineral requirements as given in Table 1. Nearly all mineral elements, whether essential or nonessential, can adversely affect an animal if included in the diet at excessively high levels (Gough et al. 1979, NRC 1980). Forage, concentrates, mineral supplements, and drinking water serve as sources of consumed mineral elements. Soil ingestion provides yet another source of soluble or extractable mineral elements (Mayland et al. 1975). The connection between minerals in the diet and health of animals has been previously covered by others, including Harris et al. 1989, Kabata-Pendias and Pendias 1992, Mayland and Cheeke 1995, Nicholas and Egan 1975, Reid and Horvath 1980, Spears 1994. This paper will generally overlook simple cases of deficiency or toxicity. Instead it emphasizes mineral interactions leading to mineral imbalances and subsequent animal health problems. Silicon will be discussed in more detail since current coverage is sparse.

Silicon

Silicon receives major emphasis in this review because its role in forage and animal nutrition has not been greatly investigated. Silicon uptake, and subsequent deposition on leaf cell-wall, and especially on the leaf perimeter provides physical support to plants. Silicon deposits also reduce susceptibility to insect and fungal attack and may also reduce animal preference or palatability for certain plants (Jones and Handrek 1967, Shewmaker et al. 1989). There is unpublished work (Mayland, unpublished) suggesting a negative relationship between forage Si and digestibility of forage. In preliminary, unverified experimentation he found that in vitro dry matter digestibility of forage grasses was decreased 4 units for each unit of Si present in the forage. Shewmaker et al. (1989) suggest the following as possible roles of Si on digestibility. Once eaten, Si may reduce digestibility of forage by 1) acting as a varnish on the plant cell wall and reduc-

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Table 1. Nutrient element concentrations normally found in cool–season grasses and legumes and their requirement by sheep and cattle.

	Concentrations in Forages[1]		Dietary requirements[2]	
Element	Grasses	Legumes	Sheep	Cattle
(g kg^{-1})				
Calcium, Ca	3– 6	3– 14	3–4	3–4
Chlorine, Cl	1– 5	1– 5	1	2
Magnesium, Mg	1– 3	2– 5	1	2
Nitrogen, N	10–40	10– 50	10–15	10– 5
Phosphorus, P	2– 4	3– 5	2	2
Potassium, K	10– 30	20–40	3	8
Silicon, Si[3]	10– 40	0.5–1.5	requirement not established	
Sodium, Na[3]	0.1 – 3.0	0.1– 2	1	2
Sulfur, S	1–4	2– 5	1–2	1– 2
(mg kg^{-1})				
Boron, B	3–40	30– 80	requirement not established	
Copper, Cu	3–15	3– 30	5–6	7 – 10
Fluorine, F[3]	2–20	2– 20	1– 2	1 – 2
Iron, Fe	50–250	50– 250	40	40
Manganese, Mn	20–100	20– 200	25	25
Molybdenum, Mo	1–5	1–10	<0.1	<0.1
Zinc, Zn	10– 50	15 – 70	25 – 40	25 – 40
(µg kg^{-1})				
Cobalt, Co[3]	50–300	200–300	100	60
Chromium, Cr[3]	200–1000	200– 1000	Trace	Trace
Iodine, I[3]	40– 800	40– 800	500	500
Nickel, Ni	200–1000	200–1000	60–70	60–70
Selenium, Se[3]	50–200	50–200	30–200	40–300

[1] Herbage data are generalized from Fageria et al. (1991), Gough et al. (1979), Jones and Thomas (1987), Marschner (1986), Mayland (unpublished), Mays (1974), and Reid and Jung (1970)

[2] Animal data are generalized from Grace (1994), Grace and Clark (1991), Jones and Thomas (1987), NRC (1980). F, while not required by animals is beneficial to bones and teeth. Dietary requirements are for growing sheep and lactating cattle. Requirements may be different for other animal classes.

[3] Required by animals but not grasses or legumes.

ing accessibility to rumen microflora, 2) complexing trace elements like Zn and reducing their availability to rumen microflora, or 3) complexing enzymes that are integrally involved in rumen metabolism.

Silicon (Si) is absorbed as monosilicic acid [$Si(OH)_4$] by plant roots, transported throughout the plant, and deposited primarily in epidermal cells, stoma and trichomes of leaves (Jarvis 1987). Some of this Si remains in soluble forms. Most Si, however, is incorporated into or onto the cell wall structure or precipitated with other elements to form amorphous crystalline deposits called phytolyths (Blackman and Bailey 1971, Moore 1984). [The structure, shape, and color of plant phytolyths differ among grass genera and may be used for classification purposes in archeological sites.] Silicon uptake is largely passive, i.e., taken up with the transpiration stream, however, recent evidence has demonstrated that some energy mediated uptake of Si occurs in grasses (Jarvis 1987, Mayland et al. 1991).

The incorporation of Si into scabrous tissue is perceived as a defense mechanism against some insects (Moore 1984) and possibly against grazing by large herbivores (McNaughton et al. 1985). Silicon taken up by forage plants may also reduce rumen microbial accessibility to cell wall structure (Smith and Nelson 1975, Harbers et al. 1981), thereby reducing apparent digestibility of herbage (Van Soest and Jones 1968). Mika (1986) reported that a water-soluble form of Si inhibits activity of cellulases and other digestive enzymes, whereas the insoluble form is chemically inert. Thus, exogenous Si from ingested soil or dust adhering to herbage probably has little direct effect on digestibility.

Silicon, in addition to affecting forage quality, is implicated in animal health (Jones and Handreck 1967). In some early research, urolithiasis in steers was related ($r^2 = 0.56$) to Si concentrations in Montana forage grasses (Parker 1957). However, Bailey (1976) later reported that frequency of urinary calculi encountered in Alberta cattle was inversely related to urine volume and water intake. This cause and effect relationship has not been resolved. Ingestion of certain Si minerals may increase the rate of tooth wear, thus reducing the effective lifetime of grazing animals (see also Soil Ingestion).

Shewmaker et al. (1989) determined the Si concentration in 31 accessions of C-3 grasses and the relationship of Si concentration to sheep preference. Silicon concentrations in leaves increase with advancing phenological maturity and are greatest in leaves, intermediate in inflorescences, and least in stems. Awns contain high concentrations of Si. Silicon concentrations in leaves of *Agropyron*, *Pseudoroegneria*, and *Thinopyrum* increase at nearly twice the rate of those in *Critesion*, *Hordeum*, *Leymus* and *Psathyrostachys* (Fig. 1). *Elymus* leaves contain higher concentrations of Si at the vegetative stage than other groups, but the accumulation rate is intermediate.

Silicon is much more soluble in NDF than ADF extractions (Shewmaker, et al.1989). They found that in vegetative grass, about 32% of total leaf Si remains in the NDF residue. However, about 76% remains in the ADF residue. Some of the Si is insoluble in both extracts. These insoluble portions of Si increase with aging. Preference relates to estimated dry matter digestibility at boot and anthesis, but is not related to fiber or Si measurements.

Leaf Si concentration ranges from 7 g kg^{-1} in *Hordeum* to 47 g kg^{-1} in bluebunch wheatgrass (*Pseudorogneria spicata* = *Agropyrum spicatum* [Pursh] Scribn. & Smith). Indian ricegrass (*Oryzopsis hymenoides* (Roemer & J.A. Schultes) ex Piper) contains 25 g Si kg^{-1} in leaves at the anthesis stage. Medusahead (*Elymus caput-medusae* L.) is very unpalatable and contains up to 113 g Si kg^{-1}, whereas cheatgrass (*Bromus tectorum* L.) contains 44 g Si kg^{-1} (Bovey et al. 1961).

Silicon accumulation in 3 groups of grasses as a function of growth stage is shown in Figure.1. The wheatgrasses (group 1) generally reach physiological maturity quicker than wildryes (with the exception of Russian wildrye) and wild barleys (group 2). Group 1 plants tend to have fewer leaves, which on average may be chronologically older than leaves of group 2 plants. These older leaves of group 1 plants may have higher concentrations of Si because passively-transported Si, taken up as a soluble component in the transpiration stream, accumulates for a longer time in leaves or because of differences in active transport (requiring energy) of Si from roots to leaves.

Silicon in tall fescue and its relation to cattle preference.

In our studies of cattle preferences among tall fescue cultivars, preference scores were not related to soluble or insoluble Si in ADF and NDF residue, nor to total Si at any phenological stage (Mayland, unpublished). Thus, cattle preference for these grasses is a function of factors other than Si components. There is

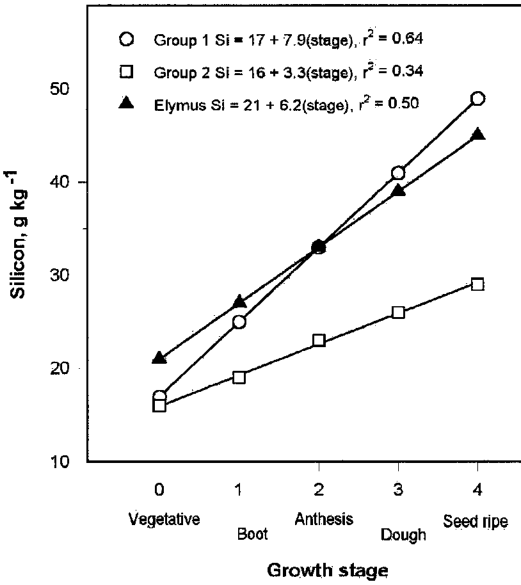

Fig. 1. Leaf silicon (Si) accumulation in C–3 grasses as predicted by growth stage. Group 1 genera include *Thinopyrum, Agropyron,* and *Pseudoroegneria,* the wheatgrasses. Group 2 genera include *Critesion, Hordeum, Psathyrostachys,* and *Leymus,* wild–barley and wildrye. Data are adapted from Shewmaker et al. 1989.

evidence that Si concentration is higher in grazed plants than ungrazed plants on the Serengeti (McNaughton and Tarrants 1983) and in western wheatgrass (*Pascopyrum smithii = Agropyrum smithii* [Rydb.] A. Love) on the northern plains (Brizuela et al. 1986). Brizuela also reports that hand-defoliated little bluestem (*Schizachyrium scoparium* [Michx.] Nash) contains lower Si concentrations than non-defoliated plants. The different Si concentrations may be a result of grazing-induced ecotypic differentiation (Detling and Painter 1983). The theory that Si is a short-term defense against large herbivores is clouded by the interaction with increased nutritional value of regrowth forage over initial forage.

Magnesium x Potassium x Calcium

Hypomagnesemic grass tetany is probably the most important metabolic problem in ruminants caused by mineral imbalances (Mayland 1988). It is characterized by low blood plasma Mg concentrations (<0.4 mmol liter^{-1}) and most assuredly by low urinary Mg concentrations (< 0.8 mmol liter^{-1}). Although 2 g Mg kg^{-1} DM is adequate to meet Mg requirements in most situations, cows and ewes near parturition and continuing into lactation, may need extra Mg (10 to 30 g Mg cow-day^{-1}, 2 to 3 g Mg ewe-day^{-1}).

Magnesium absorption by both plants and ruminants is negatively affected by K. That interaction is the basis for the K/(Mg+Ca) ratio in forages that provides a risk index. Calcium may counter some of the effects of K on Mg absorption. The risk of grass tetany increases exponentially when the herbage K/(Ca+Mg) increases above 2.2 (expressed as moles of charge basis). Other factors that reduce Mg availability to ruminants include high concentrations of N and low concentrations of total soluble carbohydrate. Prudent use of N and K fertilizers is warranted to minimize risk of grass tetany (Mayland and Wilkinson 1989, Mayland et al. 1990). Aluminum in acid soil solutions may also reduce Ca and Mg uptake by cool season grasses and increase susceptibility to grass tetany (Rengel and Robinson 1989). Restoring available soil P to concentrations adequate for good plant growth has also elevated Mg and Ca concentrations in grass leaves (Reinbott and Blevins 1994).

Severity of economic livestock losses can be reduced by delaying early spring use of grass pastures, grazing with stocker and dry cows, and supplementing animals with soluble Mg. The Mg may be provided in drinking water, licks, salt, or perhaps as a dust on the forage. On acid soils; liming with Ca-Mg limestone (dolomite) rather than calcium limestone (calcite) would increase Mg availability to plants and likely to grazing animals. The method chosen will be greatly dependent on local conditions.

An alternative to fertilization or direct supplementation is to increase Mg in forage through plant breeding (Sleper et al. 1989). Progress has been made with Italian ryegrass *(Lolium multiflorum* Lam.) (Moseley and Baker 1991, Moseley and Griffiths 1984), perennial ryegrass (*Lolium perenne* L.) (Binnie et al. 1996), and tall fescue (Mayland and Sleper 1993, Crawford et al. 1998). The new cultivars have resulted in reduced values of K/(Mg+Ca) in forage, increased levels of blood plasma Mg in animals, and in high risk situations these high magnesium cultivars have reduced the incidence of grass tetany death losses by grazing animals.

Potassium levels of 28 g kg^{-1} DM in herbage will provide near maximum herbage yield of cool-season grasses. However, increases in solution K concentration reduce uptake of both Ca and Mg by plants, even at higher solution K levels resulting in less than maximum forage yield. Smith et al. (1985) reported that Mg concentrations level out at 1.9 g kg^{-1} when herbage contains $\geq$ 25 g K kg^{-1}; whereas Ca concentration continues to decrease to a low of 6 g kg^{-1} as forage K increases to 65 g K kg^{-1}. High herbage K levels also depresses Mg and Ca absorption by ruminants.

On the other hand, K concentrations in dry-mature or winter grass (standing or harvested) may be inadequate for cattle requirements. This may occur because of weathering and leaching of K from the curing forage. Minimum critical levels for cattle are in the range of 5–10 g kg^{-1}. During summer, 20 g K kg^{-1} DM may be desired to reduce heat stress in cattle. *Prudent applications of fertilizer K are required to meet plant growth requirements, and not aggravate the risk of lowered Mg and Ca uptake by plants and absorption by animals.*

Calcium x Phosphorus

Milk fever or parturient paresis, is characterized by low blood Ca (<1.0 mmol liter^{-1}). It occurs during late pregnancy and onset of lactation. This situation can occur even though herbage contains 4.4 g Ca kg^{-1} DM. Animals must be treated parenterally with Ca for several days. Calcium:phosphorus ratio of 2:1 (wt:wt) is ideal, but 8:1 has been tolerated. In extreme situations, cattle and sheep may be observed chewing on bones. This behavior may be indicative of a P deficiency. Animal nutritional guides generally discuss ratios of Ca:P rather than absolute dietary concentrations.

Sulfur x Selenium

A blind staggers, or more correctly, polioencephalomalacea may occur if ruminants ingest excess sulfate sulfur (James et al. 1994, Mayland 1995, O'Toole et al. 1996). This occurs when ruminant organisms reduce SO_4 to the toxic H_2S form. Sulfate in drinking water should be considered suspect in these cases (Mayland 1995). Interactions of S x Se may occur when S fertilization results in forage crop yield response. The reduced Se absorption by the plant may occur because of a direct competition of S reducing the uptake of Se or may occur by dilution of Se in the plant (Mayland and Robbins 1994, Wu and Huang 1991).

Selenium

Selenium is needed for animal health in low concentrations but is toxic at high. It may occur in high to toxic (to animals) levels in herbage grown on Cretaceous geological soils, especially in the Central Plains of North America. In other areas, herbage Se concentrations may be inadequate for animal requirements. Dietary Se requirements range from 0.03 to as much as 1.0 mg Se kg^{-1} DM. The amount is dependent upon the class of animal and levels of vitamin E, S, and other factors present in the diet. The effect of Se is complemented to some extent by that of vitamin E. High levels of dietary S will counter the availability of Se to ruminants. Whole blood Se concentrations should be greater than 250 nmol $liter^{-1}$.

Selenium is the only mineral whose supplementation of food animals is regulated by the US Food and Drug Administration (FDA 1993). Effective 13 September 1993, the FDA permitted an increase of 0.1 mg Se kg^{-1} (as sodium selenite or sodium selenate) in complete feeds for animals. The use of Se boluses is not permitted. Congress and U.S. President Clinton suspended the FDA action until 31 December 1995 (Gloyd 1994). Thus, during 1995, animal and fowl feeds could contain 0.3 mg Se kg^{-1} and the osmotic Se bolus for cattle could be used as a source of Se. These on-again, off-again, changed-again regulations have not satisfactorily met Se nutrition needs of animals. The current status is that none of the regulations adequately consider the level nor bioavailability of Se in naturally occurring feedstuffs. Selenium deficiency causes white muscle disease, ill thrift, and reduced fertility, in animals. Alkali disease and acute toxicosis (selenosis) may occur when animals ingest excess Se (> 5 mg kg^{-1}) (Mayland 1994).

Copper x Molybdenum x Sulfur x Iron

Copper deficiencies may occur in grazing animals (Baker and Ammerman 1995). Reduced bioavailability of Cu occurs in the presence of increased intake and bioavailability of Mo, S, and Fe. The formation of thiomolybdates in the gut, reduces absorption of Cu by animals (Baker and Ammerman 1995). Dietary Cu intake should be decreased in those areas where herbage Mo levels are extremely low. When Mo levels are high as they might be in some meadow soils, then Cu supplementation should be increased. Copper requirements for cattle are about twice those for sheep. Several incidences of Cu toxicity in grazing sheep have been reported on recently manured pastures. These are associated with swine or poultry manures from operations where Cu-anthelmintics are used for control of intestinal parasites (McDowell 1992, Suttle and Price 1976). Copper bioavailability differs among some grasses as Stoszek et al. (1986) showed for cattle grazing tall fescue or quackgrass. Nutritionists should be alert to signs of Cu deficiency or toxicity in animals, because of the many opportunities for interaction that affect Cu bioavailability.

Cobalt, Fluorine, Iodine

The Co requirements for sheep are about twice those for cattle (Henry 1995). Lambs are most sensitive to Co deficiency. Fluorine in concentrations of 1 to 2 mg F kg^{-1}, while not required by animals, is beneficial for high tooth and bone density. Concentrations of 4 to 8 mg F kg^{-1} will cause brown staining of tooth enamel and concentrations greater than 8 mg F kg^{-1} will reduce tooth and bone density and increase tendency for breakage. Drinking water is the primary source of F. Sprinkle irrigation of forages, using high F water, is another way in which animals may ingest excess F (Wallender and Keller 1984). High F is often associated with thermal water and with rock phosphates used for supplemental P in rations. The F intake may not be a problem for adult animals. However, for young growing stock intake of excess F will weaken tooth and bone formation and livestock men should consider growing these animals in other areas where F intake is much less (Mayland, personal experience).

Animal performance can be good on pastures containing 0.3 mg I kg^{-1} DM, however, the northern half of the U.S. and Canada is generally I-deficient (McDowell 1992, Miller and Ammerman 1995). Salt (NaCl) is a common carrier of supplemental I for both human and domestic livestock and will be identified as iodized salt (Miller and Ammerman 1995). Dietary intakes of 1 to 2 mg I kg^{-1} DM must be considered when animals are eating goitrogenic plants like turnips and other *Brassica species* (Miller and Ammerman 1995).

Ultra-Trace Elements

The elements Al, As, Cr, Ni, V, Sn are presumed essential for ruminants although research data are not available. If required, the dietary concentrations must be extremely low. Using the definition of essentiality for plants; one might also add Ba, Br, F, Rb, and Sr. We have measured <0.5 mg Cd kg^{-1} DM and 0.5 to 6 mg F kg^{-1} DM in grass herbage. We are currently not aware of any factors that might affect the bioavailability of these ultra-trace elements. Several of these elements, if required by plants and animals, must be at such low concentrations in nutrient culture or in diet that it is difficult to conduct a sufficiently 'clean environment' to test their essentiality.

Interaction with Immunological Requirements

The mineral element requirement of animals is defined as the amount of bioavailable nutrient in the diet required for growth and reproduction and further that the element is the only component that can meet that animal's needs. There is increasing evidence (Mayland et al. 1987) suggesting that for some trace elements, a higher concentration of the element may be needed for maintaining the animal's immune system than is currently considered as required for good growth and performance. Experimental results, however, are mixed and possibly animal species dependent (Ward and Spears 1999). Further experimentation is required to substantiate the role of trace element requirements and the development of full immunological response levels.

Soil Contamination of Forage Soil Intake by Animals

Mineral element concentrations of analyzed herbage samples may be significantly biased by the presence of dust or soil adhering to the material (exogenous components). Such contamination is reflected by plant sample Fe concentrations greater than 250 mg kg^{-1} DM (Mayland and Sneva 1983). Laboratory personnel in the senior author's lab routinely use a level of 400 as a threshold indicator of possible soil contamination of plant samples. Soil contamination on herbage may elevate the intake of Fe, Mn, Se, Co, and other elements above the true elemental composition of the herbage. Direct soil ingestion by animals may also affect the intake of some mineral elements (Mayland et al. 1975, 1977, Sneva et al. 1983). This source of mineral elements may be important when studying trace element responses of free grazing livestock (Mayland et al. 1980). In some situations the eating of soil (a form of geophagia) is an attempt to provide a dietary buffer. In horses, it is often a behavioral response to boredom with the subsequent risk of developing an irritating and sometimes fatal case of sand collic.

Ingested soil can have another impact on animal health as is seen in the following case. Breeding cattle from one area of the Great Basin, contrasted to cattle from other areas, are routinely discounted when sold through the regional livestock auction barn. This discounting occurs because of a significantly greater loss or wearing of teeth. These animals may ingest more soil than others. A check of surface minerals from those grazing lands indicate a hardness (Moh scale) much greater than tooth enamel and thus minerals in the ingested soil serve as an abrasion to the enamel. Tooth enamel is apatite with a rating of 5, whereas talc is rated 1 and diamond is rated 10. Soil minerals range several points above or below 5.

Urolithiasis

Male sheep or cattle are more prone to kidney stones when the dietary Ca:P is less than 2:1 or ingested Si is high and water intake is limited (Bailey 1976). Supplementing Ca will reduce the incidence of this problem only if the stones are analyzed as containing high concentrations of P. Providing adequate and quality drinking water will reduce the incidence of silicosis.

Summary

Discussions of mineral nutrition of forage plants and forbs must include the elemental needs of both plant and grazing animal. Grasses require 6 macronutrients (N, K, Ca, Mg, P, and S) in concentrations exceeding 1,000 mg kg^{-1}. They also require 7 micronutrients (B, Cl, Cu, Fe, Mn, Mo, and Zn) in concentrations ranging from 0.1 to 50 mg kg^{-1}. Some ultratrace elements like Ni, Co, Si, and Na may also be needed by cool-season grasses.

Grazing animals require 8 macronutrients. This list includes the same 6 needed by plants plus Na and Cl. Animals require some of the same micronutrients as plants (Cu, Fe, Mn, Mo, and Zn) plus Co, I and Se. Animals may also require ultratrace quantities of Cr, Li, and Ni.

Grasses may exhibit macronutrient deficiencies but seldom suffer from micronutrient deficiencies. However, they may not provide sufficient macronutrients (N, Ca, Mg, P, and S), micronutrients (Cl, Cu or Zn), or other elements (I, Na or Se) and thus fail to meet the animal's nutritional needs. Paddocks of cool-season grasses are often fertilized with N and K. If N-fixing legumes are present then P may be applied to these paddocks and N fertilization is omitted. Grazing animals are generally supplemented with NaCl and may also receive additional amounts of I, Se, Zn, and Co trace mineral to supplement their forage diets. Ruminants may also receive supplementary Mg where there is considerable risk of grass tetany.

Often grass and forb diets will contain nutrient levels considered adequate, but the bioavailability of some minerals may be reduced because of interactions like K x Mg, Mo x Cu x S, and S x Se. Split applications of K fertilizer will minimize the impact of high K levels on Mg availability to the plant and subsequent animal.

Forages in some geographic areas contain sufficient mineral nutrients to maintain herbage growth, but there may be an insufficient amount of Cu, Mg, Se (not needed by plants), or Zn to meet animal requirements. For example, tall fescue is well adapted to many areas of the U.S. Soils in these areas contain little plant-available Se and plants growing on them may not take up sufficient Se to meet animal requirements (McQuinn et al.1991). Management programs that allow for direct or indirect supplementation of these nutrients to the animals should be considered.

Knowledge of mineral element requirements of forages plants and grazing animals is essential to understand the complex interactions that one element may have on another.

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Alkaloids as anti-quality factors in plants on western U.S. rangelands

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Abstract

Alkaloids constitute the largest class of plant secondary compounds, occurring in 20 to 30% of perennial herbaceous species in North America. Alkaloid-containing plants are of interest, first because alkaloids often have pronounced physiological reactions when ingested by livestock, and second because alkaloids have distinctive taste characteristics. Thus, alkaloids may kill, injure, or reduce productivity of livestock, and have the potential to directly or indirectly alter diet selection. We review 7 major categories of toxic alkaloids, including pyrrolizidine (e.g., *Senecio*), quinolizidine (e.g., *Lupinus*), indolizidine (e.g., *Astragalus*), diterpenoid (e.g., *Delphinium*), piperidine (e.g., *Conium*), pyridine (e.g., *Nicotiana*), and steroidal (*Veratrum*-type) alkaloids. Clinically, effects on animal production vary from minimal feed refusal to abortion, birth defects, wasting diseases, agalactia, and death. There are marked species differences in reactions to alkaloids. This has been attributed to rumen metabolism, alkaloid absorption, metabolism, excretion or directly related to their affinity to target tissues such as binding at receptor sites. In spite of alkaloids reputed bitter taste to livestock, some alkaloid-containing plant genera (e.g., *Delphinium*, *Veratrum*, *Astragalus*, *Oxytropis*, and *Lupinus*) are often readily ingested by livestock. Management schemes to prevent losses are usually based on recognizing the particular toxic plant, knowing the mechanism of toxicity, and understanding the temporal dynamics of plant alkaloid concentration and consumption by livestock. Once these aforementioned aspects are understood, losses may be reduced by maintaining optimal forage conditions, adjusting grazing pressure and timing of grazing, aversive conditioning, strategic supplementation, changing livestock species, and herbicidal control.

Key Words: poisonous plants, plant toxins, forage quality, diet selection, grazing management

Resumen

Los alcaloides constituyen la clase mas grande de compuestos secundarios de las plantas y ocurren en un 20 a 30% de las especies herbáceas perennes de Norte América. Las plantas que contienen alcaloides son de interés, primero porque cuando el ganado consume alcaloides a menudo producen pronunciadas reacciones fisiológicas y segundo porque tienen caracteristicas distintivas de sabor. Así, los alcaloides pueden matar, dañar o reducir la productividad del ganado y tienen el potencial para alterar directa o indirectamente la selección de la dieta. Revisamos 7 categorías principales de alcaloides tóxicos, incluyendo pirrolizidinae (por ejemplo, *Senecio*), quinolizidina (por ejemplo, *Lupinus*), indolizidina (por ejemplo, *Astragalus*), diterpenoide (por ejemplo, *Delphinium*), piperidina (por ejemplo, *Conium)*, pyridina (por ejemplo, Nicotiana), and esteroidal (tipo *Veratrum*). Clínicamente, los efectos de los alcaloides sobre la producción animal varían desde el rechazo mínimo del alimento al aborto, defectos de nacimiento, enfermedades mermantes, agalacia y la muerte. Hay marcadas diferencias entre especies en cuanto a las reacciones a los alcaloides. Esto has sido atribuido al metabolismo del rumen, la absorción del alcaloide, el metabolismo, la excreción o directamente relacionado a su afinidad con los tejidos blanco, tal como fijarse en sitios receptores. A pesar de que los alcaloides tiene reputación de ser de sabor amargo para el ganado, algunos géneros de plantas que contienen alcaloides (por ejemplo, *Delphinium*, *Veratrum*, *Astragalus*, *Oxytropis* y *Lupinus*) a menudo son ingeridas por el ganado. Los esquemas de manejo para prevenir perdidas usualmente son basados en reconocer una planta tóxica en particular, conociendo el mecanismo de toxicidad y entendiendo las dinámicas temporales de la concentración de alcaloides en la planta y su consumo por el ganado. Una vez los aspectos antes mencionados son entendidos, las perdidas se pueden reducir manteniendo condiciones forrajeras óptimas, ajustando la presión y tiempo de apacentamiento, induciendo un condicionamiento aversivo, utilizando suplementación estratégica, cambiando las especies de ganado y controlando las especies toxicas con herbicidas

Alkaloids are a chemically-diverse group of plant compounds with widely varying biological activities when consumed. Although most effects are thought to be detrimental, many alkaloids have been developed into beneficial drugs and pharmaceuticals. Range plants that contain alkaloids, poison more livestock worldwide than any other class of toxic compounds. The economic loss to the livestock industry specifically from alkaloid-containing plants is not known, but livestock losses in cattle and sheep in the western states to all toxic plants are estimated to exceed $340 million (Nielsen et al. 1988), not including horses

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Table 1. Direct and indirect economic losses from poisonous plants related to production and off take from domestic livestock and wildlife. Alkaloid-containing plants are responsible for the majority of livestock losses to poisonous plants worldwide.

Direct losses	*Indirect losses*
Death	Added fencing to restrict access
Wasting/reduced weight gains	Herding costs
Neurological incapacitation (horses)	Supplemental feeding
Abortions	Changes in grazing management
Weak/small offspring	Increased veterinary costs for treatment
Reduced fertility	Lack of immune response to vaccines
Birth defects	Lost opportunity to graze forage
Inability to sell/harvest animals	Lost nutrients in ungrazed forages
	Reduced land values
	Reduced value of grazing permits
	Herbicide costs for suppression
	Increased risk in overall enterprise

and goats. This estimate includes only death and reproductive losses (e.g., abortions), but other indirect costs also impact the livestock industry (Table 1). Our objective is to scrutinize the effects of alkaloid-containing plants on livestock production on western rangelands and outline management solutions. We sequentially review 7 major categories of toxic alkaloids, including pyrrolizidine, quinolizidine, indolizidine, diterpenoid, piperidine, pyridine, and steroidal alkaloids.

Alkaloids—Definition and Distribution

Alkaloids are difficult to define because of their diversity, but the alkaloid chemist S.W. Pelletier (1983) defined alkaloids as “a cyclic organic compound containing nitrogen...” The presence of a nitrogen atom usually makes alkaloids basic, as suggested by their name. Alkaloids are classified by their heterocylic ring structure and the location of the nitrogen atom in the ring. Ring structure is important because specific structural features are responsible for the biological activity of the individual compounds. Some alkaloids possess a close structural similarity with neurotransmitters such as acetylcholine (Ach), dopamine and serotonin. This structural similarity partially explains the toxicity of some alkaloids in the central nervous system (CNS).

Alkaloids occur in about 20% of all vascular plants, with most found in dicotyledons (Hegnauer 1963, 1988, Hazlett and Sawyer 1998). More than 33% of annual herbs in North America contain alkaloids (Levin 1976). Fortunately for livestock producers, the only monocotyledon family with significant (> 0.05% of dry weight) alkaloid concentration is Liliaceae (Robinson 1979). Obviously, this statement ignores alkaloids in monocots produced by fungal endophytes (see Thompson et al. this volume). The major alkaloid-containing plants on western ranges are classified by the type of alkaloid they contain (Table 2).

Do Alkaloids Alter Diet Selection?

Alkaloids are reported to taste bitter (Bate-Smith 1972). Garcia and Hankins (1975) argued that animals acquire natural aversions to most alkaloids because bitter taste is often linked with toxicity. Some forage plants such as reed canarygrass (*Phalaris arundinaceae* L.) and certain lupines (*Lupinus* spp.) are unpalatable because of high alkaloid concentrations (Ralphs and Olsen 1987). Nonetheless, Robinson (1979) and Glendinning (1994) concluded that alkaloids are not universally repellent to herbivores. Additionally, Molyneux and Ralphs (1992) suggest that some toxic alkaloids are not bitter tasting to livestock. Sheep (Arnold and Hill 1972), cattle (Pfister et al. 1996a, Panter et al. 1997), and pigs (Panter et al. 1985) do not necessarily avoid bitter tastes, nor do sheep form stronger aversions to bitter than to sweet flavors (Launchbaugh et al. 1993). As a rule, grazing animals are not deterred by the supposed bitterness of alkaloid-containing plants. Intake of alkaloid-containing plants is primarily regulated by positive or negative postingestive consequences (see Launchbaugh et al. this volume).

Indolizidine alkaloids

Major Plant Species

The indolizidine alkaloid, swainsonine, is the toxin in locoweeds (Molyneux and James 1982), found within the *Astragalus* and *Oxytropis* genera of the Fabaceae. There are more than 350 species of *Astragalus* and about 30 species of *Oxytropis* in North America. Of these species, only about 10 *Astragalus* and 2

Table 2. Major classes of plant alkaloids, livestock species primarily affected, body system(s) affected, and major plant genera containing the alkaloids.

Type of Alkaloid	Animal Species Primarily Affected	Body System(s) Affected	Plants Containing Toxin	
			Common name	Scientific name
Diterpene	Cattle	Muscle paralysis	larkspur	*Delphinium* species
Pyrrolizidine	Cattle, horses	Liver toxin; photosensitization	groundsel houndstongue	*Senecio* species *Cynoglossum officinale*
Steroidal (solanum type)	Cattle, sheep, horses	CNS[1] toxin; digestive tract	nightshades	*Solanum* species
Steroidal (veratrum type)	Sheep	Birth defects; lung congestion	skunk cabbage death camas	*Veratrum* species *Zigadenus* species
Piperidine	Cattle, sheep, horses, pigs	CNS toxin; birth defects	poison hemlock lupine tobacco	*Conium maculatum* *Lupinus* species *Nicotiana* species
Quinolizidine	Cattle, sheep, horses	Respiratory paralysis;birth defects	lupine	*Lupinus* species
Indolizidine	Horses, cattle, sheep	Digestive, reproductive & CNS	locoweed	*Astragalus* and *Oxytropis* spp.
Pyridine	Cattle, horses, pigs, sheep	CNS toxin; birth defects	tobacco	*Nicotiana* species

[1] CNS = central nervous system

Table 3. Major locoweed species containing indolizidine alkaloids, primary distribution in the western U.S., and range of swainsonine concentration (mg/g dry weight).

Scientific name[1]	Common name	Distribution	Range in Concentration
Astragalus			----(mg/g)----
allochrous	rattleweed	southern California east to Texas	0.7 to 11.5[2,3]
bisulcatus	two-grooved milkvetch	southern Canada south to New Mexico	0.0 to 0.4[2,3]
drummondii	Drummond milkvetch	southern Canada south to northern N.M.	0.60[3]
emoryanus	red-stemmed peavine	Utah and southwestern states into Texas	0.5 to 1[4]
lentiginosus	freckled milkvetch	western Canada to California; Rocky Mountains south into Arizona to Texas	0.05 to 0.4[3,6,7]
lonchocarpus	great rushy milkvetch	Nevada, Utah, Colorado, and southwestern states	0.0 to 4.4[2,3,5]
missouriensis	Missouri milkvetch	southern Canada south to New Mexico and Texas	0.12 to 0.18[2,3]
mollissimus	woolly locoweed	Utah and Wyoming south to Mexico	0.02 to 10.3[2,4,5,6]
praelongus	stinking milkvetch	Utah, Nevada, Colorado and southwestern states east into Texas	0.03 to 0.2[2,3,5]
tephrodes	ashen milkvetch	Nevada, southwestern Utah and New Mexico, Arizona, and California	0.0 to 0.9[2,3]
Oxytropis			
lambertii	Lambert's locoweed	southern Canada south to Arizona and New Mexico	0.2 to 1.0[2,5]
sericea	whitepoint locoweed	northwest Canada south to Nevada, New Mexico and Oklahoma	0.05 to 1.2[3,5,7]

[1] Many species have one or several varieties, but that level of detail is beyond the scope of this paper
[2] Smith et al. 1992
[3] Fox et al. 1998
[4] Davis et al. 1984
[5] R.J. Molyneux, personal communication
[6] D.R. Gardner, personal communication
[7] Molyneux et al. 1989

Oxytropis species have been found to contain swainsonine (Table 3). Many of these toxic species are located around the Colorado Plateau, the Great Basin, and portions of the Great Plains. Some *Astragalus* species contain nitro-toxins (e.g., *Astragalus miser* Dougl. ex Hook; see Majak and Benn, this volume) or selenium (e.g., *Astragalus bisulcatus* (Hook.) Gray). Other genera worldwide contain swainsonine, including *Swainsona* spp. (Colegate and Dorling 1997) and *Ipomoea* (Molyneux et al. 1995). Within the U.S., *Ipomoea* spp. (morning glory) have not been examined for swainsonine, but *Ipomoea batatas* (L.) Lam. (sweet potato) can be toxic to livestock through an unrelated mechanism.

Mechanism of Intoxication

Swainsonine has a chemical structure similar to mannose and glucose, and this similarity may be the basis of its toxicity (Colegate et al. 1989). Swainsonine inhibits several intracellular mannosidase enzymes responsible for cleaving sugar molecules from oligosaccharides (Broquist 1986). Inhibition of ∝-mannosidase and subsequent failure to trim mannose from oligosaccharides, results in accumulation of mannose-rich oligosaccharides in lysosomes and causes cellular disruption, and eventual cell death (Dorling et al. 1989, Elbein 1989). These accumulated oligosaccharides damage cells in thyroid, brain, pancreas, and kidney tissue, characterized as foamy cytoplasmic vacuolation (Van Kampen and James 1970, Stegelmeier et al. 1995a). Inhibition of Golgi mannosidase II results in abnormal glycosylation of proteins, affecting hormones, membrane receptors, and enzymes throughout the body. Once a sufficient number of cells are damaged, signs of poisoning are seen, which may occur within 3 weeks (Van Kampen and James 1970). Microscopically, damage in the CNS results from vacuolar degeneration of both neurons and glia (Stegelmeier et al. 1994). Pathological lesions appear within 1 week after locoweed feeding begins (Van Kampen and James 1970), and when locoweed feeding ceases, the cytoplasmic vacuoles disappear quickly (James and Van Kampen 1971). Residual CNS lesions may resolve quickly depending on the extent of intoxication (Pfister et al. 1996b), but once a particular threshold is exceeded, CNS damage becomes permanent (James and Van Kampen 1971), and the animal likely will display long-term abnormal behavior (Pfister et al. 1996b).

There appears to be a dose-response threshold for swainsonine, such that incomplete enzyme inhibition occurs at lower doses. Doses at or above the threshold result in similar etiology and further increases in dosage do not increase the severity of intoxication (Stegelmeier et al. 1995a); however, this threshold is low and relatively small doses have been shown to produce both clinical and histologic lesions. For example, sheep were intoxicated with average daily swainsonine doses of 0.21 mg/kg body weight/day (as ingested plant material, Pfister et al. 1996b).

Swainsonine is water-soluble, and is rapidly excreted (Stegelmeier et al. 1995b). Clearance time ($T_{1/2}$) for swainsonine from most tissues is about 20 hours; however, for the liver and kidneys it is much longer and requires about 60 hours. Swainsonine is distributed throughout all tissues and is present in many animal products. Thus, current recommendations are that animal products not be used, and intoxicated animals withheld from slaughter for about 8 days after animals discontinue locoweed ingestion ($T_{1/2}$ x 10; Stegelmeier et al. 1998a). Lactating animals that eat locoweed will excrete swainsonine into the milk within 30 min (Broquist 1986); therefore nursing young may become intoxicated (James and Hartley 1977).

Clinical Signs

The symptoms of locoweed poisoning are lethargy, muscular incoordination, intention tremors, nervousness, and excitability, progressing to emaciation, possible maniacal behavior when stressed, and death. Horses may be particularly susceptible to intoxication (James and Van Kampen 1971) and may be dangerous when handled. Abortions and water belly (i.e., hydrops amnii) often occur when pregnant animals eat locoweed (Ralphs et al. 1994b). If the fetus survives *in utero* intoxication, the newborn offspring often exhibits abnormal suckling behavior, and may not survive (Pfister et al. 1993). Grazing animals that consume locoweeds at higher elevations (e.g., > 2200 m) are increasingly susceptible to congestive right heart failure (James et al. 1983).

Locoweed poisoning may be diagnosed by determining if animals have been exposed to locoweed, and by evaluating clinical and pathological signs; affected animals show typical overt signs of poisoning while living, and have pathological lesions upon post-mortem examination. With living animals, definitive diagnostic tests using serum can verify consumption of locoweed (Stegelmeier et al. 1995b). Serum tests are not very reliable, however, if suspected animals have not recently (i.e., within 2–3 days) been eating locoweed, as serum swainsonine quickly disappears, and enzyme concentrations quickly return to normal ranges. Future work will determine if other diagnostic assays, such as determining glycosylation of specific proteins, may be better indicators of intoxication.

Effects on Livestock Nutrition and Grazing Behavior

A dominant feature of locoweed poisoning in livestock is gradual emaciation (i.e., wasting, Marsh 1909), which may not cease when animals are removed from locoweed (James et al. 1969). In studies at our laboratory, rats, sheep, cattle, and horses have all shown declines in food intake and body condition while eating locoweed, and the wasting continued after locoweed feeding ceased. Steers lost weight while grazing locoweed, and gains did not resume for 45–60 days after locoweed feeding ceased (Ralphs et al. 2000). Overtly intoxicated horses, when removed from locoweed-infested pastures, continued to decline in body condition over 4 weeks even though their appetites did not diminish (Pfister unpublished data). The loss of productive function may result directly from neurological damage because of impaired ability to prehend and masticate food (Ralphs et al. 1991b). Ralphs et al. (1991b) reported that sheep had seizures that severely disrupted prehension and mastication. The loss of body condition may also be a direct result of swainsonine on hormonal and digestive functions (Stegelmeier et al. 1995a). Both aspects probably operate simultaneously to cause weight loss, because weight loss is not fully attributable to lower food intake (Velastegui et al. 1992).

Mildly or moderately intoxicated animals can be salvaged and returned to near normalcy by removing them from locoweed, and offering supplements (Marsh 1909). This does not ensure that such animals will be fully productive and normal, but they may regain sufficient body weight to allow resale (Torell et al. 1999b). Notwithstanding, severely intoxicated animals may not regain lost body weight even with supplemental feeding, and will never be productive no matter how intensive the rehabilitation.

There are pervasive anecdotal accounts of addiction or of animals “seeking out” locoweed in preference to other desirable forage. Marsh (1909) reported that locoweed was addictive to various animals, including mules, pigs and pronghorn antelope. Lewin (1931) described livestock addiction to locoweed and to the Australian plant *Swainsona*, long before it was known that *Swainsona* and locoweed contained the same toxin. Recent reports of toxicity in South America (Peru and Brazil) from morning glory vines (*Ipomoea* spp.) indicate that livestock become addicted or dependent on these plants (Molyneux, personal communication; Tokarnia et al. 1992). Ralphs et al. (1990) reported that dried, ground whitepoint locoweed (*Oxytropis sericea* Nutt. in T. & G.) was not addictive, but some animals habituated or become accustomed to eating the plant material. The obsessive consumption that producers observe may result from locoweed being relatively more palatable than associated forage (Ralphs et al. 1993), or alternatively, locoweed may have pharmacological properties that are reinforcing (Pfister 1999).

Management and Control

Swainsonine usually occurs at very low concentrations (0.01 to 0.3% of dry weight) in locoweeds (Table 3), with much of the toxin found in the seeds. Fluctuations in swainsonine concentration as the plants mature have little effect on how much locoweed is eaten (Ralphs and Molyneux 1989). The growth habits of locoweed in relation to other available forages generally determine if and how much of the plant is eaten. Livestock producers should not over-stock or over-utilize locoweed-infested ranges, and should manage for sufficient desirable forage so that grazing pressure does not impel livestock to begin eating locoweed. When animals become overtly intoxicated, the most economical solution may be to remove them from pasture, and allow time for recovery before selling (Torell et al. 1999b).

Whitepoint locoweed (*Oxytropis sericea*)

Whitepoint locoweed begins growth in late winter and early spring on shortgrass prairie rangelands, and the green leaves are often more palatable than are dormant grasses. Livestock readily consume green locoweed leaves during the spring when cool-season grasses are just beginning growth, and warm-season grasses are dormant (Ralphs et al. 1993). Grazing of whitepoint locoweed may cease when warm season grasses begin active growth in early summer (Ralphs et al. 1993), or livestock may switch diet selection to other green locoweeds (*Oxytropis lambertii* Pursh, Ralphs unpublished data), if available. On mountain rangelands, cattle prefer immature seed pods of whitepoint locoweed, but may also eat mature pods and green leaves later in the summer, particularly if grazing pressure is excessive. (Ralphs 1987). In contrast to shortgrass prairie rangelands, whitepoint locoweed on high elevation rangelands is grazed during summer even though other forage is also green and actively growing (Ralphs et al. 1986, Ralphs et al. 1987, Ralphs 1987). Simple changes in grazing management can have profound positive impacts on losses to whitepoint locoweed. For example, Ralphs et al. (1984) reported reductions in cattle losses from over 20% to less than 3% annually from a simple change in grazing management.

Specklepod locoweed (*Astragalus lentiginosus* Dougl. ex Hook.)

Limited studies with cattle and horses (Pfister unpublished data) suggest that, during spring, likelihood of animals eating locoweed increases greatly when animals begin to search avidly for newly growing cool-season grasses (i.e., “chasing green”). Cattle prefer dormant grasses to specklepod locoweed (var. *diphysus)* during much of the spring, but once cattle begin eagerly selecting green grass, they also begin eating still-green, but drying, locoweed. During winter, cattle will even eat toxic black stems from previous growing seasons (Ralphs et al. 1988). During spring, horses intensely search for green grass,

Table 4. Characteristics, relative toxicity, and general concentration range of toxic alkaloids of the dominant larkspur species in the western U.S.

Class/Species	Typical height at maturity	Elevation	Associated plant communities	Typical risk of losses[1]	Alkaloid concentration[2]
	--(cm)--	--(m)--			--(mg/g)--
Tall Larkspurs					
D. glaucum	90–200	>2000	aspen, conifers, alpine meadows	low	1–20
D. barbeyi	90-180	>2200	aspen, conifers, alpine meadow, mountain brush, alpine tundra	moderate to severe	1–29
D. glaucescens	76–90	>2000	mountain meadows, sagebrush	low to moderate	1–12
D. occidentale	90–180	>2000	mountain brush, sagebrush, conifer, aspen	low to severe	0–18
Low Larkspurs					
D. nuttallianum	20–60	>1200	mountain brush, sagebrush, aspen, conifer, mountain and foothill meadows	low to severe	2–4
D. bicolor	20–40	>800	mountain brush, sagebrush,	low to severe	—
D. andersonii	10–60	>1200	desert shrub, mountain brush, sagebrush, pinion-juniper	low to moderate	1–4
Plains Larkspur					
D. geyeri	40-80	>1500	desert shrub, mountain brush, sagebrush shortgrass prairie	low to severe	1-4

[1] The risk of losing cattle to these species is a subjective evaluation based on plant toxicity, numbers of grazing cattle threatened during the growing season, and the geographical distribution of the larkspur species. *D. glaucescens* is relatively more toxic late in the growing season compared to mature plants of the other species.

[2] These concentrations are general values, and were determined by examining numerous samples collected over the past 6 years at the Poisonous Plant Research Laboratory. The values for low and plains larkspurs should be considered preliminary because they are based on small sample sizes. Multi-site and year analysis for low and plains larkspurs is ongoing (Gardner, unpublished data). For further references see review by Pfister et al. (1999). For concentrations in Canadian low larkspur, see Majak (1993).

and simultaneously select green locoweed. Once horses begin to eat locoweed, consumption may continue until they become very intoxicated.

Woolly locoweed (*Astragalus mollissimus* Torr.)

Woolly locoweed is not very palatable to grazing cattle, and probably is not selected by livestock unless grazing pressure is excessive (Ralphs et al. 1993). Consumption of woolly locoweed appears to cease with the growth of warm-season grasses (Ralphs et al. 1993).

Social facilitation

When some animals begin to eat locoweed, these 'locoeaters' can influence other grazing animals, including nursing calves, to begin eating locoweed through social modeling (Ralphs et al. 1994a). In most situations, ranchers should remove animals that eat locoweed to eliminate social influences, and to prevent progressive intoxication. Some producers in New Mexico with locoweed-infested pastures have reduced their locoweed losses by systematically, over several years, removing any cow from their herds seen eating locoweed, before the animal either becomes intoxicated or influences her calf or companions to eat locoweed (D. Graham, personal communication).

Aversive Conditioning

Grazing animals may be conditioned so that they will avoid toxic plants, including locoweed, in future encounters (Ralphs et al. 1997a). In this procedure, animals are given a taste of the plant in a corral, then dosed via stomach pump with a solution of lithium chloride (LiCl) at 200 mg/kg body weight. The LiCl-induced illness is associated with the taste of the toxic plant, and animals avoid eating the target species (Ralphs 1992). Averted animals must not be allowed to graze with non-averted companions, as social facilitation can quickly extinguish the aversion (Ralphs 1997).

Cyclic or "on-off" grazing

Livestock can be poisoned by low level locoweed doses given for as little as 4 weeks (Pfister et al. 1996b). Nonetheless, considering both swainsonine's rapid clearance and dose-response threshold, it may be possible to expose animals briefly to locoweed with a low-risk of intoxication, if they are then allowed to recover on locoweed-free ranges. Recent work with sheep (Stegelmeier unpublished data) shows that animals repeatedly given locoweed for 10 days with a 14-day recovery period had no detectable permanent damage. On-off grazing schemes may work, but must be approached with caution as they have not been tested under field situations.

Herbicidal control

Producers should, if possible, provide a locoweed-free pasture for spring or fall grazing when animals are most likely to eat locoweed. Herbicidal control of locoweed (Ralphs and Ueckert 1988, McDaniel 1999) in some pastures can provide a relatively "loco-free" pasture for critical times. Herbicidal treatment for this specific purpose is often economical, even though general spraying to eliminate locoweed on a ranch-wide basis is usually not economical (Torell et al. 1999a).

Diterpenoid alkaloids

Major Plant Species

Toxic C_{19} and C_{20} norditerpenoid alkaloids occur primarily in 2 genera from Ranunculaceae: larkspurs (*Delphinium* spp.) and monkshood (*Aconitum* spp.). There are over 50 species each of *Delphinium* and *Aconitum*, but only a few are known to cause livestock poisoning. Monkshoods are highly toxic plants, but we believe that most reports of livestock losses to monkshood are attributable to larkspur (Knight and Pfister 1997). The 2 plants grow together in wet mountain habitats and are easily confused; furthermore, monkshood is not usually grazed by cattle. Larkspurs are divided into 3 general categories based primarily on mature plant height and distribution: low, tall, and plains (Table 4). Most research has focused on tall larkspurs (Pfister et al. 1999). Livestock losses in the western United States to all types of larkspurs probably exceed $10 million dollars annually.

Toxic Alkaloids and Occurrence

Larkspurs contain many (> 18) norditerpenoid alkaloids of which the most toxic are methyllycaconitine (MLA), 14-deacetylnudicauline (DAN), and nudicauline (NUD; Manners et al. 1993, 1995). Both MLA and DAN occur to some extent in all classes of larkspurs, whereas NUD has not been found in tall larkspurs. A fourth alkaloid, deltaline, is relatively low in toxicity, but is the dominant alkaloid in most tall larkspurs, comprising ≥ 40% of the alkaloid composition, while MLA and DAN together comprise another 20 to 50% of the alkaloid mix in tall larkspurs. The MLA is the dominant alkaloid in low larkspurs (Majak et al. 1987, Majak and Engelsjord 1988, Bai et al. 1994).

The concentration of MLA and DAN is highest in immature larkspurs (Pfister et al. 1994a, Ralphs et al. 1997b). In tall larkspurs, MLA concentrations may exceed 20 mg/g. In a Canadian study, Majak (1993) reported high concentrations of MLA (up to 8.7 mg/g) in vegetative low larkspurs, and 2 mg/g in flowering plants. Before shattering, tall larkspur pods are relatively high in toxicity (MLA + DAN = 7 to 12 mg/g). Toxicity declines rapidly in tall larkspurs once pods begin to shatter (Gardner and Pfister 2000), whereas concentrations are relatively stable in low larkspurs after the vegetative stage (Majak 1993, Gardner, unpublished data).

Mechanism of intoxication

The primary result of larkspur toxicosis in livestock is neuromuscular paralysis, as nicotinic acetylcholine (nAch) receptors in the muscle and brain are blocked by MLA and related alkaloids (Aiyar et al. 1979, Dobelis et al. 1999). Animals usually die from respiratory failure (i.e., asphyxiation) when the muscles of the diaphragm are paralyzed or the CNS respiratory center is depressed. Larkspur alkaloid binding to nAch receptors appears to be correlated to toxicity in various tissues (Kukel and Jennings 1994), and may explain sheep tolerance to larkspur if larkspur toxins bind less avidly to nAch receptors in sheep (Stegelmeier et al. 1998b).

Toxicity, but not lethality of MLA + DAN has been established for cattle by oral doses of dried tall larkspur (Pfister et al. 1994b, 1997a). Cattle typically show clinical signs when given an MLA + DAN dose of about 20 mg/kg body weight (Pfister and Cheney 1998). A 450 kg cow may show clinical signs after rapidly eating 1.8 kg of tall larkspur (≈ 7.2 kg wet weight). Assuming the plant material used in Olsen's (1978) LD_{50} study (vegetative and early flowering tall larkspur) contained 12 mg/g of toxic alkaloid, the LD_{50} of MLA + DAN in cattle would be about 30 mg/kg. Early studies by Marsh et al. (1916) suggest that the lethal dose is lower when tall larkspur is given repeatedly over 3 to 4 days.

Clinical Signs

Clinical signs of intoxication include muscular weakness and trembling, straddled stance, periodic collapse into sternal recumbency, respiratory difficulty, and finally death while in lateral recumbency. Moderately-intoxicated animals will periodically collapse while moving, and be in sternal recumbency for 10 to 30 min; when the temporary paralysis subsides, affected animals may show muscular trembling, but will be able to walk and graze. Severely-intoxicated animals will be laterally-recumbent, and will be unable to do more than thrash about. Marsh et al. (1916) reported that bloat seldom occurs in intoxicated animals, but our observations suggest that bloat can be a significant component of larkspur fatalities. Bloating may occur as a result of paralysis of the rumen eructation (belching) mechanism. Cattle may die from bloat alone or asphyxiation from aspirated rumen contents while recumbent from larkspur paralysis. Some success of early remedies for larkspur poisoning (e.g., bacon fat and turpentine given orally, Glover 1906) may have been due to bloat reduction.

Diagnosis and Treatment

Diagnosis of larkspur poisoning is usually by association, as dead or sick animals are found near larkspur plants. Because larkspur poisoning causes no tissue lesions, pathological examination can only rule out other possible causes of death. Currently, no field test exists to determine if animals have been poisoned by larkspur. Blood or rumen fluid may contain larkspur alkaloids (Holstege et al. 1996); even so, cattle can eat substantial quantities of larkspur without ill effect, and the presence of alkaloids in body fluids only suggests larkspur intoxication.

A variety of remedies have been applied by ranchers (e.g., bleeding by cutting the tail), but most are without scientific rationale. Treated animals probably survive because they did not eat a lethal dose of larkspur and did not bloat. Drugs that increase acetylcholine concentration at the neuromuscular junction have potential for

Table 5. Relative pyrrolizidine alkaloid (PA) concentration and toxicity of various PA-containing plant species on western U.S. rangelands.

Scientific name	Common name	Distribution	Concentration[1]	Lethal Dose[2]
			---mg/g---	---mg/g---.
Cynoglossum officinale	houndstongue	widespread weed in North America	0.5 to 21[3]	5 to 60[4]
Senecio				
longilobus	threadleaf groundsel	midwest south into Texas and west into New Mexico and Arizona	1 to 87[5]	10 to 13[6]
riddellii	Riddell's groundsel	midwest south into west Texas and New Mexico	2 to 180[5]	15 to 45[7]
jacobaea	tansy ragwort	weed in northwestern U.S.	0.2 to 9[5]	2 to 3[8]
vulgaris	common groundsel	weed in western U.S.	2 to 3[5]	Not available

[1] The concentration of total pyrrolizidine alkaloids (N-oxide and free base) in dry plant material. Concentrations vary greatly depending on growing conditions and plant part. The high value for *S. riddellii* (180 mg/g) is the highest recorded concentration of any type of alkaloid in any plant yet recorded (Molyneux and Johnson 1984).

[2] Lethal dose may be acute (short-term) or chronic (long-term) depending on dose, because toxicity from pyrrolizidine alkaloids may be delayed by weeks or months from the time animals ingest the plant.

[3] Pfister et al. 1992; Van Damm et al. 1994

[4] Baker et al. 1991; Stegelmeier et al. 1996

[5] Johnson et al. 1985a; Molyneux and Johnson 1984

[6] Johnson and Molyneux 1984

[7] Johnson et al. 1985b; Molyneux et al. 1991

[8] Johnson and Smart 1983

reversing larkspur toxicity. The cholinergic drug, physostigmine (0.08 mg/kg i.v.), has been successfully used under field and pen conditions to reverse clinical larkspur intoxication (Nation et al. 1982, Pfister et al. 1994c). Our current recommendation is that ranchers not attempt to move partially-paralyzed or recumbent animals, as stress is detrimental. If intoxicated animals bloat, passing a stomach tube or puncturing the rumen with a knife or trocar will relieve gas pressure.

Impacts on Animal Nutrition and Behavior

Larkspur poisoning is acute, rather than chronic, thus, animals that survive show essentially no long-term detrimental effects. Ingestion of larkspur at sub-acute doses has no negative impact on ruminal fermentation or digestive function (Pfister et al. 1989). Larkspur poisoning probably has no long-term effect on diet selection or grazing behavior, although previously-poisoned animals eat less larkspur and other forage for a few days after a toxic episode (Pfister et al. 1997a, Pfister and Cheney 1998). Eventually, larkspur consumption returns to previous levels, and animals may be intoxicated again.

Grazing Management

Tall larkspur (*D. barbeyi* Huth and *D. occidentale* (Wats.) Wats.)

Cattle eat little or no tall larkspur before the plant has elongated flowering racemes (Pfister et al. 1988a, 1997b). Cattle generally begin consuming tall larkspur after flowering racemes are elongated, and consumption increases as larkspur matures. Consumption usually peaks during the pod stage of growth in late summer, when cattle may eat large quantities (25 to 60% of diet, Pfister et al. 1988b).

The period of greatest risk on tall larkspur ranges extends from the flower stage into the pod stage. Many ranchers typically defer grazing on tall larkspur-infested ranges until the flower stage to avoid death losses. This approach wastes much valuable forage, and often places cattle into larkspur-infested pastures when risk of losses is high. An additional 4 to 6 weeks of grazing may be obtained by grazing these ranges early, before larkspur elongates flowering racemes (Pfister et al. 1997b). The risk of losing cattle is low when grazing before flowering even though larkspur is very toxic, because larkspur consumption is very low. Once pods are mature and begin to shatter, larkspur ranges can usually be grazed with impunity because pod toxicity declines rapidly, and leaf toxicity is low (Gardner and Pfister 2000).

Low larkspur (*D. nuttallianum* Pritz.) and Plains larkspur (*D. geyeri* Greene)

Consumption of low larkspur by cattle appears to increase once low larkspur has flowered, and higher grazing pressure will increase amounts of low larkspur eaten (Pfister and Gardner 1999). Spring grazing of low larkspur-infested ranges can be problematic, as there may not be sufficient forage growth to graze these ranges before larkspur flowers, but risk appears to increase once flowering occurs. Fortunately, in most years low larkspurs are short-lived, so producers must avoid heavily infested areas for about 4 weeks during peak toxicity. Four years of grazing studies on plains larkspur-infested ranges have shown few distinct patterns of consumption by lactating cows (Pfister, unpublished data).

Other Management Options

Aversive Conditioning

Cattle can be trained to avoid eating tall larkspur through aversive conditioning (Ralphs 1997), as previously noted with locoweed. Social facilitation, whereby one animal influences another to eat a particular plant, will quickly extinguish the aversion, thus, averted cattle must be grazed separately from non-averted cattle (Lane et al. 1990, Ralphs 1997). Animals experienced in eating larkspur may also be successfully averted, although the aversion is initially more difficult to induce and may be more fragile and less persistent than for naive animals (Ralphs 1997).

Grazing Sheep Before Cattle

Marsh et al. (1916) recommended that ranchers graze sheep before cattle to take advantage of the low toxicity to sheep, and Aldous (1917) noted that sheep grazing on immature *D. occidentale* in Nevada had reduced the poisoning risk to cattle. On tall larkspur-infested ranges where larkspur grows as discrete patches, sheep can be herded into or bedded on the patches to reduce larkspur availability or acceptability to cattle (Ralphs et al. 1991a, Ralphs and Olsen 1992). In those areas where larkspur is uniformly spaced over a pasture, sheep must eat immature larkspur and leave sufficient feed for cattle. This can be problematic, because early growth tall larkspur may not be palatable to sheep (Ralphs et al. 1991a). Sheep grazing has successfully reduced cattle losses on ranges with *D. glaucescens* in southwestern Montana (J. Helle, personal communication).

Herbicidal Control

Larkspur losses can be economically reduced if dense larkspur populations are controlled by herbicides. Picloram, metsulfuron, and glyphosate have proven to be effective in killing tall larkspurs when applied at specific growth stages (Mickelsen et al. 1990, Ralphs et al. 1991c, 1992). These herbicides do not reduce toxic alkaloid concentrations in treated larkspur plants, and metsulfuron may increase toxicity (Ralphs et al. 1998). Therefore, sprayed areas should not be grazed until larkspur has withered and decomposed.

Pyrrolizidine Alkaloids

Major Plant Species

Pyrrolizidine alkaloids (PAs) occur on western U.S. rangelands primarily in *Senecio* spp. (Asteraceae), and in *Cynoglossum officinale* L., (houndstongue, Boraginaceae). In the southeastern U.S., *Crotalaria* spp. (Fabaceae) also contain pyrrolizidine alkaloids. Worldwide, PAs are probably the most economically-important plant toxins impacting human health, as PAs contaminate grain for poultry, ruminant, and non-ruminant livestock, and human consumption, as well as herbal teas (Huxtable 1989). About 3% of the flowering plants in the world (> 6000 species) contain PAs (Smith and Culvenor 1981), and there are currently nearly 300 individual known PAs (Roitman and Panter 1995). The alkaloid concentrations in range plants and subsequent toxicity vary widely (Table 5).

Mechanism of intoxication

The PAs occur in either the free-base or N-oxide form in plants, but neither of these forms is toxic to animals *per se* (Winter and Segall 1989). The toxicity of PAs is due to the formation of toxic metabolites in the liver termed pyrroles. Pyrroles are formed as a detoxification intermediate through the action of liver enzyme systems, primarily mixed function oxidases (MFOs), but the exact mechanism is not clear (Winter and Segall 1989). Pyrroles form adducts within the liver with hepatic proteins and nucleic acids, and damage liver cells, causing enlarged hepatocytes, abnormal bile secretion, and fibrosis (Stegelmeier et al. 1996). A dysfunctional liver leads to other syndromes such as chronic wasting disease and photosensitization. The PAs can also cause lesions in the lungs and brain.

Clinical Signs and Diagnosis

Poisoning from PAs may be either acute (high-dose and short-term) or chronic (lower-dose and long-term). Acute intoxication is less common, as most animals poisoned by PAs develop clinical signs slowly over many weeks or months (Cheeke 1989). Acute intoxication can kill animals within 1 day if sufficient plant material is ingested (Baker et al. 1991). Chronic intoxication usually results from ingestion of the PA-containing plant for several weeks (Baker et al. 1991, Stegelmeier et al. 1996). Typical clinical signs include depression and lethargy, anorexia, and ascites (fluid accumulation in abdomen). None of these signs are specific for PA–induced toxicity, thus, the diagnosis is usually made from a liver biopsy and associated histopathology. Enlarged liver cells were the dominant lesion seen in horses 6 months after they were dosed with a low dose of alkaloids. Serum chemistry changes may be dramatic, as many liver enzymes are altered, but these changes are also not specific for PA-poisoning. Wasting disease (i.e., severe emaciation) as a result of liver damage is commonly noted, as is "hard, yellow liver" disease; all these conditions may be related to PA-induced damage to the liver, but can be caused by other toxic plants and diseases (Stegelmeier et al. 1996).

Younger animals are more susceptible to PA-induced toxicosis because the higher metabolic activity of growing liver tissue encourages pyrrole formation and results in more extensive liver damage (Cheeke 1989). The PAs are transferred in milk to nursing young, and there is a danger of human consumption via milk (Molyneux and James 1990). There are marked species differences in tolerance for PAs, as goats and sheep are relatively more resistant to PA-poisoning than cattle and horses (Cheeke and Huan 1995). Detoxification of PAs occurs to a limited extent in the rumen (Wachenheim et al. 1992), but the liver appears to be the major site of detoxification (Cheeke 1994).

Impacts on Animal Nutrition and Behavior

Poisoning by PAs clearly has a great impact on the nutrition of grazing and pen-fed animals. Animals with compromised liver function will generally show slow weight loss over a long period of time (perhaps years). Further, PA-intoxication may interfere with mineral and vitamin nutrition to further degrade animal performance (Cheeke 1989).

Intoxication by PAs can affect animal behavior directly. For example, horses may show typical "head pressing" behavior as a result of ammonia toxicity from liver damage (Cheeke 1989). Intoxicated animals may become intractable and difficult to handle as the disease progresses; in the final stages of poisoning animals may stagger greatly. Liver damage can lead to secondary photosensitization, and as affected animals are sensitive to sunlight, they become solitary and spend excessive amounts of time seeking shade instead of grazing. Severe sunburn may occur especially on exposed areas such as the nose, vulva, udder, etc. Photosensitized, lactating cows will often develop very inflamed and sensitive udders, especially light-pigmented animals, and will prematurely wean their nursing young.

Management and Control

Senecio species

Managing rangelands so that plant communities are in good condition and adequate forage is available is crucial to reducing losses to *Senecio* spp. (Merrill and Schuster 1978). Generally, senecios are not very palatable, and are avoided by grazing livestock if other forage is available. Drought stress and overgrazing can increase populations of threadlleaf groundsel, as the plant is an aggressive invader (Sharrow et al. 1988). Drought is an especially dangerous time because other forage may be lacking and the toxic alkaloid concentration in senecio plants increases during drought (Molyneux and Johnson 1984), so grazing animals may ingest higher quantities of more toxic forage. *Senecio* species are also most toxic when plants are reproducing, thus avoiding pastures when these plants are in bud, flower, or seed is prudent. Proper grazing management must consider stocking rates, as improper stocking may increase the amount of toxic plant consumed when alternative forages become limited. Excessive stocking may lead to degradation of the desirable plant community allowing *Senecio* species to increase. Herbicidal control may alleviate some problems if incorporated into an overall management program (Sharrow et al. 1988).

Houndstongue (*Cynoglossum officinale*)

Houndstongue is not only a toxic plant, but also a noxious weed that is increasing in North America. The plant spreads from bur-like seeds that cling to animals and humans alike, and invades disturbed areas. Houndstongue is generally unpalatable when growing on rangelands, but we have observed lactating cows eat green houndstongue when other forage was adequate (Pfister unpublished observations). When houndstongue contaminates hay, it is readily eaten by cattle and horses, and is quite toxic (Baker et al. 1989).

Quinolizidine Alkaloids

Major Plant Species

The most problematic plant genera with quinolizidine alkaloids is *Lupinus* (Fabaceae). Although lupine is cultivated in some parts of the world as forage or grain (so-called sweet lupine), in the western U.S. many wild lupine species are toxic to livestock because of high alkaloid concentrations (Keeler 1989). Wink et al. (1995) recently reported on the alkaloid concentration of 36 lupine species from North America; most contain quinolizidine alkaloids, but a few also contain piperidine alkaloids or both types of alkaloids.

Mechanisms of Intoxication

Quinolizidine alkaloids are both toxic and teratogenic (i.e., causing birth defects) to livestock (Panter and James 1995). Lupines cause respiratory failure in sheep (Kingsbury 1964), but the mechanism is unknown. Lupine alkaloids bind differentially to both nicotinic and muscarinic Ach receptors (Schmeller et al. 1994), and affect Na^+ and K^+ ion channels (Wink et al. 1995), but a specific relationship to toxicity has not been developed. Birth defects are apparently caused by the effects of 2 different, but related, alkaloids, anagyrine (a quinolizidine alkaloid, Table 6) and ammodendrine (a piperidine alkaloid; Panter et al. 1992). For unknown reasons, cattle are uniquely sensitive to the effects of anagyrine, and ingestion of alkaloid-rich lupine causes the condition "crooked calf disease" in bovine offspring (Table 6, Keeler 1989, Panter et al. 1994). Crooked calf disease has been associated with *Lupinus laxiflorus* Douglas ex Lindl., *L. caudatus* Kellogg, and *L. sericea* Pursh (Panter et al. 1992). Crooked calf disease is caused by reductions in fetal movement during a susceptible period in gestation (Panter et al. 1988a). This reduction in fetal movement at the critical time is likely to interfer with bone, muscle and ligament development, resulting in mild to lethal skeletal malformations and cleft palate in calves (Panter et al. 1990, 1988a). Even though many calves are born alive, most of these deformities make them virtually worthless, and most deformed calves are destroyed shortly after birth.

Table 6. Potentially teratogenic Lupinus species on western U.S. rangelands[1]. Ingestion by pregnant cattle of *Lupinus* species with teratogenic alkaloids (quinolizidine or piperidine) from gestation day 40–100 may cause severe deformities in calves (i.e., crooked calf disease).

Scientific name	Common name
Lupinus	
albicaulis	pine lupine
albifrons	white face lupine
alpestris	mountain silvery lupine
andersonii	Anderson's lupine
argentous	silvery lupine
arbustus[2]	spur lupine
bakeri[2]	
burkei	Burke's lupine
caudatus	tailcup lupine
densiflorus	
elatus	
elagans	
excubitus	
erectus	tall silvery lupine
evermannii	Everman's lupine
formosus[2]	Lunara lupine
holosericeus	
humicola	lowland lupine
latifolius	broadleaf lupine
laxiflorus	looseflower lupine
leucophyllus	velvet lupine
longifolius	
montigenus	Mt. Rose lupine
nootkatensis	Nootka lupine (Alaska)
polyphyllus	Washington lupine
rivularis	stream lupine
ruber	red lupine
sericeus	silky lupine
sulphureus	yellow lupine

[1] Adapted from Davis (1982), Davis and Stout (1986) and Wink et al. (1995). Species were listed if they contain any of the quinolizidine alkaloid, anagyrine.

[2] These species contain piperidine alkaloids (e.g., ammondendrine) that are also teratogenic when eaten by cattle (Panter et al. 1998b).

Clinical signs

Lupine toxicity is seen clinically as a neurologic disease that progresses from depression and lethargy to muscular weakness, collapse, respiratory failure and death (Panter et al. 1999). Animals that survive for 1 or 2 days may recover completely (Panter et al. 1999), or they may succumb several days later (Kingsbury 1964). Pregnant cows that eat small amounts of lupine may not show clinical signs of intoxication, but give birth to deformed offspring (e.g., cleft palate, Panter et al. 1994). While sheep, goats, and cattle may show signs of acute lupine toxicity such as depression and death, the anygyrine-containing lupines cause birth defects in cattle only (Panter et al. 1998b).

Impacts on Animal Nutrition

Many lupines are not toxic to livestock, and plant breeders have conducted extensive breeding programs to enhance lupines nutritional properties and to reduce their alkaloid content for both livestock and human consumption (Aniszewski 1993). Lupines, being legumes, may contain > 20% crude protein (Panter et al. 1999). So-called "sweet" lupines are relatively low in alkaloid concentrations, and are an excellent source of protein for livestock (Stanford et al. 1996). Range-grown lupines, particularly the seed pods, are a good source of nutrition if they are low enough in alkaloids that toxicity problems do not develop (Panter et al. 1999).

Management and Control

Losses of livestock from lupine poisoning can largely be prevented by understanding 2 interrelated aspects. First, the highest concentrations of toxic alkaloids tend to occur in immature lupine plants and seed pods. Anagyrine concentrations are highest (> 5 mg/g) in early growth, and decline to less than 0.5 mg/g after seed shatter, except that concentrations increase when lupine seeds ripen (Keeler 1976). Second, pregnant cattle are susceptible to the teratogenic effects of alkaloids during a window from days 40 to 70 of gestation, occasionally extending to 100 days (Panter et al. 1997). Birth defects in cattle can be prevented by using breeding or grazing programs that avoid placing pregnant cattle in lupine-dominated pastures in the first trimester of gestation (Keeler et al. 1977, Panter et al. 1992, 1999). Alternatively, risk can be reduced by allowing only short-term access to lupines by pregnant cattle in some form of rotational grazing scheme (Panter et al. 1999). Herbicidal control of lupines is feasible (Ralphs et al. 1991d), but chemical control is usually more expensive than altering a grazing management program.

Acute toxicity problems are less common now, but large sheep losses occurred frequently 100 years ago (Chesnut and Wilcox 1901). Deaths losses usually occur when livestock, usually sheep, ingest a large amount of seed pods in a short period of time (James et al. 1968). This can occur from contaminated hay or from hungry animals gaining access to lupine-dominated forage, and can be prevented by using lupine-free hay and avoiding lupine-dominated ranges when other forage is scarce. During some years, lupine populations will temporarily expand on rangelands not normally problematic. Livestock producers need to be aware of lupine populations and be sufficiently alert to alter grazing or breeding programs when these eruptions occur. Lupine populations increased dramatically during 1997 in Washington, Oregon, Idaho, and Montana, causing severe losses. For example, producers in Adams County, Washington lost over 30% of their calves (> 4000 calves) from lupine-caused birth defects (Panter et al. 1999).

Piperidine Alkaloids

Major Plant Species

Piperidine alkaloids are broadly distributed in nature, but only a few range plants have sufficient amounts to cause toxicity problems for domestic livestock. Several *Lupinus* species (Fabaceae) contain piperidine alkaloids (Table 6), in addition to quinolizidine alkaloids (Roitman and Panter 1995). The suspected toxic piperidine alkaloids in *Lupinus* are ammondendrine and N-methyl hystrine (Panter and James 1995). Recently, 8 yearling steers died after eating *Lupinus argenteus* Pursh containing high levels of ammondendrine and N-methyl ammodendrine (Panter, personal communication). These cattle began grazing *L. argenteus* after grasses were depleted.

The most prominent species containing piperidine alkaloids is poison hemlock (*Conium maculatum* L., Apiaceae). Only 1 species of *Conium* grows in North America, and should not be confused with water hemlock (*Cicuta maculata* L.). Poison hemlock grows in disturbed areas, waste land, and along waterways, invading perennial hayfields and pastures. The first alkaloid ever characterized (coniine) was isolated from poison hemlock in 1827 (Panter and Keeler 1989). In addition to coniine, poison hemlock contains 4 other alkaloids, of which the most toxic alkaloid is ϒ-coniceine, the biogenic precursor for the other *Conium* alkaloids (Panter and Keeler 1989). The ϒ-coniceine is about 8 times more toxic than coniine (Bowman and Sanghvi 1963, Panter et al. 1998a), and this difference has important management implications.

Alkaloid Occurrence

The alkaloid concentration and distribution of alkaloids in poison hemlock are affected by many factors, including environmental changes and plant maturity (Cromwell 1956, Leete and Olson 1972). Drought stress increases total alkaloid concentrations (Fairbairn and Challen 1959). Immature poison hemlock often has a high concentration of ϒ-coniceine, which may then be converted predominately into coniine during active growth. During flowering, concentrations of ϒ-coniceine also shift to coniine. Thus, coniine is the major alkaloid in mature plants and seed, whereas ϒ-coniceine dominates the alkaloid mix in early growth and fall regrowth. Leaves from young or regrowing plants contain 3 to 6 mg/g of toxic alkaloids, whereas immature and mature fruit may contain > 10 mg/g (Cromwell 1956).

Mechanism of Intoxication

Poison hemlock alkaloids act on both smooth and striated muscle; the effect on skeletal muscle is a curare-like neuromuscular blockage, similar to larkspurs. Unlike larkspur alkaloids, blockage occurs only after initial muscular stimulation (Bowman and Sanghvi 1963). When the dose is sufficient, the blockage causes muscular paralysis, resulting in depressed respiration. The specific site of blockage at the neuromuscular junction is not known, nor is the exact mechanism (Panter and Keeler 1989). Poison hemlock alkaloids are also potent teratogens, and ingestion during pregnancy induces skeletal malformations that are virtually indistinguishable from those caused by lupines (Panter et al. 1988b). The mechanism of fetotoxicity is thought to be the same, namely reductions in fetal movement during critical phases of gestation (Panter et al. 1988a).

Clinical Signs and Diagnosis

Poison hemlock causes initial CNS stimulation with frequent urination and defecation, dilated pupils, increased heart rate, muscular weakness and trembling and ataxia. This initial stage is followed by depression with further muscular weakness, collapse, and death due to respiratory paralysis (Panter et al. 1988b). Although animals exhibit tremors, muscular weakness and collapse, they do not have true seizures and may recover quickly if a sublethal dose was eaten. Although poison hemlock is fetotoxic to pregnant animals as are lupines, *Conium* is more universally teratogenic, affecting cattle, sheep, goats, and pigs (Panter and Keeler 1989). Most pregnant animals that later develop terata after ingesting poison hemlock also show initial signs of acute toxicity, and many are fatally intoxicated, unlike the teratogenesis from lupine alkaloids. The severity of birth defects varies according to the dose and the animal species. Sheep are less sensitive than are cattle, goats, and pigs (Panter et al. 1988b). Similar birth defects can be caused by genetic, traumatic, or other environmental toxins and the clinical signs and lesions are nonspecific. Because there are no definitive pathological lesions, the diagnosis of poison hemlock toxicity is made from a knowledge of exposure to the plant, and from clinical signs. Additionally, many reports suggest that affected animals have a “mousy” odor on their breath or urine. Alkaloid screening can detect the presence of poison hemlock alkaloids in body fluids, providing confirmation that animals were ingesting the plant (Galey et al. 1992).

Management and Control

The most critical time of the year to avoid poison hemlock is spring because the plant often appears before other forage has emerged. Green seed pods may be eaten in mid-to-late summer (Panter and Keeler 1989). Furthermore, poison hemlock may regrow in fall after seed shatter. Ingestion during fall may coincide with fetotoxicity in pregnant cattle, if they are in the first trimester (days 30–75, Panter et al. 1988b). If poison hemlock has invaded hay fields, the contaminated hay can poison livestock. Even though toxicity decreases upon drying, sufficient toxin may be retained to poison livestock (Galey et al. 1992). Cattle appear to be particularly susceptible because of their acceptance of the plant and their sensitivity to the teratogenic alkaloids. Poison hemlock can be easily controlled with phenoxy herbicides (Panter et al. 1988b).

Impacts on Grazing Behavior

Poison hemlock is reported to be habituating or even addictive (Kingsbury 1964, Panter and Keeler 1989). Goats (Copithorne 1937), cows (Penny 1953), and pigs (Panter et al. 1985) readily eat fresh hemlock, even when intoxicated. Panter (1983) reported that intoxicated pigs “relished” the plant, and seemingly developed a craving for poison hemlock.

Related Pyridine Alkaloids

Tree and wild tobacco (*Nicotiana* spp., Solanaceae) are the primary toxic plants in the U.S. that contain pyridine alkaloids, closely related to piperidine alkaloids (Roitman and Panter 1995). Several species of *Nicotiana* poison livestock in the western U.S. (Kingsbury 1964), including *N. tabacum* (Burley tobacco), *N. glauca* (tree tobacco), *N. trigonophylla* (wild tobacco) and *N. attenuata* (wild tobacco). Tree and wild tobacco plants are generally not palatable to livestock grazing on rangelands (Panter et al. 1992). These plants contain nicotine, a well-known toxin, and more importantly, the teratogenic piperidine alkaloid, anabasine (Keeler 1979). Anabasine causes fetal malformations virtually indistinguishable from those caused by *Lupinus* and *Conium* (Panter and James 1995).

Steroidal (*Veratrum*-type) Alkaloids

Major Plant Species

The steroidal veratrum-type alkaloids are found primarily in *Veratrum* species (false hellebore) and *Zigadenus* species (death camas, Liliaceae). Western false-hellebore (*Veratrum californicum* Durand) is the dominant species in the western U.S., and occurs in moist mountain meadows, and along slopes and stream banks. Death camas grows on plains, prairies, and foothill ranges throughout the western U.S. There are several species of death camas, and all should be considered toxic even though toxicity can vary within and among species (Panter and James 1989).

Alkaloids and Mechanism of Intoxication

Veratrum species

False hellebore has long been recognized as a toxic plant for livestock (Hall and Yates 1915), although false-hellebore-induced fetotoxicity in sheep was not reported until 1962 (Binns et al. 1962). The primary teratogen is cyclopamine; the closely-related alkaloid veratramine is very toxic but does not produce abnormalities (Keeler 1983). Ingestion of false hellebore by pregnant sheep on gestation day 14 results in “monkey-faced” or cyclopian lambs with potentially severe craniofacial defects (Binns et al. 1962). The facial defects result from the toxic insult to the neural tube such that the embryonic forebrain fails to divide normally. *Veratrum* alkaloids have a structural resemblance to cholesterol. Recent work suggests that a disruption in cholesterol transport within cells prevents brain cells from recognizing signals to divide properly (Incardona et al. 1998). Other work suggests that cyclopamine may act by competitive binding at Ach receptors (Keeler 1988). Other defects and fetal death are possible at later stages of gestation up to 33 days (Keeler et al. 1986). Sheep are primarily affected because of their propensity to eat false hellebore but cattle and goats are also susceptible. A single dose of 1.5 g of purified alkaloid will cause deformities in sheep (Keeler 1983).

Death camas

Zygadenine was the first steroidal alkaloid found in death camas, but the toxicity has been attributed to zygacine, an acetyl ester of zygadenine (Majak et al. 1992, Makeiff et al. 1997). Zygacine concentrations range from 2 to 4 mg/g, and are highest in vegetative tissue and pods (Majak et al. 1992). Majak et al. (1992) also reported that 2 related forms of zygadenine were not detected in vegetative plants, but concentrations of these alkaloids increased dramatically in pods. The mechanism of action is not known. Zygadenine and numerous related alkaloids were found in death camas (Lang and Smith 1998) collected at the site where 23 cows died in Nebraska (Collett et al. 1996).

Clinical Signs and Diagnosis

Veratrum species

Clinical signs of acute false hellebore poisoning, relatively rare in livestock, include salivation, recumbency, reduced heart rate, and dyspnea (Kingsbury 1964). The fetotoxic effects of false hellebore are not generally overt for the dam. If fetal deformities are severe, the hormonal signals inducing parturition are disrupted and the dead and deformed fetus will be carried well beyond term. These ewes will eventually show clinical signs from the extended gestation and usually die (James 1999).

Death camas

Death camas toxicity is characterized by excessive salivation, frothing around the mouth, nausea and sometimes vomition (Kingsbury 1964, Panter et al. 1987). If the dose is sufficient, muscular weakness is followed by ataxia, recumbency, and death. Affected animals have a rapid, weak heartbeat, and respiratory distress. Death is from heart failure (Panter et al. 1987). Diagnosis is made by recognizing the clinical signs of poisoning, association of affected animals with populations of grazed plants, and pathological examination of tissues from dead animals (Panter and James 1989).

Management and Control

Veratrum species

Livestock management to avoid losses to false hellebore are relatively simple. First, since the window of fetotoxicity is relatively narrow (i.e., 14 to 33 days gestation), pregnant animals (particularly sheep) should not be allowed access to veratrum-infested pastures during this period. Cattle rarely eat the plant, therefore no special management is needed. For sheep, false hellebore is quite palatable, and herders must keep bred sheep from ingesting false hellebore for about 1 month after the rams are removed (Panter et al. 1992). This is not difficult to accomplish because false hellebore is limited in distribution to moist mountain habitats and grows in easy to identify dense patches. Although effective herbicidal control is available (Williams and Cronin 1981), it may not be practical given the location of the major populations in National Forests and the ease with which the problem can be solved by grazing management.

Death camas

Death camas is one of the first plants to grow during spring, and animals may graze the plant if other forage is lacking. Generally, recognizing the presence of death camas and understanding the acutely toxic nature of the plant will aid in avoiding problems. Panter et al. (1987) identified 3 contributing circumstances that resulted in loss of over 250 sheep in one band. First, hungry ewes with lambs were driven through the death camas-infested pasture. Second, sheep were bedded near the death camas, so the plant was readily available for grazing. Third, the herder stressed the sheep by rapidly driving them from the area, thus increasing the death loss (Panter et al. 1987). Death camas can be controlled by phenoxy herbicides (Ralphs et al. 1991d).

Conclusions

Alkaloid-containing plants exact a heavy economic toll on livestock production in rangelands of western North America. Losses to these plants can be reduced or eliminated by recognizing the toxic plant responsible for specific losses, understanding when livestock graze the plant and how the toxin affects animals, altering management schemes or animal species to reduce the risk of losses, or using herbicidal control. Management of each toxic plant species is based on knowledge of the temporal and spatial dynamics of alkaloid concentration and consumption by livestock. Losses may be reduced by ensuring that livestock are not exposed or have reduced exposure either during periods of greatest risk (e.g., highest toxin concentrations), or when they are most likely to eat the plant in amounts sufficient to cause toxicity.

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Anti-quality effects of insects feeding on rangeland plants: A review

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Abstract

The anti-quality effects of the major groups of insects that utilize rangeland plants for food is discussed. The biology, ecology, geographical distribution and economic thresholds of grasshoppers, crickets, Western harvester ants, ranch caterpillars, big-eyed or black grass bugs, and white grubs are reviewed. Also discussed are practical pest management strategies if they exist. Most of these rely on the integration of good range management practices and the control strategy.

Resumen

Se discuten los efectos anti-calidad de los principales grupos de insectos que utilizan las plantas del pastizal como alimento. También se revisó la biología, ecología, distribución geográfica y umbrales económicos de chapulines, grillos, hormigas cosechadoras del oeste, orugas de rancho y pulgas ojonas o chibches negras de zacate y gusanos blancos. También se discuten las estrategias practicas del manejo de plagas, si ellas existen. Muchas de ellas se basan en la integración de buenas practicas de manejo del pastizal y la estrategia de control.

Key Words: Grasshoppers, harvester ants, range caterpillar, big eyed bugs, rangeland insects.

In the United States, over 1,500 species of insects have been noted as being in association with the range ecosystem (Kumer et al. 1976, Thomas and Werner 1981). Fortunately, most of these are not economic in terms of detrimental effects on range plants. The best known damaging species belong to the insect order of Orthoptera—grasshoppers, Hymenoptera—ants and termites, Lepidoptera—caterpillars, Coleoptera—beetles, and Homoptera—leafhoppers. Insects are a significant factor in energy flow, nutrient cycling, water utilization and vegetative changes in a range ecosystem.

Many entomology textbooks refer briefly to range insects, but the 2 major publications that deal specifically and exclusively with the subject are Haws et al. (1982) “An Introduction to Rangeland Insects of the Western United States” and Watts et al. (1989) “Rangeland Entomology”. This latter publication has been noted as the world’s most authoritative treatment on the important role of insects in rangeland ecosystems. Another publication of note is Pfadt (1994) “Field Guide to Common Western Grasshoppers”. This publication contains colored plates of adult and nymphs of the major rangeland grasshoppers, and the text details the biology habitat and feeding choices for each species. This publication by itself is a Wyoming Experiment Station Bulletin, but it is included in the USDA—APHIS Technical Bulletin 1809 “Grasshoppers Integrated Pest Management User Handbook”. This latter publication contains material by numerous authors on range management considerations to reduce damage from grasshoppers and/or to reduce grasshopper numbers based on range management techniques (Anonymous 1996).

Grasshoppers are the most serious of the insect groups that contribute to the anti-quality of range plants. While there may be 50 or more species present at a certain type of range, only 8 or 9 species are really causing economic losses. Some species are considered beneficial in that they fed only on plants that are considered detrimental to the range. For example, *Hypochlora alba* (Dodge) feeds primarily on Louisiana sagewort, *Artemsia ludoviciana* Nutt., and secondarily on Western ragweed, *Ambrosia psilostacka* D.C. The genus Hesperottix feeds mainly on Western ragweed and Missouri goldenrod, *Solidago missouriensis* Nutt., (Campbell et al. 1974).

Grasshoppers are classified as grass feeders, mixed feeders or forb feeders based on the mandibular type. Generally, the outbreak populations belong to the mixed feeder group. Another classification is slant-face, to which most of the grassfeeders belong, and the spur throat to which most of the mixed feeders belong, and band-wings, which are mostly large grasshoppers that may be either mixed or forb feeders.

There are 3 life stages in the grasshopper life cycle—egg, nymph and adult. Eggs are deposited in soil and a frothy, sticky material is secreted with egg deposition which forms an insulated pod composed of soil particles. The number of pods and eggs per pod varies with species. Some species deposit eggs in soil surrounded by roots of grasses; other species select open areas with accumulations of surface debris.

Most grasshopper species overwinter in the egg stage, but a few overwinter as nymphs. Hatching time is influenced by temperature and can be correlated with soil temperature. In the Northern Plains states, cool-season grasses such as needlegrasses *(Stipa spp.)*, wheatgrasses *(Agropyron spp.)* and bluegrasses *(Poa spp.)* begin growth before grasshoppers become very active. By the time grasshoppers begin to defoliate plants, these grasses have completed growth and have enough energy reserves needed for spring growth the following year. The warm-season grasses such as the bluestems *(Agropogan spp.)*, grama grasses *(Bouteloua spp.)* and buffalograss *Buchloe doctyloides* (Nutt.) Engelm., do not begin growth until May and grow most rapidly when temper-

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atures reach 85–95°F, which coincides with the greatest grasshopper feeding activity.

Grass responses to defoliation includes stoppage of root growth and nutrient uptake for several days if more than half of the green herbage is removed. "Shutdown" or "slow-down" periods in roots increase as severity and frequency of defoliation increase. Removing more than 65% of the green herbage one time during the growing season can reduce total root length by 30% or more. If this occurs over several years, plants become weak and die (Campbell et al. 1998).

Damage caused by grasshoppers is more than actual consumption of forage. They cut stems and blades while eating only part of them. They eat closer to the ground than livestock and may kill growing tips of grasses. They cut off seed stocks, reducing seed production, and soil erosion may result from denudation by heavy populations.

Personnel from the Bureau of Entomology and Plant Quarantine kept seasonal grasshopper density records for western ranges from 1932—1952. They estimated that the average number of 1.2 grasshoppers/m^2 would eat or destroy 14.65 million tons of forage on the 262 million acres of western rangeland. This would have provided feed for another 4.9 million animal units (unpublished data Cowan and Bell 1973).

Crickets are close relatives of grasshoppers and have had sporadic outbreaks for over a century. In outbreak years, they increase in number and form great migratory bands (Watts et al. 1982). During these outbreaks, they may denude the rangeland of practically all plants. They have been reported to feed on 250 species of range plants (Cowan and Shipman 1947). They seem to have a preference for flower and seed parts reducing the reseeding potential of the plants, and if denuding occurs later in the year, the plant wouldn't be able to store nutrients in the roots for overwintering. The Morman cricket has a similar life cycle to grasshoppers except that they are wingless. All crickets in the migratory band move in the same direction, and the movement is about 0.8 km per day or 40 km (25 miles) in a season (Ueckert 1970).

Western Harvester Ants

The genus *Pogonomyrinex* is the primary group of harvester ants in North America. Cole (1968) has described 22 species. This group ranks next to grasshoppers in terms of rangeland damage. Lavigne and Fisser (1966) indicate the mounds created by the ants may be a foot high and 30 feet in diameter. The area around the mound is denuded of all vegetation. Not only is the vegetation destroyed, but wind erosion increases in the denuded areas. The ants also collect seeds that may affect plant production, particularly with annual plants. Colonies survive for 15–20 years, and one mound may consist of as many as 60 chambers. Winged reproductive ants may appear in May after a rain, but some also appear in the summer and fall. New colonies are formed by mated queens usually in later summer. After mating, the queen sheds her wings and digs a burrow several inches deep in the soil. The first brood is composed mostly of female workers. This brood forages, enlarges the colony, cares for the young and protects the mound. The workers move the eggs of the second brood to newly-constructed chambers which have been stocked with seeds and insect parts as a food source.

Most of the mound expansion is in the spring, but there is no regrowth in the denuded area later in the season. Lavigne and Fisser (1966) estimated that a single acre of rangeland supported as many as 15 colonies. Worker ants from this number of colonies stripped vegetation from as much as one-seventh of an acre. As is true for grasshoppers, overgrazed range suffers the most damage from the red harvester ant. Grazing management will serve to slow the increase of new mounds. Insecticides can be used to treat the mounds, but this is labor intensive and should be approached from an area-wide control effort to be successful.

Rangeland Caterpillar–Hemilenca oliviae Cockerill

The range caterpillar has 3 discontinuous populations, one in Mexico, one in southcentral New Mexico and the third in northeastern New Mexico, Colorado, Oklahoma and Texas. Dubach et al. (1988) and Shaw et al. (1987) believe these were once a continuous population. Currently the distribution of the 3 populations are separated by brush-infested areas which may have been devoid of brush in earlier times. The caterpillar distribution is generally in blue grama-dominated rangeland at elevations between 1,350 and 2,400 meters. The northern distribution into Colorado is probably limited by decreasing late summer precipitation.

Caterpillars consume grass, often down to the crown, waste unconsumed portions of leaves as do grasshoppers, and in addition, discourage grazing because of urtrication spines from both the larvae and their shed skins. These spines cause irritation around the mouth and nose of livestock. The larvae may tie several grass stems together with the cast skin. Livestock tend to avoid grazing in these areas because of the spines.

As the populations become larger, food consumption is heavy. They may destroy all of the green grass down to and including some of the crown. If drought conditions exist, there is little regrowth, and the roots are unable to store nutrients for the winter, and there is no reseeding of annual plants.

As they search for food, caterpillars gather in bands a meter or more wide and several kilometers in length. Ranchers refer to the feeding of these bands as "windrowing". The range caterpillar feeds on 40 or more species of grass (Wildermuth and Caffrey 1916, Capinera 1978). Huddleston et al. (1976) established the economic threshold as 2 large larvae/m^2. Similar values were derived by laboratory and model studies (Bellows et al. 1983, Capinera et al. 1983, Riley et al. 1984).

The adult range caterpillar is a buff to brown moth with a wing span of 50–70 mm. The female mates and deposits eggs and dies within about 3 days. Eggs are deposited in cylinder-shaped clusters on plants. Larvae undergo six molts before pupating. This takes 12–14 weeks if hatch occurs in the spring but only 7 or 8 if the hatch occurs in the summer.

The range caterpillar has in the past been considered cyclic which is probably true in the sense of large populations in extensive areas. In recent years, some extensive damage has occurred in localized areas virtually every year.

Control has changed from massive aerial spray programs over large areas to smaller mist applications of pyrethroids to localized areas. If the infestation is early and appropriate timing of insecticide applications occurs in a year with at least some moisture, grassy vegetation may recover.

White Grubs

Beetles from the family Scarabaeidae are among the most numerous on range. Those beetles that have grubs as the immature stage are the most damaging. In most species, plant damage occurs from the grubs feeding on roots which kills the grass; however, adults of a few species also cause plant damage. Kumer et al. (1976) collected 37 species from shortgrass prairie in northeastern Colorado. Only 9 species of the group were associated with root feeding, most of the rest were dung beetles. The *Phyllophaga* spp. complex are the best known plant damaging group (Anonymous 1971a, 1971b).

The white grubs (May–June beetles) are creamy white with a shiny brown head, have 6 prominent legs and are generally shaped like a "C". Much of the damage on rangeland probably goes unnoticed if it is of moderate intensity. It is generally diagnosed as plant stress as a result of drought.

Heavy damage may occur only in spots ranging from 10—100 meters in diameter. In some areas such as the Nebraska Sandhills, damage may occur only in wet meadows that are a valuable hay or grazing source. In addition to destruction of the grass, other problems may occur. Annual weeds often invade and dominate the area for a number of years (Randolph and Garner 1961). Drake (1964) suggests that feeding by white grubs creates a mode of entry for bacterial and fungal diseases that kill the weakened plant.

Skunks and other rodents may cause further damage to plants by digging up grubs as a food source. This occurs in Nebraska in the wet meadow areas. Although there are certain cultural or chemical control measures that reduce grub numbers, they would only be economical to employ where a crop such as wheat is concerned. There is no practical economic method for control of white grubs on rangeland.

The life cycle of the white grub may take 3–4 years dependent on the species and climate. Most of the damage is done in the second year. The beetles deposit eggs in late spring or early summer. Some feeding occurs the first season. Grubs move below the frost line until spring, then move close to the surface to feed on roots. The same procedure occurs each year in the cycle. When the larval cycle has been completed, an earthen cell is prepared and pupation occurs within the cell. The adults remain in the cell until spring when they emerge and start another generation.

Miridae (Plant bugs)

Many species of this family are associated with range plants. They have piercing sucking mouth parts with which they suck juices from plants.

The black grass bugs are the best known of this group of insects. They are also called big-eye bugs because their eyes appear to be bulging from the side of their heads. There are 34 species from 2 genera; *Labops* and *Irbisia* in this group (Kelton 1980).

Insects such as black grass bugs that feed by sucking fluids from the cell have considerable impact on range plant quality, quantity and plant survival (Haws et al. 1982). The adults of this group are about 6 mm long and are blackish grey, with buff margins around the edges of the wing. *Labops* have vestigial hind wings, but *Irbisia* have well-developed wings.

Adult females of the big-eyed bugs deposit eggs into grass stems in the fall. The nymphs hatch in the spring in the warmer lower areas and later in the cooler upland areas.

The black grass bugs were first noted as pests around 1950 when range improvement programs were replacing native grasses with introduced grasses especially wheatgrasses. The large areas of a single species of grass provided an excellent niche for the black grass bugs (Higgins et al. 1977). A density of 156/m^2 reduced seed head production in intermediate wheatgrass by 56% (Malechek et al. 1977). Ansley and McKell (1982) showed the black grass bug feeding reduced leaf length, seedhead height and carbohydrate reserves in root crowns in crested wheatgrass.

Control strategies include application of insecticides, (Hagen 1975, Dickerson 1978) or heavy grazing in the spring, (Kamm and Fuxa 1977, Hagen 1975). Insect resistant varieties have also been evaluated. Hewitt (1980) reported that tall, slender, intermediate and pubescent wheatgrasses were somewhat tolerant to feeding by the black grass bugs.

There are many other insect species that may sporadically cause severe damage to rangeland in some limited areas. Termites, armyworms, army/cutworms, leafhoppers, plant hoppers, spittle bugs, wireworms, billbugs and numerous others feed on range plants, but generally are not numerous enough to warrant expensive control techniques.

One other group of insects I was requested to mention are blister beetles. Blister beetles are generally considered beneficial in that the larvae of several species are predacious on grasshopper eggs. Others are predaceous in the cells of ground-dwelling species of bees.

Adult blister beetles tend to be gregarious, and several may be noted feeding on the same flowering alfalfa plant. They also feed on soybeans and blooming goldenrod and probably other plant species found in a range plant complex.

Adult blister beetles vary in size and color, but are easily recognized by the elongated, narrow, cylindrical and soft bodies. When viewed from above, they have a constriction at the back of the head where it attaches to the narrowed anterior end of the thorax (Bauernfeind and Breeden 1984). The life cycle of blister beetles is complex with several different immature forms. Clusters of eggs are deposited in the ground. Newly-hatched larvae move through the soil feeding on grasshopper egg pods. This larval stage is termed triungulin. Within a month, the larvae pass through three more stages with each becoming more sedentary. Finally, they change to the pseudopupae which is the overwintering stage. As temperature and moisture increase in the spring, they enter the final immature pupal stage from which adults emerge. There is 1 generation per year.

The interest in the blister beetles is not from the standpoint of damage to range plants but because of the injury to horses or other livestock. They may actually ingest a blister beetle. The bodies of the blister beetles contain a vesicant substance called cantharidan. This substance causes blisters on skin tissue upon contact. It is usually ingested with the consumption of alfalfa hay. Horses are very susceptible to blister beetle poisoning. Portions or all of the horse digestive tract can be severely irritated bringing about secondary infections and bleeding (Bauernfeind and Breeden 1984). Cantharadin is absorbed and excreted through the kidneys, thus irritation of the kidney, ureter, urinary bladder and urethra could be followed by secondary infections and bleeding. The substance also lowers calcium levels and causes damage to heart muscle tissue.

Capinera et al. (1985) conducted cantharadin analysis on several species of blister beetles commonly found in Colorado. There were differences in amounts found between species and sexes. Males apparently produce cantharadin and pass it to females at mating. The minimum lethal dose of catharadin is about 1 mg/Kg. Thus a few beetles with a high catharadin level would kill a small horse, but quite a few with a low level would be required to kill a large horse.

Extension entomologists field quite a few questions yearly from either horse owners or alfalfa producers on how to avoid buying or selling alfalfa hay that contains blister beetles. Generally, blister beetles are present at the second and third cuttings, but probably will not be in the first or fourth cuttings; however, in 1998 in Nebraska, blister beetles were still present at the time of the fourth cutting. Inspection of bales is not practical because the gregarious behavior of the beetles might cause one bale to have a large number of beetles, and the next bale might not have any. For the same reason, chemical control is probably not practical either unless hay for horses was bringing a premium price. Dead beetles are still toxic. Killing the beetles doesn't reduce the toxicity.

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Effects of proanthocyanidins on digestion of fiber in forages

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Abstract

The ability of proanthocyanidins (PA) to form insoluble complexes with proteins and polysaccharides affects fiber digestion and analysis. This review discusses these effects in relationship to the application of the detergent system of forage analysis. A fraction of the PA in plants remains after extraction for analysis. Insoluble PA may be a natural part of the plant cell wall or may be insoluble because of high molecular weight and post harvest reactions. These reactions increase the amount of insoluble PA and decrease the amount of soluble PA. The butanol-HCl assay is the most suitable method for analysis of insoluble PA. Insoluble PA are associated with negative apparent digestion coefficients for acid-detergent lignin (ADL), neutral-detergent insoluble N and acid-detergent insoluble N. The addition of sodium sulfite to neutral detergent eliminates insoluble PA from NDF. However, the addition of sodium sulfite to neutral detergent will give misleading results in relationship to true digestibility of protein. The difference between fiber fractions that are prepared with and without the addition of sodium sulfite to neutral-detergent may estimate the amount of PA/protein complex associated with NDF. A better understanding of the relationship between PA structure and function is necessary to manipulate PA in forages through breeding or genetic engineering. The interaction between PA and fiber analysis and digestion is an important component of this research.

Key Words: condensed tannins, neutral detergent, acid detergent, lignin, polyphenolics

Resumen

La capacidad de las proantocianidinas (PA) para formar complejos insolubles con proteínas y polisacáridos afectan la digestión de la fibra y su análisis. Esta revisión discute estos efectos en relación a la aplicación del sistema de detergente del análisis de forrajes. Una fracción de las PA en las plantas permanecen después de la extracción para el análisis. Las PA insolubles pueden ser una parte natural de la pared celular de la planta o pueden ser insolubles debido al alto peso molecular y reacciones post-cosecha. Estas reacciones aumentan la cantidad de PA insoluble y disminuyen la cantidad de PA soluble. El método de Butanol-HCL es el mas apropiados para el análisis de PA insolubles. Las PA insolubles son asociadas con coeficientes negativos de digestión aparente de la lignina acido detergente (ADL), N insoluble neutro detergente y N insoluble acido detergente. La adición de sulfito de sodio a l detergente neutro elimina las PA insolubles de la NDF. Sin embargo, la adición de sulfito de sodio al detergente neutro producirá resultados erróneos en relación a la digestibilidad verdadera de la proteína. La diferencia entre las fracciones de fibra que son preparadas con y sin la adición de sulfito de sodio al detergente neutro pueden estimar la cantidad del complejo PA/proteína asociado con la NDF. Se necesita un mejor entendimiento de la relación entre la estructura y función de las PA para manipular las PA en los forrajes a través del mejoramiento o ingeniería genética. La interacción entre las PA,el análisis de fibra y la digestión es un componente importante de esta investigación.

Proanthocyanidins (PA) are naturally occurring plant polyphenols that strongly influence the nutritive value of forages. In general, PA and condensed tannins are synonyms. Phytochemists prefer to use proanthocyanidin because, as discussed below, this term is more closely related to their chemical structure. Most nutritionists use “condensed tannins” because tannins are defined as water-soluble polymeric phenolics that precipitate proteins (Haslam 1989). However, many soluble phenolics that have structural and chemical properties that are similar to PA do not precipitate proteins. There are also high molecular weight PA that have structures related to tannins but that are not water-soluble (Bate-Smith 1973, Stafford and Cheng 1980).

Proanthocyanidins in forages have both negative and positive effects on nutritive value (Reed et al. 1990, Mueller-Harvey and McAllan 1992). In high concentrations, PA reduce intake, digestibility of protein and carbohydrates, and animal performance (Barry and Duncan 1984, Reed et al. 1990). In low to moderate concentrations, PA prevent bloat and increase the flow of non-ammonia nitrogen and essential amino acids from the rumen (Egan and Ulyatt 1980, Barry and Manley 1984, Waghorn et al. 1987, McNabb et al. 1993). The positive effects of tannins on protein utilization have practical importance because problems associated with extensive proteolysis and (or) deamination in the rumen limit production in modern feeding systems (Beever et al. 1989). Proanthocyanidins may also protect ruminants against helminthiasis. Undrenched lambs grazing sulla (*Hedysarum coronarium* L.), a forage that contains PA, had lower fecal egg counts and *Trichostrongylus colubriformis* worm burdens and higher average daily gains than undrenched lambs grazing alfalfa (*Medicago sativa* L.), which does not contain PA (Niezen et al. 1995). Several useful reviews on the nutritional effects of PA and tannins in the diets of ruminants have been written in recent years (Mueller-Harvey and McAllan 1992, Reed 1995, Waghorn et al. 1999).

Research on the relationship between concentration of PA in forages and parameters of nutritive value is complicated by inadequate methodology for quantification and structural analysis. The ability of PA to form strong complexes with proteins is the most important aspect of their nutritional and toxic effects (Hagerman and Butler 1981). The strength of these complexes depends on characteristics of the PA and protein (molecular weight, tertiary structure, isoelectric point, and compatibility of binding sites). Proanthocyanidins have a large number of free phenolic hydroxyl groups that form strong hydrogen bonds with

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proteins and carbohydrates (Haslam 1989). Proanthocyanidins also complex with proteins through hydrophobic bonding (Oh et al. 1980). In addition, PA form covalent bonds with proteins through oxidative polymerization reactions as a result of heating, exposure to ultraviolet radiation and the action of polyphenol oxidase (Haslam 1989). The ability of PA to form insoluble complexes with proteins and polysaccharides leads to several effects on fiber digestion and analysis. This review discusses these effects in relationship to the application of the detergent system of forage analysis.

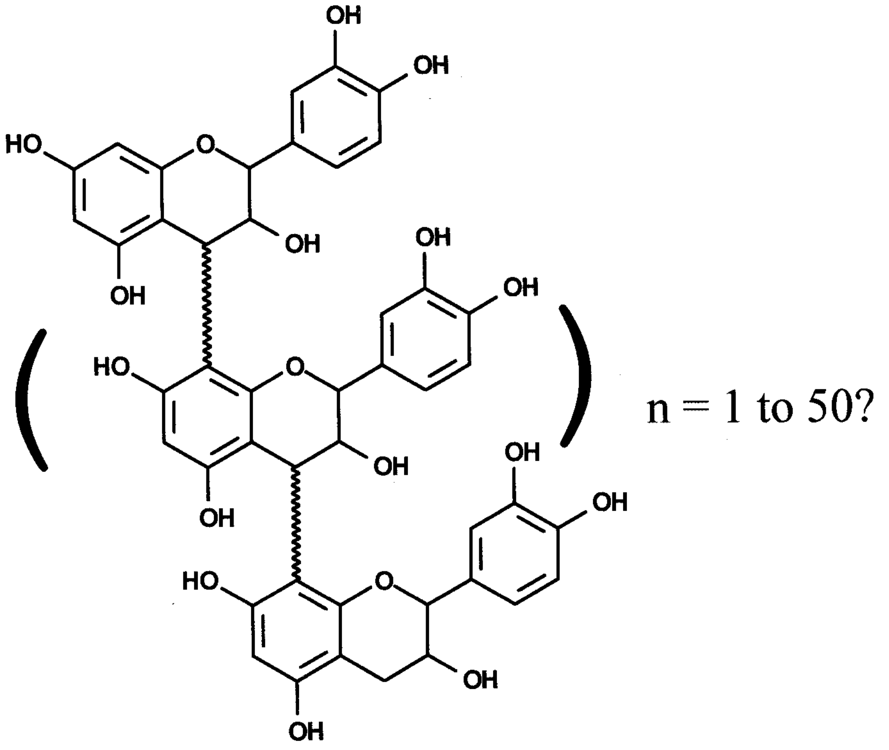

Fig. 1. Structure of proanthocyanidin polymers.

Chemistry and Nomenclature of Proanthocyanidins

Proanthocyanidins are polymers that belong to the class of secondary plant compounds known as flavonoids (Harborne 1994, Haslam 1989, Stafford 1990, Foo et al 1982). Monomeric and polymeric flavonoids are ubiquitous in higher land plants and have many ecological and nutritional effects on animals (Harborne 1993). The principal structure of PA is based on repeating units of polyhydroxy flavan units linked by C bonds between carbons 4 and 8 of the ring structures (Fig. 1). These covalent bonds are resistant to hydrolysis and no known enzyme is capable of cleaving the interflavan bond.

However, PA undergo a cleavage reaction upon heating with strong acids. This reaction is an auto-oxidation to form an intermediate that undergoes oxidation to an anthocyanidin. The term proanthocyanidin (PA) is prefered over condensed tannin because their discovery and distribution in plants was determined by this characteristic auto-oxidation reaction. Therefore, PA are defined as colorless plant compounds that form anthocyanidins upon heating in solutions of strong acids. Specific names for PA are given based on the type of anthocyanidin formed during the autoxidation reaction. Proanthocyanidins that yield cyanidin are termed procyanidins and those that yield delphinidin are termed prodelphinidin (Fig. 2). These 2 PA are the most common but many diverse PA occur in plants including propelargonidin and proluteolinidin. One problem with this nomenclature is that it implies that the proanthocyanidins are homopolymers. However, as we learn more about the structure of PA it is clear that many heteropolymers occur in nature. Proanthocyanidins have been described with glycosylation, acylation with gallic acid, and other substitutions (Porter 1994).

The solubility and extraction of PA in forage legumes were initially studied by Bate-Smith (1973). This research demonstrated that substantial amounts of PA are not extracted by aqueous organic solvents and remain in the fibrous residue after extraction. The origin of these insoluble PA remains somewhat controversial. Haslam (1989) proposed that PA are a natural part of the plant cell wall with covalent bonds to cell wall polysaccharides. On the other hand Stafford (1988) suggests that PA are insoluble because of high molecular weight and post harvest condensation reactions with proteins and cell wall polysaccharides. Regardless of the mechanism, a fraction of the PA in most plants remains after extraction for analysis. This fraction has a large effect on the analysis of fiber and its relationship to nutritive value and is the main topic of this paper. In species such as sainfoin (*Onobrychis viciifolia* Scop) and *Gliricidia sepium* (Jacq.) Stewd., the insoluble fraction represents the greatest amount (Bate-Smith 1973, Giner-Chavez et al. 1997, Jackson et al. 1996).

The proportion of insoluble PA in plants also appears to be under genetic control. In group II genotypes of sorghum all of the PA in the grain are insoluble in aqueous organic solvents unless HCl is added to the extraction procedure (Price et al. 1978). Our research on the inheritance of PA among interspecific crosses of *Sesbania sesban* (L.) Merr. and *S. goetzei* Harms also indicates that insoluble PA is a heritable characteristic (Table 1). *Sesbania goetzei* has a large quantity of insoluble PA in comparison to *S. sesban*. The hybrid had the same levels of insoluble PA as *S. goetzei* and a higher amount of soluble PA in comparison to *S. sesban* (Table 1).

Table 1. Extractable and insoluble proanthocyanidins (PA) in leaves from *Sesbania sesban* and *S. goetzei* and their interspecific crosses.

Species	Extractable PA	Insoluble PA
	$(A_{550})^1$	$(A_{550})^2$
S. sesban	0.503	0.263
S. goetzei	0.556	0.727
S. sesban x *S. goetzei*	0.928	0.821
S. goetzei x *S. sesban*	0.807	1.029

[1] Absorbance at 550 nm from the butanol–HCl reaction of the extract of 100 mg of DM in 15 ml of aqueous acetone.
[2] Absorbance at 550 nm from the butanol HCl reaction on 5 mg of neutral–detergent fiber.

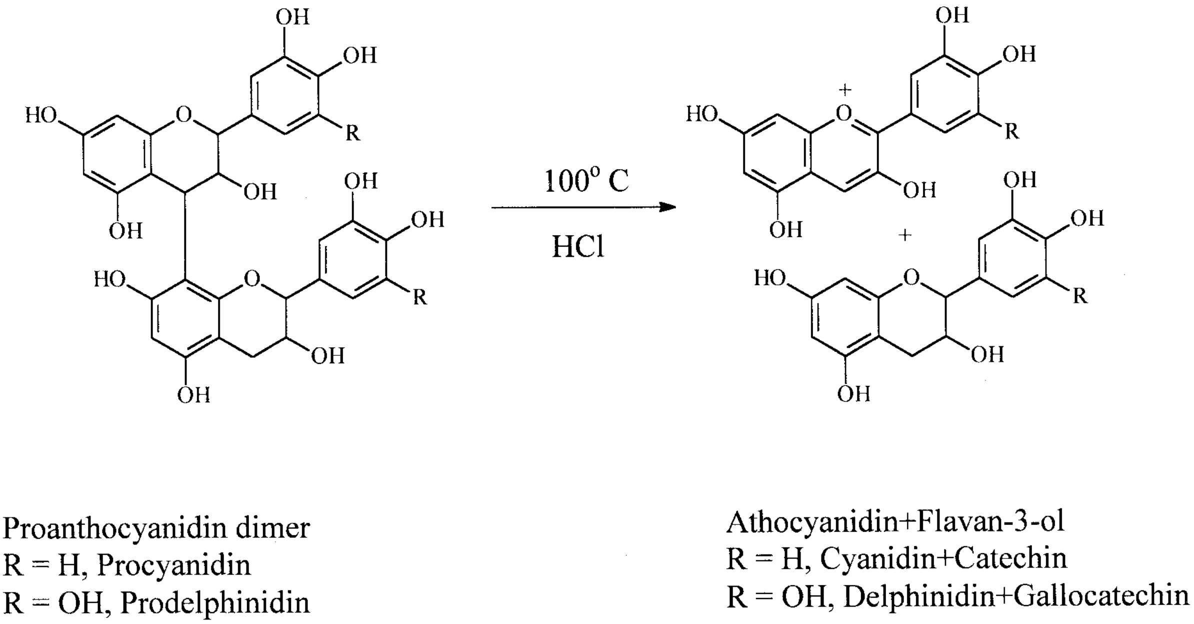

Fig. 2. Butanol–HCl reaction of proanthocyanidins.

Analytical Methods

The quantification of PA in plants is essential to studies on their nutritional and ecological effects (Feeny and Bostock 1968, Swain 1979, Horvath 1981, Martin and Martin 1982, Waterman and Mole 1994). However, the commonly used methods of colorimetric analysis have many problems (Tempel 1982, Martin and Martin 1982). There are a growing number of analytical methods for the determination of PA in plants (Waterman and Mole 1994). However, no single method will give satisfactory results for quantitative analysis in relationship to nutritional effects because the chemical properties that are involved in the reactivity of PA in colorimetric and (or) precipitation assays differ from the properties that underlie their nutritional or toxic effect. Animal species also differ in nutritional response ingesting plants that contain PA (Hagerman et al. 1992). Sample preparation also has a large influence on the determination of PA and related polyphenols in plants. Proanthocyanidins in fresh samples are likely to have low complex formation and oxidative polymerization and high solubility in aqueous organic solvents. If storage is necessary, freezing is preferred over other methods as long as the samples are not allowed to thaw before extraction (Mould and Robbins 1981). In some situations, drying is the only means of preserving material. At low temperatures (< 40° C), enzymes may still function leading to oxidation. At temperatures above 60° C, heat damage and polymerization may occur (Haslam 1966). These post harvest reactions increase the amount of insoluble PA and decrease the amount of soluble PA. If the researcher does not attempt to assay for insoluble PA then the total amount will be severely underestimated in the case of oven drying.

The most commonly used colorimetric procedures for the analysis of PA are the the vanillin-HCl reaction (Broadhurst and Jones 1978) and the butanol-HCl reaction (Bate-Smith 1973, 1975). The vanillin-HCl reagent is specific for flavan-3-ols and proanthocyanidins. The reaction is based on the condensation of the phenolic aldehyde (vanillin) with the phloroglucinol structure of flavan-3-ols and proanthocyanidins under acidic conditions in methanol or ethanol. The butanol-HCl reaction is specific to the proanthocyanidins and is the prefered method because of its close relationship to the accepted nomenclature. The butanol-HCl method can also be applied to insoluble PA by placing the fibrous residues after extraction into the solution. After heating, the red pigments formed during the auto-oxidation reaction go into solution.

These colorimetric procedures share the analytical problem of lack of suitable standards. The most commonly used standards are catechin for the vanillin-HCl reaction and quebracho tannins for the butanol-HCl reaction. However, the extinction coefficients for the chromophores produced in the reaction with these standards usually are different than the compounds from the plant extracts. This difference can lead to large under and over estimations of the content of PA and is probably the single largest cause for the great deviation in concentrations that are reported in the literature (Giner-Chavez et al. 1997). Another problem is that the mechanism that leads to the reaction of PA with the analytical reagent is unrelated to the mechanism underlying their nutritional effects (Reed 1995). The most suitable method is to use the butanol-HCl assay and isolate the PA from the plant species under investigation for use as a standard. Reversible adsorption of PA from plant extracts onto Sephadex LH-20 is a commonly used method for isolating PA from plants (Hagerman 1991, Giner-Chavez et al. 1997). Reed et al. (1985) developed a gravimetric method based on the ability of trivalent ytterbium to selectively precipitate PA from plant extracts. The advantage of Yb precipitation is that the precipitate can be easily dissolved to yield a solution of the PA. These solutions are used for colorimetric analysis (Giner-Chavez et al. 1997), chromatography, enzyme inhibition studies and in vitro and in vivo assays for inhibition (Reed et al. 1985). The results from the assays on the dissolved PA also relate to an equivalent weight of PA precipitate. The 2 methods for isolating PA give similar results for several species of forages (Giner-Chavez et al. 1997).

Effects of Proanthocyanidins on Fiber Analysis

The extraction of PA from plant samples is a problem that is often overlooked in PA analysis. Bate-Smith (1973) showed that, in sainfoin (*Onobrychis viciaefolia*), a significant percentage of the PA is not extracted by aqueous organic solvents. The extraction is improved by fine milling and using hot methanol, but there is always a substantial amount of PA which remains in the fibrous residue after extraction. High molecular weight PA may be completely insoluble in aqueous organic solvents (Stafford and Cheng 1980).

Much of the PA remains in the neutral-detergent fiber (NDF) after sequential extraction of several browse species with aqueous acetone (7:3, acetone:H_2O) followed by neutral detergent (Reed et al. 1982, Reed 1986). This problem is common in several types of feeds that contain PA (Terrill et al. 1992). Insoluble PA in the NDF of sorghum grain was inversely correlated with soluble PA ($r = -.69$, $p < .01$, $n = 16$) in brown and red varieties (Reed 1987). These results suggest that analysis of extractable PA may underestimate the total PA content in many samples.

The amount of PA in the fiber fractions can be estimated by using the butanol-HCl assay (Bate-Smith 1973, Reed et al. 1982, Terrill et al. 1992). The nutritional effects of the insoluble PA have not been adequately studied. They are associated with negative apparent digestion coefficients for acid-detergent lignin (ADL), neutral-detergent insoluble N and acid-detergent insoluble N in browse legumes (Reed et al. 1990, Wiegand et al. 1995). Increased total fecal excretion and increased fecal excretion of water, fat, and nitrogen were observed in rats fed carob pod concentrate that contained non-extractable condensed tannins (Bravo et al. 1993).

Terrill et al. (1992) developed a method to determine the extractable PA, protein-bound PA and fiber-bound PA in forages and protein concentrate meals. The method uses a modified butanol-HCl procedure. Protein-bound PA in the fiber remaining after extraction with aqueous acetone is extracted with a solution of sodium dodecyl sulphate (SDS) and 2-mercaptoethanol. The fiber-bound PA is determined directly on the residue after extraction with SDS. The ratio of extractable PA to protein-bound PA to fiber-bound PA was highly variable among these feeds but in each case the fiber-bound fraction was the lowest (Table 2). Similar results were obtained for tropical tree, shrub and forage legumes by using this method (Jackson et al. 1996). Similar results were also obtained by Giner-Chavez et al. (1997) by using a different methodology. *Gliricidia sepium* had the highest proportion of protein-bound and fiber-bound PA in the studies of Jackson et al. (1996) and Giner-Chavez et al. (1997).

Table 2. Extractable, protein-bound and fiber-bound proanthocyanidins in species of forages.

Source and Species	Extractable	Protein–bound	Fiber–Bound
	- - - - - - - - - - - - - - - - - -	(g/kg)	- - - - - - - - - - - - - - - - - -
Terrill et al 1992:			
Lotus pedunculatus	59	14	1
Lotus corniculatus	7	13	1
Hedysarum coronarium	23	13	1
Jackson et al 1996:			
Calliandra calothyrsus	103 to 158	10 to 28	4 to 8
Flemingia macrophylla	19 to 198 1	6 to 98	3 to 32
Desmodium ovalifolium	82 to 197	16 to 30	8 to 10
Giner–Chavez et al 1997:			
Desmodium ovalifolium	63 to 272 1	4 to 35	1 to 10
Gliricidia sepium	0 to 43	21 to 120	2 to 29
Manihot esculenta	22 to 126	12 to 22	0 to 1

The assumption in the butanol HCl reaction of the insoluble and fiber bound PA is that the stoichiometry of the reaction is identical to the extractable PA that was isolated from the plant species for use as a standard. This is unlikely to be the case. The butanol HCl reactivity for the fiber bound PA is likely to be much lower than the extractable PA that was used as a standard. The formation of an insoluble complex between PA and protein or polysaccharide is likely to decrease the reactivity of the PA in the auto-oxidation reaction that occurs in the butanol HCl reagent. This difference in reactivity would lead to an underestimation of the amount of fiber-bound PA.

Effect on Fiber Digestion

Proanthocyanidins reduce cell wall digestibility by binding bacterial enzymes and (or) forming indigestible complexes with cell wall polysaccharides (Barry and Manley 1984, Barry et al. 1986, Reed et al. 1990). Digestibility of fiber fractions was low for sheep fed *Acacia cyanophylla* Lindl., a tree legume with a high content of PA when compared to sheep fed forages that did not contain PA. Digestibility of acid detergent lignin in *A. cyanophylla* was negative (Reed et al. 1990).

The recovery of PA in digestion balance studies with forage legumes that contain PA also presents an analytical problem. Studies carried out with ^{14}C labeled PA indicate that they are not absorbed from the digestive tract of chickens (Jimenez-Ramsey et al. 1994) and sheep (Terrill et al. 1994). Terrill et al. (1994) recovered 92% of the labeled PA in the digesta and no label was found in the blood. However, only 42% of the PA could be accounted for by direct analysis of PA by butanol-

Table 3. Soluble and insoluble proanthocyanidins and digestibility of acid–detergent lignin (ADL) by rams in 3 accessions of *Sesbania sesban* (10865, 15019, and 15036) and 1 accession of *S. goetzei* (15007). Rams were supplemented with leaves from *S. sesban* or *S. goetzei* to supply 3 levels of crude protein.

	Sesbania accession				
	10865	15019	15036	15007	
Soluble PAs[1] (A$_{550}$/g DM)	13	35	93	95	
Insoluble PAs[1] (A$_{550}$/g DM)	24	48	71	271	
Level of CP from *Sesbania* (g/day)					mean
	----------------------	----------------------	% ADL	----------------------	----------------------
25	15.1	–26.8	–69.3	–100.2	–45.3
50	7.1	–40.2	–95.2	–163.4	–72.9
75	11.2	–46.1	–110.7	–166.7	–78.1
mean	11.2	–37.7	–91.7	–143.4	–65.4

[1] Values for proanthocyanidins were determined by analysis with butanol–HCl and expressed as absorbance units per g of dry matter analyzed.

HCl analysis of feed and digesta. The reactivity of PA in butanol-HCl is most likely altered in the process of digestion. This change in reactivity may be related to the increase in ADL and detergent insoluble nitrogen fractions of digesta and feces that is observed in ruminants fed forages that contain PA (Reed et al. 1990, Yocum and Reed 1994, Yocum 1995, Wiegand et al. 1995).

Proanthocyanidins and the Detergent System of Forage Analysis

Research on the use of 3 accessions of *Sesbania sesban* and 1 accession of *S. goetzei* as sources of protein in diets for sheep demonstrated the effects of PA on the application of the detergent system of forage analysis (Wiegand et al. 1995). Accessions with a high content of PA had negative digestion coefficients for neutral-detergent insoluble nitrogen (NDIN) and acid-detergent lignin (ADL) (Table 3). Higher amounts of ADL and NDIN excreted in the feces than consumed are a result of the formation of these fractions in the digestive tract. The origin of the NDIN in the feces may be from dietary or endogenous sources. Reed et al. (1990) also observed negative digestion coefficients for NDIN in sheep fed diets containing forage from 2 tree species, *Acacia cyanophylla* and *A. sieberiana* DC., that had high levels of PA.

Linear regression of the apparent digestible amount of N and the amount of N in the diet can estimate true digestibility of nitrogen. Uniform feed fractions have a constant true digestibility and the metabolic amount in the feces is estimated by the intercept of this linear regression. The slope of this regression in forages that do not contain PA is approximately 0.88 and indicates that the forage N has uniform nutritional availability and high true digestibility (Van Soest 1967). The negative intercept is an estimate of N of endogenous origin and is approximately 0.5% of dry matter intake. The slope and intercept of the regression analysis for the accession of *S. sesban* with the lowest content of PA were similar to the expected values. The high r^2 and low standard error indicates that the N in this accession was digested in a nutritionally uniform manner. The lower slope and r^2 and higher standard error for the regression analysis of accessions that contained higher levels of PA indicated that the N in these accessions was not digested in a nutritionally uniform manner. These results indicate that, as the level of PA increase, forage N becomes nutritionally non-uniform and true digestibility of N can not be predicted by regression analysis. Similar effects of PA on true digestibility of N were observed for *Acacia cyanophylla, A. sieberiana* and *A. seyal* Del. that contained high levels of PA (Reed et al. 1990).

The increased excretion of fecal NDIN and negative digestion coefficients also indicates that the N in the sesbania accessions that contain high levels of PA is digested in a nutritionally non-uniform manner. Fecal excretion of NDIN was highly correlated to intake of insoluble PA. These results indicate that PA cause the formation of detergent insoluble complexes in the digestive tract. Intake of PA

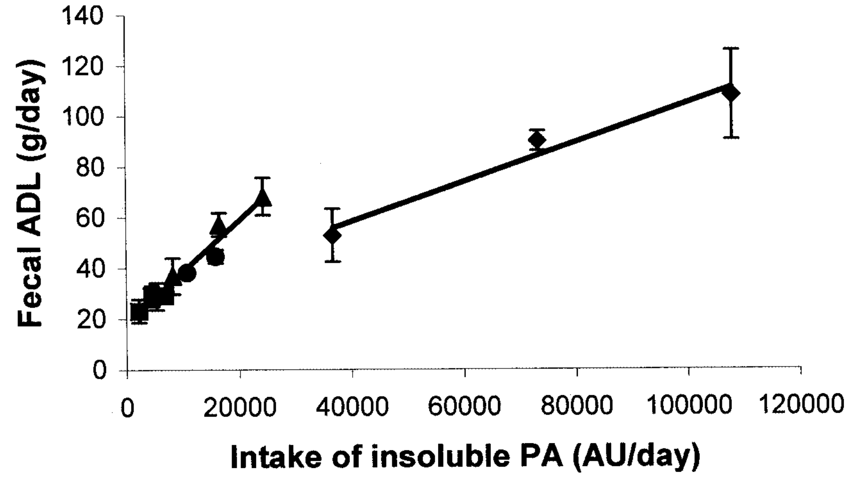

Fig. 3. Excretion of acid–detergent lignin (ADL) and intake of insoluble proanthocyanidins (PA) in sheep fed 3 accessions of *Sesbania sesban* (10865, squares; 15019, circles; and 15036, triangles) and 1 accession of *S. goetzii* (15007, diamonds) at 3 levels of crude protein offered from each accession.

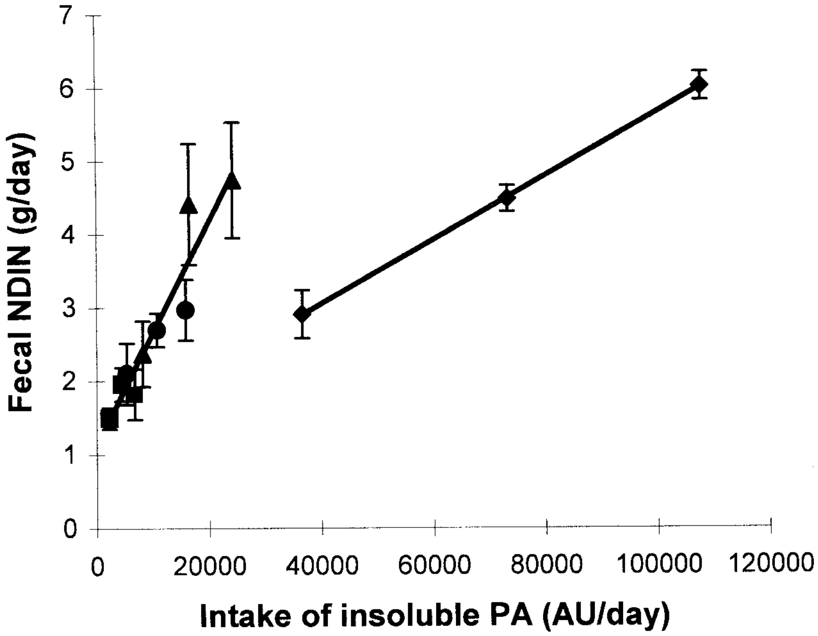

Fig. 4. Excretion of neutral–detergent–insoluble N (NDIN) and intake of insoluble proanthocyanidins (PA) in sheep fed 3 accessions of *Sesbania sesban* (10865, squares; 15019, circles; and 15036, triangles) and 1 accession of *S. goetzii* (15007, diamonds) at 3 levels of crude protein offered from each accession.

Table 4. Insoluble PA (A550 g^{-1}) with (+) and without (–) addition of sodium sulfite to neutral detergent (Krueger et al 1999).

	Neutral Detergent Insoluble Proanthocyanidin		
	Sulfite Trt.		
	–	+	Difference
		(g/kg)	
Sericea (AU Donnely)	130	1	129
Sericea (Serala)	216	2	215
Crownvetch	38	2	36
Sainfoin (Eski)	36	3	33
Sainfoin (Remont)	27	3	24
Birdsfoot trefoil (Viking)	21	2	19
Birdsfoot trefoil (Norcen)	17	1	16

was highly correlated to fecal excretion of ADL and NDIN, and fecal ADL and NDIN were also highly correlated.

Proanthocyanidins cause the formation of detergent insoluble complexes that elevate fecal excretion of NDIN and ADL. The formation of these complexes violates 2 of the basic principles of the application of detergent analysis for estimating the nutritive value of forages. The first principle is that neutral-detergent solubles and crude protein are nutritionally uniform and have high true digestibility. The second is that fiber fractions are of plant origin and cannot originate in the digestive tract (Van Soest 1967). The violation of these principles in forages that contain PA does not invalidate the use of the detergent system of analysis. These results suggest that the deviation from ideal behavior in the detergent system may be a useful technique to determine the effects of PA on protein digestion. This conclusion is supported by the high correlation between intake of insoluble PA and fecal excretion of ADL ($r = .88$, $p < .01$, $n = 36$) (Fig. 3), and NDIN ($r = .94$, $p < .01$, $n = 36$; Wiegand et al 1995; Fig. 4).

Sodium Sulphite in Neutral Detergent and Insoluble Proanthocyanidins

Alfalfa (*Medicago sativa* L.), red clover (*Trifolium pratense* L.), birdsfoot trefoil (*Lotus corniculatus* L.), sainfoin (*Onobrychis viciifolia* Scop), crownvetch (*Coronilla varia* L.), cicer milkvetch (*Astragalus cicer* L.), sericea lespedeza [*Lespedeza cuneata* (Dum.-Cours) G. Don], and kura clover (*Trifolium ambiguum* M. Bieb.) were subjected to sequential detergent fiber analysis to investigate the effects that the addition of 0.5 g sodium sulfite to neutral detergent has on the recovery and composition of fiber and lignin from forage legumes that vary in levels of PA (Krueger et al. 1999). Soluble, insoluble, and neutral detergent insoluble PA (NDIPA) concentrations were highest in sericea, moderate in crownvetch, sainfoin, and birdsfoot trefoil and absent in alfalfa, cicer milkvetch, red clover, and kura clover. Addition of sodium sulfite reduced levels of neutral detergent fiber (NDF), acid detergent fiber (ADF), acid detergent lignin (ADL), neutral detergent insoluble nitrogen (NDIN), and acid detergent insoluble nitrogen (ADIN) recovered from most forages tested. The addition of sodium sulfite effectively eliminated NDIPA from NDF (Table 4). The difference between fiber fractions prepared without and with the addition of sodium sulfite during the neutral detergent procedure was related to PA concentration. Neutral detergent fiber difference was positively correlated with insoluble PA ($r = 0.905$, $p = 0.0001$) and NDIPA ($r = 0.913$, $p = 0.0001$; Fig. 5). The addition of sodium sulfite to neutral detergent in sequential detergent analysis of PA containing species eliminates the insoluble PA frac-

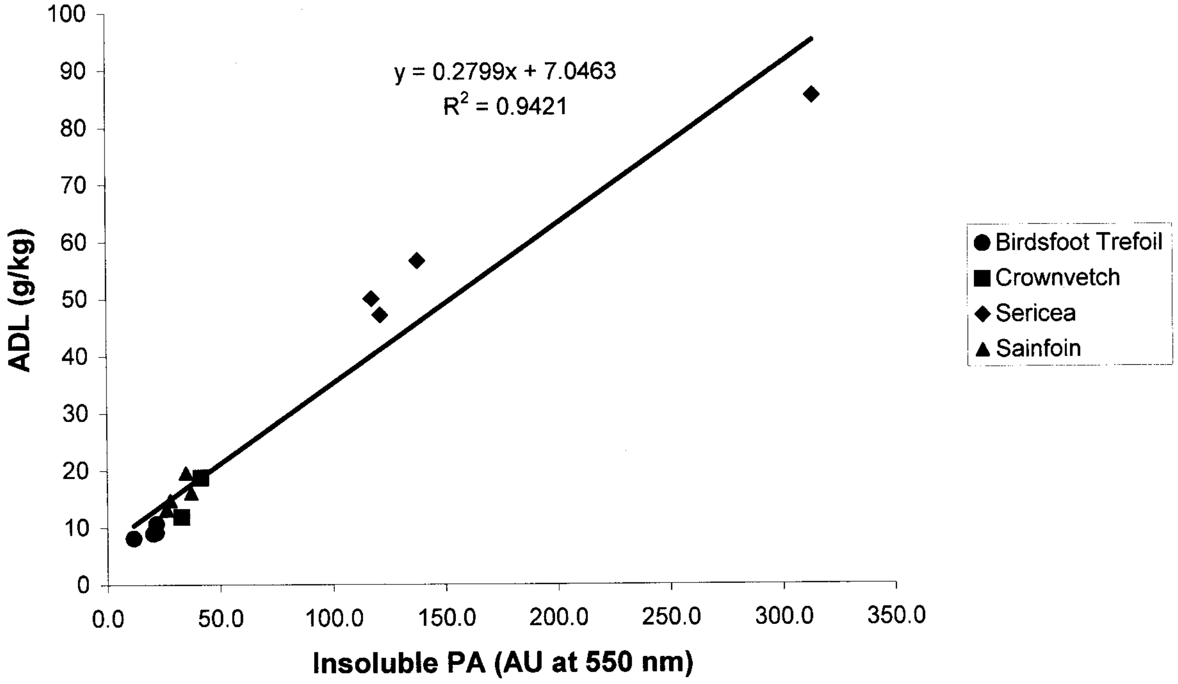

Fig. 5. Difference in sequential acid–detergent lignin (ADL) and insoluble PA with and without addition of Na_2SO_3 to Neutral Detergent.

tion and decreases the amount of lignin and detergent insoluble N.

There are 2 applications for the detergent system of analysis. First, NDF provides an estimate of the plant cell wall fractions. Acid detergent fiber estimates the cellulose and lignin, while ADL estimates lignin. For this application the presence of PA/protein complexes in the fiber residues interferes with the estimate of the plant cell wall and the addition of sodium sulfite to neutral detergent when analyzing plant species that contain PA may be advisable.

The second application of neutral detergent is to partition feed into fractions that reflect their bioavailability and nutritional uniformity. Protein in forages that do not contain PA are nutritionally uniform, have high true digestibility and are soluble in neutral detergent (Van Soest 1967). However, the true digestibility of protein is reduced in forages that contain PA and the protein is nutritionally non-uniform. This behavior of protein in forages containing PA is associated with an increase in NDIN, ADIN and ADL in both forages and feces. The recovery of PA/protein complexes in NDF reflects the nutritional non-uniformity of protein. The addition of sodium sulfite to neutral detergent will therefore give misleading results in relationship to the true digestibility of protein. On the other hand, the difference between fiber fractions that are prepared with and without the addition of sodium sulfite to neutral-detergent may estimate the actual amount of PA/protein complex associated with the NDF. Therefore, both analytical approaches may be used to study the effects of PA on protein digestion in forages.

Management Implications

A better understanding of the relationship between PA structure and function is necessary to manipulate PA in forages through breeding and selection or through genetic engineering. The interaction between PA and fiber analysis and digestion is an important component of this research. There is a fine line between the potentially positive effects of PA and their negative effects on intake, digestion and animal performance. The review by Waghorn et al. (1999) clearly outlines the magnitude of the problem and the research required. Topics include defining the chemical structure of PA in relationship to reactivity with proteins and enzymes, determining optimal concentrations and types of PA for ruminants, surveys of grasses, herbaceous plants, trees, browse shrubs and seed coats to determine PA concentration and reactivity. The effect of PA on the nutritive value and adaptation of rangeland species in the diets of ruminant herbivores is another important research topic. Products to overcome the negative effects of PA and related polyphenols on ruminant production on rangelands are sold in South Africa, Australia and Zimbabwe. However, the manipulation of range vegetation in relationship to PA content would be very difficult because many dominant woody species contain high levels of PA and related polyphenolic compounds.

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Anti-quality factors associated with alkaloids in eastern temperate pasture

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Abstract

The greatest anti-quality associated with eastern temperature pasture grasses is the result of ergot alkaloids found in endophyte-infected (*Neotyphodium ceonophialum*) tall fescue (*Festuca arundinacea* Schreb.) The relationship between the grass and the endophyte is mutalistic with greater persistence and herbage mass as a result of the endophyte. Ergot alkaloids reduce growth rate, lactation, and reproduction in livestock. Significant effects are the result of elevated body temperature and reduced peripheral blood flow such that necrosis may result. Perturbations also occur in a variety of body systems. Planting new pastures with seed containing a "non-toxic" endophyte appears to be a potential solution. Ergotism results from the ingestion of the scelerotia of *Claviceps purpurea* containing ergot alkaloids found on seed heads. Ergotism resembles the effects of endophyte-infected tall fescue. Endophyte-infected perennial ryegrass (*Lolium perenne* L.) contains ergot and lotirem alkaloids that result in reduced growth and tremors. Reed canarygrass (*Phalaris Anundinacba* L.) contains tryptamine, hordenine and gramine alkaloids that reduce growth. Annual ryegrass (*Lolium multiplorum* L. may contain galls with cornetoxins which result in neurological signs.

Key Words: tall fescue, ergotism, perennial ryegrass, reed canarygrass, annual ryegrass

Resumen

El principal factor anti-calidad asociado con los de zacates templados del este que se utilizan para praderas es el resultado de los alcaloides Ergot encontrados en el pasto Alta fescue infectado de hongo endófito (*Neotyphodium ceonophialum*). La relación entre el pasto y el endófito es mutualista, con mayor persistencia y masa de forraje como resultado del endófito. Los alcaloides Ergot reducen la tasa de crecimiento, la lactación y la reproducción del ganado. Los efectos críticos son el resultado de la elevada temperatura corporal y el reducido flujo periférico de sangre que puede ocasionar en necrosis. También ocurren perturbaciones en una variedad de sistemas corporales. El plantar praderas nuevas con semilla libre del hongo endófito parece ser una solución potencial El Ergotismo resulta de la ingestión de la esclerotia de Claviceps purpuerea que contiene alcaloides Ergot la cual se encuentra en las estructuras de la planta que contienen las semillas. El Ergotismo asemeja los efectos producidos por el zacate Alta fescue infectado por el hongo endófito. El ryegrass perenne infectado con el endófito contiene alcaloides ergot y lotirem que resultan en un crecimiento reducido y temblores. El zacate "Reed canarygrass" contiene los alcaloides triptamina, hordenina y gramina los cuales reducen el crecimiento. El rye grass anual puede contener agallas con cornetoxinas las cuales resultan en síntomas necrológicos.

The term "eastern temperature grass" is somewhat subjective and could be defined to include any grass species grown in temperate zones or species that originate and predominate within the temperate regions of the world. Numerous grass species contain anti-quality compounds as defense mechanisms, so this discussion will be limited to grasses that are utilized in the eastern half of the United States, have origins in temperature climatic regimes, and contain the C_3 photosynthetic pathway common to cool-season grasses. Using this definition of the term, this discussion will focus on 2 grass species, i.e., tall fescue (*Festuca arundinacea* Schreb.) and perennial ryegrass (*Lolium perenne* L.) that form mutualistic associations with other organisms resulting in anti-quality products, and 1 grass species, reed canarygrass (*Phalaris anundinacea* L.), in which anti-quality products are an endemic function of the plant genome. In addition, ergotism and annual ryegrass (*Lolium multiflorum* L.) toxicosis are the result of organisms parasitizing forages.

Tall Fescue

The most notorious grass-related livestock anomaly in the United States is fescue toxicosis, affecting over 8.5 million beef cows and 700,000 horses (Ball et al. 1996). The economic impact of grazing endophyte-infected (E+) tall fescue upon the beef industry has been estimated to exceed $700 million per annum (Hoveland 1990). Further economic impacts occur upon the horse and sheep industry. The agronomic attributes of tall fescue (*Festuca arundinacea* Schreb.) make it an attractive forage species because of its ability to withstand drought, poor soil conditions, and intensive defoliation from grazing. It is utilized on approximately 14 million hectares of pasture and hayfields, most of which are located in the eastern half of the United States. Fescue toxicosis occurs when the plant is infected with the constitutive clavicipitaceous endophytic fungus, *Neotyphodium coenophialum* (Glenn et al. 1996, formerly called *Acremonium*). The endophyte lives in intercellular spaces of sheath, stem, leaf, and seed tissues. There is no invasion of plant cells nor does the endophyte become pathogenic. It is passed from generation to generation via seed, so infected plants beget infected

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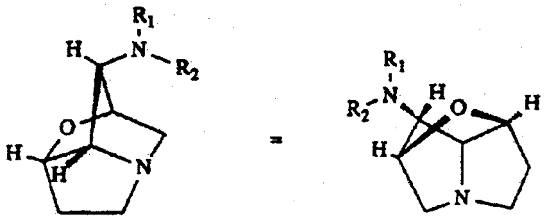
offspring and thus perpetuate the association. In a survey of over 1500 pasture samples obtained throughout the United States, more than 70% of the samples had 60% or more endophyte infection rates (Shelby and Dalrymple 1987). Seeds which were tested generally had the same rate of presence as pasture samples, but nearly 90% of the seed samples had less than 20% viable (living) endophyte. The obvious question then is, "Why are fields highly infected if the endophyte does not survive in the seed from which they were planted?" Older tall fescue stands are typically highly infected because in mixed stands of endophyte-free (E-) and E+ plants, E+ plants choke out and replace the E- plants and hence, pastures convert from low-infection rates to high-infection rates as the process continues.

The grass benefits from the endophyte-grass association in part by a group of alkaloids produced by the endophyte or by the plant in response to the endophyte. Ergot (Fig. 1) and clavine alkaloids, peramine, and saturated aminopyrrolizidine (lolines) alkaloids (Fig. 2) are all biologically active compounds that serve as feeding deterrents and decrease reproduction and growth by both mammals (Porter 1994, Stuedemann et al. 1989) and insects (Clay et al. 1985, Clay 1989, Siegel et al. 1991, Porter 1994). Protection from defoliation suggests solar energy capture and retention is a paramount priority in this association. Reduced insect or livestock grazing results in more photosynthetically active leaf area, resulting in greater energy capture, greater energy reserves, and greater regrowth capacity when infected with the endophyte (Hill et al. 1990). Endophyte-infected tall fescue has greater forage and seed productivity than the E- form (Hill et al. 1991) and is more drought tolerant (West et al. 1993).



	R_1	R_2
LOLINE	CH_3	H
N-ACETYLLOLINE	CH_3	$COCH_3$
N-FORMYLLOLINE	CH_3	CHO
N-ACETYLNORLOLINE	H	$COCH_3$
N-METHYLLOLINE	CH_3	CH_3

Fig. 2. Loline alkaloids found in endophyte–infected tall fescue (Porter 1994).

The endophyte receives a home and a food supply in return for its contribution to the plant. This means the endophyte is never subjected to environmental forces and is only dependent upon plant health for its survival (Hill 1994). Hence, it is in the plant's interest to provide the needs for the endophyte; and the endophyte to provide protection to the plant against climatic and biological forces (e.g., insects) that may be threatening.

Animal Toxicosis-Tall Fescue

The impact or effects of consumption of E+ tall fescue have been reviewed (Bush et al. 1979, Stuedemann and Hoveland 1988, Schmidt and Osborn 1993, Stuedemann and Thompson 1993). Readers are referred to those reviews for specific information on the impact of E+ tall fescue on animal response. A compendium of the effects of the endophyte on animal response variables is presented in Tables 1 (performance and production), 2 (animal behavior), 3 (physiological) and 4 (sera or plasma). In cases where extensive data exist, only a few selected articles were referenced to illustrate effects.

The presence of ergot and perhaps other alkaloids in forage resulting in depressed body weight gains in livestock grazing E+ tall fescue particularly during the warm season is often referred to as summer fescue toxicosis. Affected animals have an unthrifty appearance, long rough hair coats, excessive salivation and elevated respiratory rates and spend less time grazing during daylight hours (Stuedemann and Hoveland 1988). Calving rates are also decreased (Porter and Thompson 1992) as well as milk yield in dairy cows (Strahan et al. 1987). Fescue foot and fat necrosis are 2 other conditions in cattle associated with E+ tall fescue. Fescue foot is a gangrenous condition of the hooves, tail and occasionally ears that occurs primarily during the winter months (Yates 1983). Fat necrosis occurs in mature cows and is associated with masses of hard fat in the abdomen, leading to poor digestion and calving problems (Bush et al. 1979). We postulate that both fat necrosis and fescue foot are symptoms of fescue toxicosis.

Milk Production and Calf Growth. Milk production was reduced as much as 60% in dairy cows consuming an E+ ryegrass-tall fescue hybrid compared to the same E- hybrid (Hemken et al. 1979). There was also an associated decrease in forage intake. In a subsequent study daily milk production was significantly reduced in mid-lactation Holsteins on E+ compared to E- tall fescue (Strahan et al. 1987). There was also an associated significant decrease in daily dry matter intake on E+ (7.1 kg) compared to E- (9.1 kg) tall fes-

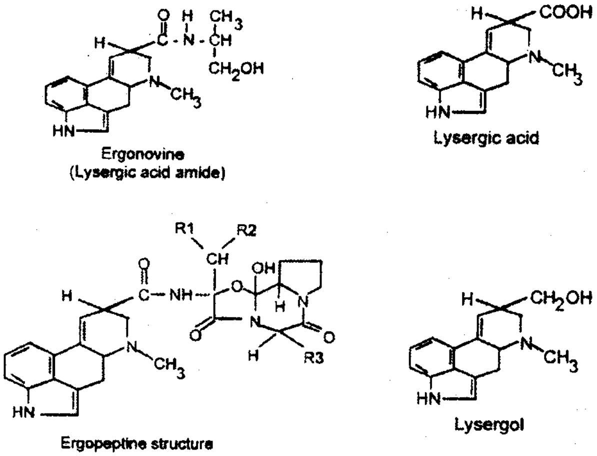


Fig. 1. Ergot alkaloids found in endophyte–infected tall fescue (Porter 1994).

Table 1. Effects of endophyte–infected fescue on animal performance criteria.

Response criteria	Endophyte level		Ergovaline		Response				
	Low E	High E	Low E	High E	Low E	High E	Feedstuff	Animal	Reference[a]
Average daily gain	(%)		(mg d^{-1})		(Kg day^{-1})				
	0	100			.96	.20	Seed	Steers	Schmidt el al. 1982
	2	>90			.83	.45	Pasture	Steers	Hoveland et al. 1983
	8	91			.97	.46	Pasture	Steers	Read and Camp 1986
	<1	98			.21	–.05	Pasture	Cows	Gay et al. 1988
	<10	>70			.66	.43	Pasture	Steers	Tolley et al. 1990
	0	>85	.45	3.50	–.08	–3.5	Pasture	Cows	Peters et al. 1992
	0	>85			.89	72	Pasture	Suckling calves	Peters et al. 1992
	25	58			.46	30	Pasture	Steers	Stuedemann et al. 1993
Pregnancy Rate					(%)				
	1	98			95	55	Pasture	Cows	Gay et al. 1988
	21	77			89	74	Pasture	Cows	Tucker et al. 1989
	0	>85	1.45	3.50	91	72	Pasture	Cows	Peters et al. 1992

[a] Some values were adapted from specific research reports.

cue. Cows receiving E- tall fescue gained 12.0 kg during the experiment compared to a weight loss (–11.7 kg) in cows fed E+ tall fescue. The authors suggested that there was no endophyte threshold level below which milk production in dairy cows would not be adversely affected.

Milk production was 75% greater in beef cows grazing E- compared to E+ tall fescue (Schmidt et al. 1984). At 100 days postpartum, primiparous beef cows grazing E+ tall fescue had 50% lower milk production than those grazing E- tall fescue (Schmidt et al. 1986). Beef cows grazing E+ KY 31 tall fescue had a 25% reduction in milk production compared to cows grazing E- Mozark tall fescue or orchard grass, (6.0 and 8.0 kg/day, respectively) (Peters et al. 1992). Calf growth associated with nursing cows grazing E+ tall fescue was also significantly reduced compared to the other 2 groups. A similar reduction in calf weights associated with nursing cows grazing E+ tall fescue was reported by Gay et al. (1988). These effects of E+ tall fescue are most detrimental to calf-weaning weights considering that cow-milk production accounts for approximately 66% of the variance in calf-weaning weight. In this regard Danilson et al. (1986) calculated a 0.15 kg reduction in milk production for each 10% increase in pasture endophyte-infection level. Grazing E+ tall fescue also reduced milk production in ewes (Stidham et al. 1982).

The effect of grazing E+ tall fescue on calf-birth weight either had no effect (Schmidt et al. 1986) or there was a reduction in birth weight (Bolt and Bond 1989).

Reproduction in Beef Cattle. This subject has been reviewed (Porter and Thompson 1992, Schmidt and Osborn 1993). In studies summarized by Schmidt and Osborn (1993), lactating beef cows grazing E+ tall fescue both lost weight and had reduced pregnancy rates compared to cows grazing E- tall fescue. A decline in cow body condition postpartum negatively affects reproduction and results in a prolonged interval from parturition to first estrus (Wiltbank et al. 1964). In a 3-yr cow study Gay et al. (1988) reported calving rates were 95 and 55% for the E- and E+ tall fescue groups, respectively. In another 3-yr study Washburn and Green (1991) reported that 65% and 39% of cows on low vs. high endophyte, respectively, raised a calf each year. Similarly, Boling (1985) reported cows grazing low-endophyte infected Kenhy tall fescue had calving rates of 86% compared to 67% for E+ tall fescue.

A greater negative effect from grazing E+ tall fescue upon reproduction occurred in beef heifers compared to cows. Heifers raised on E+ tall fescue had delayed onset

Table 2. Effects of endophyte–infected tall fescue on behavioral response criteria.

Response criteria	Endophyte level		Ergovaline		Response				
	Low E	High E	Low E	High E	Low E	High E	Feedstuff	Animal	Reference[a]
Intake	(%)			Kg day^{-1}					
	0.0	100			6.6	4.2	Pasture	Steers	Stuedemann et al. 1989
	0.0	96			6.0	3.2	Seed	Steers	Osborn et al. 1992
			(mg/d)		(% of BW)				
	0.0	>85	1.45	3.50	2.40	2.25	Pasture	Cows	Peters et al. 1992
			(mg/kg $BW^{.75}$)						
			0.0	0.053	2.55	1.76	Seed & hay	Sheep	Aldrich et al. 1993b
Water intake					(Lis in day^{-1})				
			0.0	0.053	4.2	5.3	Seed & hay	Sheep	Aldrich et al. 1993b
			0.0	0.05	49.3	48.9	Seed	Heifers	Aldrich et al. 1993b

[a] Some values were adapted from specific research reports.

Table 3. Effects of endophyte–infected fescue on physiological response criteria.

Response criteria	Endophyte level		Ergovaline		Response		Feedstuff	Animal	Reference[a]
	Low E	High E	Low E	High E	Low E	High E			
Skin Vaporization	(%)		(ppb)		Kcal m^2 hour^{-1}				
			<50	381	113.7	91.3	Seed	Heifers	Aldrich et al. 1993a
			<50	285	41.9 (at 22°C)	34.4	Seed	Steers	Aldrich et al. 1993b
			<50	285	87.2 (at 32°C)	47.1	Seed	Steers	Aldrich et al. 1993b
Respiration rate					(breath min^{-1})				
	0.0	96			62	70	Seed & hay	Steers	Osborn et al. 1992
Heart rate					(beats min^{-1})				
	0.0	96			68	51	Seed & hay	Steers	Osborn et al. 1992
Rectal temperature					(°C)				
	0.0	96			39.4	39.7	Seed & hay	Steers	Osborn et al. 1992
			(mg/kg BW$^{.75}$)						
			0.0	0.053	40.0	40.4	Seed	Sheep & hay	Aldrich et al. 1993b
Core body Temperature			0.0	0.053	38.3	39.3	Seed & hay	Sheep	Aldrich et al. 1993b

[a] Some values were adapted from specific research reports.

of puberty and decreased first-service conception rates (Washburn et al. 1989). Similarly, in another study there was a 96% conception rate in beef heifers raised on E- tall fescue compared to a conception rate of 55% on E+ tall fescue (Schmidt et al. 1986). In the following year, only 33% of the then primiparous cows grazing E+ tall fescue were successfully rebred compared to 93% on E- tall fescue.

The adverse effect of the endophyte upon reproduction in cattle is mediated partially at least, by increased early embryonic mortality. Cattle embryos transferred into heifers grazing E+ tall fescue had decreased survival compared to embryos transferred into heifers grazing E- tall fescue (Rahe et al. 1991). Similarly, cattle embryos taken from cows grazing E+ tall fescue had decreased in vitro cleavage, rate of development and quality compared to those from cows grazing E- tall fescue (Nasti et al. 1994).

Impact on Horses. The pregnant mare is very sensitive to the effects of grazing E+ tall fescue (Cross 1997). Mean gestation length in mares consuming E+ tall fescue was lengthened 27 days (Monroe et al. 1988). Others reported similar effects (Putnam et al. 1991, Redmond et al. 1994). Severe dystocia frequently occurs with prolonged gestation in mares on E+ tall fescue. Putnam et al. (1991) reported that 10 of 11 mares grazing E+ tall fescue experienced dystocia. Supplementing pregnant mares on E+ tall fescue with shelled corn had no effect on gestation length or incidence of dystocia (Earle et al. 1990). Placentas from affected mares were thickened, reddish colored and heavier (Monroe et al. 1988, Brendemuehl et al. 1994b). Surviving foals were large-framed and emaciated in appearance, with premature eruption of teeth and overgrown hooves (Monroe et al. 1988, Putnam et al. 1991). Mares should be removed from E+

Table 4. Effect of ingestion of endophyte–infected tall fescue on sera or plasma constituents of cattle.

Response criteria	Direction	Reference
Alkaline phosphatase	reduced	Bond et al. 1984 Boling et al. 1989
Amylase	increased	Nutting et al. 1992
Asparatate aminotransferase	reduced	Dougherty et al. 1991
Cholesterol	reduced	Bond et al. 1984 Stuedemann et al. 1985a Lipham et al. 1989 Tolley et al. 1990
Cortisol	unchanged	Aldrich et al. 1993a
Creatine kinase	reduced	Dougherty et al. 1991
Growth hormone	unchanged	Elsasser and Bolt, 1987 Lipham et al. 1989
	increased	Thompson et al. 1987
Insulin–like growth factor^{-1}	reduced	Filipov et al. 1999
Lactic dehydrogenase	reduced	Dougherty et al. 1991
Luteinizing hormone	unchanged	Mizinga et al. 1992
Melatonin	reduced	Hurley et al. 1981 Porter et al. 1990
Prolactin	decreased	Hurley et al. 1981 Elsasser and Bolt, 1987 Thompson et al. 1987 Lipham et al. 1989
Thyroid stimulating hormone	unchanged	Elsasser and Bolt, 1987
Thyroxine	unchanged	Aldrich et al. 1993a
Triiodothyronine	unchanged	Aldrich et al. 1993a

tall fescue at least 30 days prior to expected foaling (Taylor 1993).

Following foal delivery mares grazing E+ tall fescue had a high incidence of either agalactia or reduced milk yield (Monroe et al. 1988, Putnam et al. 1991). The milk from such mares was off-colored (straw-colored with an oily appearance), rather than the white milk of normal mares. This milk lacked normal immunoglobulin concentrations and, consequently, foals did not have normal passive immunity (Cross 1997).

Grazing E+ tall fescue alters the reproductive endocrinology of the pregnant mare (reviewed by Cross 1997). Serum concentrations of the pituitary hormone, prolactin, that is necessary for the onset of lactation (lactogenesis) were depressed. Serum progesterone concentrations were also lowered, but serum concentrations of estradiol were increased. This indicates that placental function is altered because progesterone and estradiol are secreted from that organ.

Grazing E+ tall fescue did not increase body temperature in horses (Monroe et al. 1988), perhaps because of the ability of horses to dissipate heat by sweating. Putnam et al. (1991) observed increased sweating in pregnant mares grazing E+ tall fescue. A relationship between grazing E+ tall fescue and laminitis has been suggested based upon epidemiologic and pathologic reports (Rhorbach et al. 1995). McCann et al. (1992a) reported no reduction in growth of yearling horses grazing E+ tall fescue supplemented with concentrate. In contrast, average daily gain was reduced by 57% in yearling horses grazing E+ tall fescue without supplementation (Aiken et al. 1993). Relative to mare fertility (Brendemuehl et al. 1994a) reported that mares grazing E+ tall fescue had reduced fertility and increased early embryonic mortality rates.

Behavior, Intake and Digestibility. During daylight, cattle on E+ tall fescue pastures spent less time grazing (Stuedemann et al. 1985b, Lipham et al. 1989). In sunlight, steers on E+ tall fescue grazed 5–21% of the time between 1200 and 1600 hours compared to 43–65% for steers grazing E- tall fescue (Stuedemann et al. 1985b). This effect persisted for at least 26 days after the steers were moved from E+ to E- pastures. There is no known explanation for this residual behavior.

Much of the reduction in animal performance has been attributed to reduced intake. The presence of the endophyte reduced intake in cattle (Hemken et al. 1981, Schmidt et al. 1982, Stuedemann et al. 1989, Osborn et al. 1992) and sheep (Hemken et al. 1979, Aldrich et al. 1989). An 8% depression in intake in steers fed E+ tall fescue hay resulted in a 58% suppression in average daily gains (Schmidt et al. 1982). Steers grazing E- tall fescue had a 43–69% greater dry matter intake compared to steers on E+ tall fescue (Stuedemann et al. 1989).

While the negative effect of the endophyte upon intake may due to palatability or secondarily to increased body temperature (Beede and Collier 1986), a separate neural mechanism is probable. Metoclopramide, primarily a dopaminergic antagonist with some anti-serotinergic activity (Freeman et al. 1992), increased intake in lambs held at 32°C fed a high endophyte diet with no alteration in body temperature (Aldrich et al. 1989).

The effect of E+ tall fescue on intake is exacerbated by elevated environmental temperatures (Hemken et al. 1981). When calf intake of E+ and E- tall fescue forage was compared in environmental chambers, the E+ forage decreased intake only when environmental temperatures exceeded 31°C. In a similar experiment with calves in environmental chambers at 21°C and 32°C, and fed an endophyte-free tall fescue diet with added ergotamine resulted in reduced intake at both temperatures (Osborn et al. 1992).

In vitro dry matter digestibility was superior for E+ hay compared to E- tall fescue hay (Schmidt et al. 1982). Chestnut et al. (1991) found no difference in organic matter digestibility of E+ and E- tall fescue in steers and Harmon et al. (1991) found no endophyte effect on dry matter and nitrogen digestibility in steers. Others, however, found that diets containing E+ tall fescue had reduced dry matter and organic matter digestibility in sheep (Hannah et al. 1990, Fiorito et al. 1991, Westendorf et al. 1993), cattle (Aldrich et al. 1993a), and rats (Larson et al. 1991), which could be ambient temperature-dependent (Hannah et al. 1990).

A metabolic cost has been associated with the endophyte. This was revealed by pair-fed experiments where the intake of animals receiving E- diet was maintained at the intake level of the E+ tall fescue seed-based diet group. Using this strategy with rats and cows, a depression in body weight gains occurred in the animals receiving E+ diets (Mizinga et al. 1992, 1993). Therefore, growth in rats and cattle are affected by the endophyte in some manner beyond intake. This could be due to increased hepatic mixed function oxidase activity related to detoxification as found in sheep on E+ diets (Zanzalari et al. 1989).

Body Temperature, Respiratory and Heart Rates. Inclusion of the endophyte in fed diets has resulted in increased rectal temperature and respiratory rate. In this regard, the effects of the endophyte were investigated using temperature controlled rooms (Hemken et al. 1981, Rhodes et al. 1991, Osborn et al. 1992, Aldrich et al. 1993b, Cornell et al. 1990). Calves consuming a toxic ryegrass-tall fescue hybrid at increased ambient temperatures had increased rectal temperatures, respiratory rates and depressed body weight gains compared to those fed a non-toxic hybrid (Hemken et al. 1981); however, at lower ambient temperatures there were no differences in respiratory rate and rectal temperatures. In a later experiment using steers fed E-, E+ or E- diets plus ergotamine at both a thermoneutral temperature (21°C) and a heat stressed environment (32°C), Osborn et al. (1992) reported both temperature and endophyte increased rectal temperature and decreased heart rate, but no significant interaction occurred between endophyte and temperature. Respiratory rate was increased with the endophyte only at the elevated temperature. Ergotamine induced changes similar to those found by feeding E+ diets. Both the endophyte and added ergotamine decreased peripheral body temperature; this was attributed to reduced peripheral blood flow. Similar changes in rectal temperature in cattle resulted from feeding E+ or E- tall fescue diets when animals were exposed to diurnal temperature changes (Aldrich et al. 1993a). Interestingly, this experiment also revealed that there was a significant interaction between diet and environmental temperature on skin vaporization; with skin vaporization increased only in the E- group at an elevated temperature. Therefore the effect of the endophyte reduces the ability to remove excess body heat. A relationship was established between dietary ergovaline concentrations fed to cattle and rectal temperatures (Cornell et al. 1990). Ergovaline at 50 ppb, lowest concentration, resulted in increased rectal temperature only at 30°C ambient temperature and above.

Ergot alkaloids can increase body temperature by a direct effect upon the temperature regulating areas in the brain (Nickerson 1970, Loew et al. 1978). This central effect upon body temperature occurs at a lower dosage compared to that necessary to mediate vasoconstriction. Spiers et al. (1995) investigated the effects of injecting rats with ergovaline in both a cold environment (7–9°C) and hot environment (31–33°C). Treatment in the cold environment resulted in a decrease in both rectal and tail temperature whereas treatment in the hot environment resulted in an elevation of rectal temperature, but a reduction in tail temperature.

The effects of ergot alkaloids are complicated as they are adrenergic and dopaminergic agonists as well as both serotinergic agonists and antagonists (Muller-Schweintzer and Weidmann 1978). Receptors for these activities are widely dispersed. In this regard treatment of previously dewormed heifers fed E+ diets treated with ivermectin, an anthelmintic that binds to g-amino butyric neural receptors (Barragry 1984), had reduced core body temperature and increased intake upon heat exposure (Dr. Spiers, University of Missouri, personal communication). Treatment of cattle grazing E+ tall fescue with ivermectin topically before grazing and again at 56 days after beginning the experiment had increased weight gains (Bransby 1997). In some experiments this treatment resulted in increased gains in cattle on E- tall fescue in spite of very low fecal egg counts. Therefore, while ivermectin resulted in a positive effect in cattle on E+ tall fescue, this effect may not have a specific effect against alkaloids in the forage. Interestingly, a combination of an anabolic ear implant containing estradiol and progesterone plus ivermectin to cattle overcame the growth depressant effect of E+ tall fescue.

Vasoconstriction. In vitro ergot alkaloids mediated vasoconstriction of bovine dorsal pedal veins via α-2 adrenergic properties (Solomons et al. 1989). N-acetyl loline had some effect in this regard (Oliver et al. 1990). A subsequent study (Dr. Jack Oliver, University of Tennessee, personal communication) demonstrated extreme potency of ergovaline in this regard. Most interestingly, Oliver et al. (1998) demonstrated that venous preparations from cattle on E+ diets had an enhanced contractility to an alpha-2 adrenergic agonist. Dyer (1993) reported ergot alkaloids mediated vasoconstriction upon cattle uterine and umbilical veins via a serotinergic mechanism.

Vasoconstriction is important in the pathogenesis of fescue foot. Yates et al. (1979) showed that administration of toxic anion fractions from fescue resulted in decreased coronary band temperatures in cattle. Decreased blood flow to the digit would result in decreased nutrient delivery and tissue death. A mechanism for the vasoconstriction is found in the thickening of the smooth muscle layer of the arterioles in cattle following ingestion of the endophyte (Oliver and Schultze 1997). In this regard bovine vascular smooth muscle proliferated in vitro in response to both ergot alkaloids and N-acetyl loloine (Strickland et al. 1996).

Prolactin, Neural Function and Hair Coat. Serum prolactin is reduced in livestock species consuming E+ diets (Hurley et al. 1981, Bolt et al. 1983, Thompson et al. 1987, Lipham et al. 1989, McCann et al. 1992b). Pituitary secretion of prolactin is inhibited by dopamine and ergot alkaloids are potent dopaminergic agents (Lamberts and Macleod 1990). Ergot alkaloids were ranked relative to competitive binding to dopamine receptors on pituitary cells (Larson 1997). Ergovaline shared potency with other ergopeptines in this regard and the ergopeptine alkaloids had 10-fold greater activity compared to ergine and ergonovine.

Depressed serum prolactin with E+ diets indicates an impact of ergot alkaloids on both pituitary and neural function. While prolactin is required for the onset of lactation, it is not importantly related to growth (Eisemann et al. 1984). The central nervous system and pituitary have an abundance of dopamine receptors. Metoclopramide (dopamine antagonist) given to steers grazing E+ tall fescue increased serum prolactin, improved hair coat quality, body weight gains and more time was spent grazing (Lipham et al. 1989). The dull and shaggy hair coat changes associated with fescue toxicosis may also result from depressed serum prolactin. Administration of prolactin to hamsters following pituitary removal resulted in hair changes appropriate for the photoperiod under which they were maintained (Niklowitz and Hoffmann 1988). In sheep, increased daylight length that results in increased serum prolactin, which is importantly related to a spring moult and production of a summer coat (Lincoln 1990). As a specific cellular mechanism upon neural function, ergovaline inhibited Na+/K+ ATPase activity in a dose dependent manner in rat brain homogenates (Moubarak et al. 1993).

Hepatic/Insulin-Like Growth Factor/-Energy Production. The major anabolic effect of growth hormone (GH) secreted from the pituitary is expressed via stimulating secretion of insulin-like growth factor-1 (IGF) prominently from the liver (Hossner et al. 1997). Secretion of IGF is modulated by diet and intake (Elsasser et al. 1989). Circulating IGF has a negative effect upon GH secretion. The effects of E+ tall fescue intake on serum GH have been variable (Oliver 1997). Both ergotamine and ergonovine elevated plasma GH in steers (Browning et al. 1997). Serum IGF was reduced in steers grazing E+ tall fescue (Filipov et al.1999, Hazlett et al. 1998), suggesting this may be an important mechanistic effect whereby the ergot alkaloids suppress growth.

Ergot alkaloids may also alter energy metabolism and electrolyte movement in the liver, as both ergonovine and ergotamine inhibited Ca^{2++}-activated bovine mitochondrial ATPase activity (Moubarak et al. 1998). As previously mentioned, E+ intake increased mixed function oxidases in the liver of sheep (Zanzalari et al. 1989).

Fat Metabolism. Serum cholesterol is reduced by grazing E+ tall fescue in cattle (Studemann et al. 1985a, Lipham et al. 1989) and sheep (Bond et al. 1988). It is unknown whether this was the result of increased cholesterol uptake by the tissues or decreased hepatic secretion. The ergot alkaloids may decrease lipolysis by an adrenergic receptor activity in the liver (Oliver 1997). An association was made between high-nitrogen fertilization of E+ tall fescue, reduced serum cholesterol and the incidence of fat necrosis in cattle (Stuedemann et al. 1985a). Serum triglyceride levels were also reported to be decreased in cattle on E+ diets (Oliver 1997). Together these studies indicate that ingestion of E+ diets alters lipid metabolism.

Serum Enzymes. Several serum enzymes, alkaline phosphatase, aspartate amino transferase, alanine amino transferase, and lactic dehydrogenase, are frequently reduced in cattle on E+ diets (reviewed by Stuedemann and Thompson 1993, Oliver 1997). This general decrease in enzymatic activity by E+ diets has been attributed to increased hepatic α-2 adrenergic activity (Oliver 1997). Other possible mechanisms include inhibitors of enzymatic action, effects on cell proliferation, increased clearance via the liver or kidney, loss of enzymatic cofactors and alterations in conditions that might inhibit enzymatic action, e.g. pH and tonicity (Schultze et al. 1999). Dougherty et al. (1991) reported that circulating gamma glutamyltransferase, as well as aspartate aminotransferase and creatinine kinase were reduced in cows fed E+ tall fescue seed. Gamma glutamyltransferase is produced specifically in the liver in the bovine species (Duncan et al. 1994). It is pertinent to recognize that only an increase in the circulating concentration of these enzymes is an indication of inflammation of the organ(s) of origin.

The reduction of alkaline phosphatase as the result of E+ diets is rather consistently observed (Bond et al. 1984, Boling et al. 1989, Jackson et al. 1997, Gould and Hohenboken 1993, Schultze et al. 1999). A steady decrease in the concentration of alkaline phosphatase was observed in steers grazing E+ tall fescue (Schultze et al. 1999). This enzyme catalyzes the hydrolysis of monophosphate esters under alkaline conditions (Duncan et al. 1994). Quantitative isoenzyme determinations of this enzyme obtained from cattle grazing E+ indicated that the decrease in this enzyme was due to lowered activities of intestinal and bone isoenzymes (Schultze et al. 1999). Therefore, an effect upon serum enzymes extends beyond the liver.

Copper Status. Consumption of presumably high-endophyte tall fescue resulted in rapidly decreased circulating copper (Cu) and ceruloplasmin oxidase activity in cattle (Stoszek et al. 1979); however, body weight gains were not improved by Cu supplementation. Recent work indicates serum Cu concentrations were decreased in E+ compared to E- tall fescue (Dennis et al. 1998, Oliver et al. 2000). In a related report, steers grazing E+ compared to E- tall fescue had reduced ceruloplasmin and serum Cu (Saker et al. 1998). The steers grazing E+ tall fescue also had lowered indices of immunological competency (lowered phagocytic activity and MHC class II expression). Copper supplementation increased the MHC class II expression regardless of forage endophyte status. Additionally, Cu is required for hair pigmentation and red blood cell production (Barragry 1994). Perhaps the decreased circulating Cu levels contributes to the bronzed hair coat observed in Angus cattle grazing E+ tall fescue.

Blood Cells. The results of a 3 year grazing study indicate that the effect of E+ tall fescue was an increase in numbers of circulating red blood cells, however, there was a reduction in both mean red blood cell volume and hemoglobin concentration in each cell (Oliver et al. 2000). These changes in red blood cell volume and hemoglobin are congruous with a decrease in circulating Cu. Earlier work (Steen et al. 1979, Bond et al. 1984) indicated the hematocrit was likely suppressed in cattle grazing E+ tall fescue. In contrast, circulating numbers of red blood cells were not reduced in cattle on endophyte containing diets (Rhodes et al. 1991). Since Cu is related to red blood cell production, a Cu deficiency could alter red blood cell parameters. Oliver (1997) indicated both total circulating leukocytes and individual types of leukocytes (neutrophils, lymphocytes, eosinophils and monocytes) were lowered in calves on E+ tall fescue, suggesting lowered immunocompetence. However, in a later report (Oliver et al. 2000) only eosinophil numbers were reduced by E+ tall fescue.

Immunological effects. Saker et al. (1998) indicated cattle on E+ tall fescue had lowered indices of immunological function. Additionally, a decreased antibody titer in response to tetanus toxin occurred in steers grazing on E+ tall fescue (Dawe et al. 1997) and in rats on E+ diets challenged with sheep red blood cells (Dew et al. 1990). In contrast, Rice et al. (1997) reported greater antibody response in challenged cattle grazing E+ tall fescue. Further evidence of immunosuppression is indicated by the decreased serum globulin concentrations in steers grazing E+ (Schultze et al. 1999). Both the alpha and gamma globulin fraction decreased, but the largest decrease occurred in the gamma globulin fraction. Since gamma globulins are of lymphoid origin (Duncan et al. 1994), this could explain decreased immune responses. In support of these experimental observations, Purdy et al. (1989) reported that steers that had been on E+ had increased morbidity and mortality following movements to feedlots.

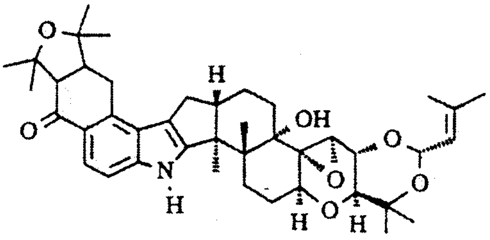
Pathogenesis. Necropsy changes observed in cattle that had grazed E+ tall fescue were mostly limited to a thickening of the smooth muscle layer of the arterioles (Oliver and Schultze 1997). There were GI tract lesions in several animals indicating abscesses, enteritis and colitis. Similarly, in earlier findings in cattle that had grazed E+ tall fescue, Garner and Cornell (1985) reported swollen arterioles upon necropsy. Therefore, changes in cattle on E+ tall fescue are largely referable to the cardiovascular system. The pathogenesis associated with ergotism is also described as due to stimulation of smooth muscles in blood vessels (primarily arterioles) with congestion proximal to the resulting vasoconstriction and ischemia distal to the vessel spasm (Osweiler 1981).

Ergot alkaloids mediated cytotoxicity upon the endothelial portion of blood vessels in cattle grazing E+ tall fescue (Oliver 1997). The vascular endothelium is a known target for the ergot alkaloids (Thompson et al. 1950). The endothelial cells are metabolically active and serve as an interface for toxic agents (Gimbrone 1986). Biologically active agents of endothelial origin, endothelin, von Willibrand factor, and angiotensin converting enzyme, were elevated in sera of cattle grazing E+ tall fescue (Oliver 1997). Endothelin is a potent vasoconstrictor agent and is mitogenic (Anggard et al. 1990). Angiotensin converting enzyme results in the production of angiotensin II, a potent vasoconstrictor enzyme (Hoorn and Roth 1993). Von Willibrand factor is an adhesion molecule for platelets during vascular injury (Blann 1993). Additionally, thromboxane B_{2a} (stable metabolite of thromboxane A_2) a potent vasoconstrictor from platelets, was reportedly elevated in the sera of cattle on E+ tall fescue (Oliver 1997). This agent also has bronchoconstrictive effects in the lung (Campbell 1990). Recently, it was found that steers grazing E+ compared to E- tall fescue had a greater response to lipopolysaccharide as measured by increases in tumor necrosis factor, a catabolic agent (Filipov et al. 1999); indicating that E+ tall fescue sensitizes the animal to other excitatory agents.

In summary, the pathogenesis of fescue toxicosis appears to originate from damage to the vascular endothelium. Endothelial cells release mediators that result in smooth muscle cell proliferation in the arterioles. Further exposure of blood vessels results in vaso-constriction with ischemia so that nutrient flux is altered and dissipation of heat is reduced. The decrease in blood perfusion to the skin and lungs would contribute to heat stress while the same effect upon the GI tract would result in altered nutrient flux. The more distal portions of the body would be most compromised by this scenario with the resultant loss of tail tips and limb digits. The effects upon reproduction could be either as a direct effect of ergot alkaloids upon embryos, decreased nutient delivery to the uterus, or altered uterine environment. A direct effect of ergot alkaloids upon the brain may lead to increased body temperature and decreased intake.

Ergotism

Ergot toxicity or ergotism occurs as the result of ingestion of the scelerotia of *Claviceps purpurea* found on feed grains and pasture grasses. Ergot alkaloids identified with the toxicosis have been identified (Porter et al. 1987). The major ergot alkaloids found in sclerotia on fescue, wheat, and barley were ergotamine, ergocristine and ergosine. Additionally, ergocornine and ergocryptine were associated ergotized annual ryegrass (Schneider



LOLITREM B

Fig. 3. Alkaloids found in endophyte–infected perennial ryegrass (ergot alkaloids not shown)(Porter 1994).

et al. 1996). The scelerotia of the fungus replaces some of the seedhead and appear as elongated dark-brown bodies of variable size.

The signs of ergotism resemble fescue toxicosis (Robbins et al. 1986, Schneider et al. 1996). This similarity in signs is natural as both are the result of ergot alkaloid toxicity. Hyperthermia, decreased intake, peripheral vasoconstriction leading to lameness and gangrene of distal portions of the body especially in the hind limb characterize both conditions in cattle (Coppock et al. 1989, Mantle 1978a, Robbins et al. 1986). Barley ergot fed to heifers resulted in tail sloughing, retained winter coats, increased salivation, and respiratory rates during hot weather (Skarland and Thomas 1972). Cold weather predisposed cattle fed ergot to lameness and gangrene (Mantle 1978b). Pregnant heifers fed ergot failed to abort (Mantle 1978b), however, some ewes aborted following ergot feeding (Greatorex and Mantle 1974). Sheep fed either ergot or ergotamine had anorexia, hyperventilation, excessive salivation, cold extremities, and some had necrosis of the tongue (Greatorex and Mantle 1973). Ergotism has resulted in severe loss of milk production associated with loss of body mass and infertility occurred in dairy cows (Schneider et al. 1996). A reduction in serum prolactin was associated with the toxicity.

Gross and microscopic changes associated with ergot resemble the vascular changes in fescue toxicosis. In cattle, constriction of arterioles, endothelial damage, vascular stasis, thrombosis, ischemia, and gangrene are described (Burfening 1973). Another cattle report included areas of skin necrosis at the base of the ear, flanks, tailhead, and around the distal portions of the limbs (Coppock et al. 1989). Microscopically arterioles were thickened. Grossly there was distal swelling of the limbs with a demarcating line between viable and non-viable tissue. In another report, gangreneous lesions on the rear of the fetlock characterized ergotism in cattle (Woods et al. 1966). Intestinal inflammation has been observed in both cattle and sheep with ergotism (Coppock et al. 1989, Greatorex and Mantle 1973). The pathogenesis of ergotism and fescue toxicosis is identical with the disturbances resulting from endothelial damage to the vascular system. Reference is made to the pathogenesis of fescue toxicosis for this discussion.

Perennial Ryegrass

Perennial ryegrass (*Lolium perenne L.*) is of minor significance as an eastern temperate forage grass (Balasko et al. 1995). It's primary region of adaptation is the wet and cool climate of the northeastern United States and seed production regions of the Willamette Valley in Oregon. As with tall fescue, perennial ryegrass is infected with a mutualistic endophyte, *Neotyphodium lolii*, and E+ ryegrass has increased growth and density compared to the non-infected forms (Cunningham et al. 1993). Insect resistance mediated by the endophyte can have a significant impact on the agronomic qualities of a pasture, as Argentine stem weevil (*Listronotus bonanensis*) kills the growing points of the E- grass plant (Prestidge and Gallagher 1988). The alkaloids found in *N. coenophialum* infected tall fescue are also found in *N. lolii* infected perennial ryegrass, but in addition, *N. lolii* produces tremorgenic indolediterpene alkaloids (lolitrems) (Fig. 3). These tremorgenic alkaloids produce involuntary convulsing when animals are stressed by excitation (Fletcher 1982). Hence, livestock producers utilizing perennial ryegrass are faced with the same dilemma as those utilizing tall fescue in that they can use a toxic forage base (endophyte-infected) or a non-sustainable endophyte free variety.

Animal Toxicosis–Perennial Ryegrass. The effect of grazing endophyte-infected (E+), lolitrem B-free E+ and E- varieties of perennial ryegrass upon animal performance and the incidence of ryegrass staggers has been reported (Fletcher 1993, Cunningham et al. 1993).

Animal Performance. Live weight gains were reduced in sheep grazing E+ perennial ryegrass in the absence of ryegrass staggers (Fletcher and Barrell 1984); indicating a direct effect of the endophyte. Depressed body weight gains occurred only in association with summer conditions and the endophyte. Reduced serum prolactin also was associated with the endophyte, presumably as the result of ergovaline (Davies et al. 1993b). Grazing the lolitrem B-free varieties of E+ perennial ryegrass over an extended period did not result in improved live weight gains over other perennial ryegrass endophyte associations, however, animals grazing the endophyte-free variety had the greatest gain (Fletcher and Sutherland 1993a). Therefore, other anti-quality factor(s) associated with the endophyte depressed gains in the absence of lolitrem B.

Staggers. Ryegrass staggers is a neuromuscular disease that is of major animal health significance in sheep, cattle and horses in New Zealand and Australia. It is most prevalent in warm drought conditions and is associated with close grazing (less than 2.5 cm) and when animals are disturbed (Keogh 1973). Ryegrass staggers occurs sporadically in most years on E+ perennial ryegrass in Australia (Cunningham et al. 1993). Severe outbreaks have resulted in substantial livestock losses with the greatest loss in young lambs suggesting altered lactation (Foot et al. 1988).

Animals with ryegrass staggers may appear normal or have a fine tremor of the head and neck at rest. When affected animals are excited they move with a stiff, uncoordinated, jerky gait that affects either the front limbs or all limbs. Severely affected animals may collapse with tetanic seizures, but rise and move normally within a few minutes once the source of excitement is removed (Mortimer and di Menna 1985). Generally there are few deaths in affected livestock unless associated with misadventure and animals generally recover when moved to E- pastures (Cunningham et al. 1993). Lesions associated with this condition are primarily biochemical, however, muscle fiber degeneration and degeneration of Purkinje's cells in the cerebellum have been microscopically described (Munday

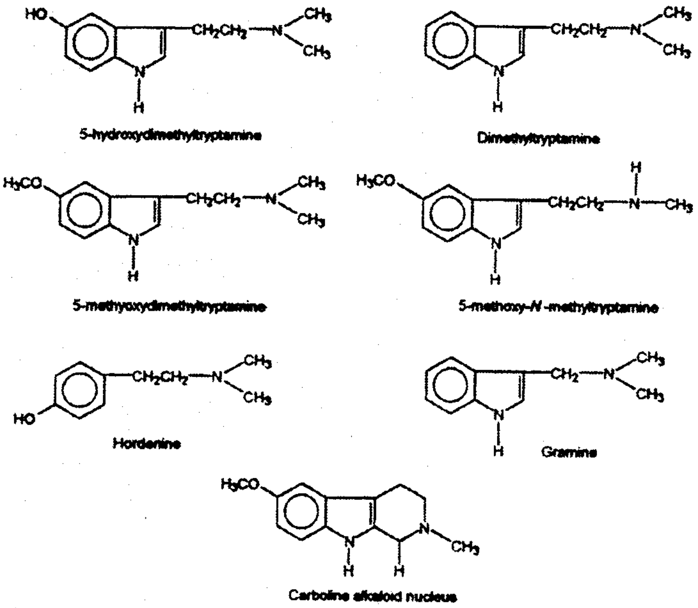


Fig. 4. Alkaloids found in reed canary grass (*Phalaris sp.*) that are similar to serotonin (Cheeke 1998).

et al. 1985). These changes are considered the result of altered neuronal metabolism, neuronal exhaustion, and anoxic conditions during seizures. The tremorgenic action of several mycotoxins including paxilline have been attributed to binding to the gamma amino butyric acid (GABA) receptors in neural tissue and inhibiting GABA stimulation of Cl^- uptake (Gant et al. 1987). The significance of this inhibitory effect is found in the fact that GABA is the major inhibitory neurotransmitter in the nervous system. Consequently, receptor blockade of the GABA system results in increased sensitivity to stimulii.

Heat Stress. Increased respiratory rates and rectal temperatures have been associated with grazing E+ perennial ryegrass (Fletcher 1993). The rectal temperature increase in a stressed environment was greatest in the animals grazing E+ ryegrass compared to E-, however, rectal temperatures were intermediate in lambs on E+ lolitrem B-free ryegrass. This increase in rectal temperature was attributed to ergovaline in the E+ lolitrem-free forage. Animals with the greatest increase in respiratory rates grazed forage with the largest concentration of ergovaline. It is presumed that the presence of ergovaline results in the effects as described for fescue toxicosis.

Fecal Contamination and Fly Strike. Fecal contamination of wool and flystrike involving flies laying eggs in the skin beneath fecal contaminated areas is a major economic problem in New Zealand associated with grazing E+ perennial ryegrass (Fletcher and Sutherland 1993b). Lambs grazing E- perennial ryegrass did not have these problems whereas this occurred in 29–31% of the animals on E+ perennial ryegrass.

Phalaris Species (Reed Canarygrass)

Reed canarygrass (*Phalaris arundinacea L.*) is utilized primarily in the northern half of the United States (Sheaffer and Martin 1995). It is adapted to poorly drained or flooded areas and can be invasive in these habitats (Merigliano and Lesica 1998). Its primary utilization is in low lying areas where spring melting snows or streambanks provide moist habitats. Reed canarygrass is also drought intolerant and, therefore, has limited use in the southeastern U.S. (Sheaffer and Martin 1995). Reed canarygrass may contain methoxy-methyl tryptamine, 2 methyl tryptamine, 2 methoxy-tetrahydro-b-carboline, hordenine, and gramine alkaloids (Marten 1973). Structures of these alkaloids are in Fig. 4 (Cheeke 1998). These alkaloids are concentrated in the immature leaf sheaths and blades (Woods et al. 1979). They reduce palatability of the grass, and thus serve as animal deterrants to prevent overgrazing (Marten et al. 1976). The tryptamine and carboline alkaloids create digestive disorders resulting in a greater incidence of diarrhea in sheep compared to either the hordenine or gramine alkaloids (Marten et al. 1981). Hordenine and gramine alkaloids simply reduce average daily gains. Hence, there are metabolic differences in modes of action; however, forage refusal correlates better with total alkaloid concentration than with the individual alkaloid classes (Marten et al. 1976). The alkaloids in reed canarygrass are under simple genetic control and are highly heritable (Marum et al. 1979, Woods et al. 1979). Fortunately, low alkaloid cultivars are commercially available. Therefore, the obvious solution for prevention of *Phalaris* staggers is to replant with low-alkaloid cultivars.

Field outbreaks of *Phalaris* toxicity have been reported for sheep and cattle (Bourke et al. 1990, Nicholson et al. 1989). In sheep 2 toxicological entities occur: a "sudden death" syndrome and a nervous syndrome (Bourke et al. 1988). The "sudden death" is characterized by sudden collapse especially when excited and is associated with cardiac abnormalities, cyanotic mucous membranes and disturbed respiration. Affected sheep either die immediately or recover spontaneously (Gallagher and Koch 1964). The problem occurred when *P. aquatica* L. dominated the pasture with rapidly growing plants (Blood and Radostits 1989). Signs have occurred within 4 hours of going on pasture but usually between 12 and 72 hours after exposure. The cardiac disorder associated with "sudden death" has been attributed to an unknown toxin other than the tryptamine alkaloids (Bourke et al. 1988). The cardiac syndrome or "sudden death" was regarded to be the result of forced exercise in sheep already exhibiting nervous signs. Anderton et al. (1994) suggested N-methyltyramine (structurally related to hordenine) is causative. Both tryptamine and tyramine alkaloids being monoamine oxidase inhibitors provides a mechanism for a cardiotoxic effect.

The typical nervous form occurs after more protracted exposure, usually 2–3 weeks after sheep are put on new growth pasture (Blood and Radostits 1989). The following signs were described: thoracic limb paresis, pelvic limb paresis, disturbed equilibrium, hypermetria of the thoracic limbs, fine mild tremors and a bounding pelvic gait (Bourke et al. 1990). Affected sheep often are conscious and frightened when approached. If they are recumbent, they struggle in an attempt to rise. New cases have occurred in association with forced exercise for as long as 12 weeks after removing sheep from the pasture (Blood and Radostits 1989). The nervous signs were replicated following administration of the *Phalaris* alkaloids, 5-methoxy dimethyltryptamine, gramine and hordenine, with the former being the most potent (Bourke et al. 1990). *Phalaris* alkaloids act by binding to neural serotinergic receptors that inhibit neurotransmission in those pathways. Provision of cobalt to iodinized salt is preventive (Duynisveld and Wittenberg 1993).

Signs of toxicosis in cattle include stiffness of the hocks, dragging the hind feet, incoordination of the tongue and lips which results in eating difficulty. Consequently, affected bulls died after a wasting disease associated with *P. caroliniana* (Nicholson et al. 1989). Microscopically degenerative lesions of spinal cord tracts and in the cerebellum of sheep have been observed (Blood and Radostits 1989). Also, an abnormal greenish pigment has been seen in the renal medulla and in parts of the brain.

Animal Production. Total indole alkaloid concentration (gramine, tryptamines and carbolines) was inversely correlated with weight gains in lambs and steers (Marten et al. 1976). Marten et al. (1981) indicated that a total alkaloid concentration greater than 2.0 mg/g dry weight of forage reduces animal gains. Similarly, palatability was correlated with total alkaloid concentration (Simons and Marten 1971). Recently released cultivars of reed canarygrass, 'Rival' and 'Venture', contain only gramine and hordenine (Duynisveld and Wittenberg 1993). Lamb gains were superior on these cultivars early in the grazing season compared to 'Frontier' reed canarygrass, a cultivar containing the methoxy derivatives of the tryptamines and B-carbolines; however, overall ADG was similar for the 3 cultivars. Gramine concentration exceeded 2.0 mg/g during a portion of the trial in all 3 cultivars and this was assumed to be the factor that reduced gains in Rival and Venture in the latter half of the grazing season.

Ryegrass Toxicosis

Annual ryegrass (*Lolium multiflorum* Lam., *Lolium rigidum* Gaud. in Australia) is grown on approximately 1 million hectares in the United States, of which over 90% is found in the southeast (Balasko et al. 1995). Annual ryegrass is infected with an endophytic fungus whose dissemination is fastidious compared to endophytes belonging to the genus *Neotyphodium*. The endophyte resides in the basal 2 mm of the tiller, and is troublesome to locate in developing seedheads, but it is passed from one generation to the next in a limited number of seed within the raceme (Latch et al. 1987, Nelson and Ward 1990). The endophyte has no adverse effects on livestock (Hickey and Hume 1994) nor does it provide resistance to insect predation (Prestidge 1991). While the endophye is termed "Acremonium-like" there is no taxonomic evidence suggesting a common ancestry with *Neotyphodium*.

Animal Toxicosis. Annual ryegrass (*Lolium rigidum*) toxicosis in livestock is a neurological disease caused by grazing annual ryegrass parasitized by the nematode, *Anguina agrostis* (McIntosh et al. 1967). The causative agents are corynetoxins (Fig. 5) produced by the bacterium, *Clavibacter toxicus*, which is carried into the seedhead by the nematode (Riley and Ophel 1992). The infected flower does not produce seed, but is replaced by a gall. There appears to be a requirement for the bacteria to be infected with a bacteriophage before the toxin can be produced (Ophel et al. 1993). The bacterium produces a yellow slime on the seed heads. Toxic nematode galls are orange in color whereas, the non-toxic gall is dark brown or black. Nematodes in the gall may be visualized microscopically following addition of water to the dry gall (McKay and Riley 1993).

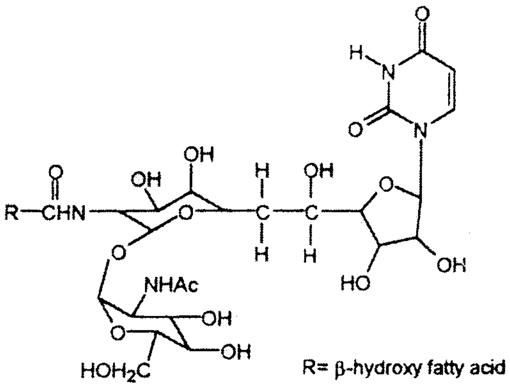


Fig. 5. Corynetoxin alkaloids found in toxic galls on annual ryegrass (Cheeke 1998).

The mechanism of action of the corynetoxins involves inhibition of an enzyme, uridine diphospho-N-acetylglucosamine:dolichol-phosphate N-acetyl-glucosamine phosphate transferase (UDT) necessary for glycosylation of proteins (Jago et al. 1983). Therefore, toxicity results from depletion or reduced activity of essential glycoproteins found in enzymes, hormones, components of the cell membrane and membrane receptors (Jago et al. 1983).

Toxicosis may appear as soon as 2 days or as late as 12 weeks after grazing the toxic forage. Signs in sheep associated with this toxicosis include a high stepping gait, lack of coordination and convulsions (Cheeke 1998). An animal may have a convulsion and recover or remain recumbent and die with their feet in a paddling motion. Signs appear most obvious when the animals are excited and resemble ryegrass staggers, however, a substantial mortality is associated with annual ryegrass toxicosis. Convulsions and lack of coordination has been described for cattle and horses that had access to galls found on chewing red fescue (*Festuca rubra commutata* Gaud.) (Galloway 1961). Annual ryegrass toxicosis per se has also been reported in horses (Creeper et al. 1996).

The lethal dose of corynetoxins given orally to sheep was 5 mg/kg. This total lethal dose was the same whether administered as a single dose or as repeated smaller doses with a maximum interval of 9 weeks between doses being examined (Jago and Culvenor 1987). Therefore, the toxic effect is cumulative. Corynetoxins result in extensive damage to the cerebellum via damage to the endothelial cells in capillaries (Finnie and Mukherjee 1987). Gross and microscopic pathology includes lipid deposition in the liver, diffuse hemorrhages, and perivascular edema particularly in the cerebellar meninges (Blood and Radostits 1989).

Hepatic damage determined by increases in the serum concentration of 2 hepatic enzymes, aspartate amino transferase (AST) and glutamate dehydrogenase (GLDH) occurred in ewes given sublethal doses of corynetoxins (Davies et al. 1996).

There was no effect of this treatment on body weight and reproduction was not adversely affected. However, wool growth and wool fiber diameter were reduced. Anorexia and rumen stasis has been reported in acutely affected sheep (Berry et al. 1976).

Some protective effect from corynetoxins was found by dosing sheep with cobalt sulfate (4.0 Mg/Day^{-1}) (Davies et al. 1993a). Cobalt treatment prevented the rise in the serum concentration of AST and GLDH but did not prevent the suppression of UDT in the liver. It was thought that cobalt treatment would enhance the growth of microorganisms in the rumen that would metabolize corynetoxins, although there was no evidence presented to indicate cobalt had this effect. Normally corynetoxins are not readily metabolized in the rumen (Vogel and McGrath 1986).

Management Options to Overcome or Reduce Fescue Toxicosis

A. Pasture and/or animal management

1. Dilution with other forages including Bermudagrass or clovers. The major problem associated with dilution with clovers is that the potential for utilizing clover varies greatly among regions. Clovers are sensitive to viruses and other diseases, plus, they are comparatively shallow rooted and are consequently subject to drought stress which often occurs during summer months.
2. Although research is limited, it appears that increased stocking rates on E+ tall fescue may improve animal performance and production.
3. Friendly endophytes. Endophyte infected cultivars, i.e., those containing nontoxic endophytes will be commercially available. Limited research suggests they will improve animal productivity; however, knowledge regarding stand persistance is unknown.
4. Withdrawal of pregnant mares from E+ tall fescue at least 30 to 60 days prior to expected foaling date should reduce problems assocated with foaling.

B. Feed treatment and/or dietary additives

1. Ammoniation of hay. Ammoniation of hay has resulted in consistent improvement in animal performance.
2. Energy supplementation. Supplementation with concentrated feedstuffs may overcome much of the negative effects.
3. Mineral supplementation. Supplementation with selenum or copper have not given consistent results. Research with other mineral supplements is either limited or non-existent.
4. Ensiling. Limited research suggests it does not overcome the toxicosis.
5. Others. The use of thiamine supplementation, zeranol, aluminosiliates and activated charcoal have either given negative results, inconsistent results or have not been researched.

C. Pharmacologic compounds

1. Ivermectin. The anthelmintic appears to have some positive effect, although its mechanism of action and method of administration has not been fully researched.
2. Domperidone. It appears domperidone is an effective treatment for equine fescue toxicosis.

D. Immunologic protection

1. Although experimentation with vaccines has resulted in positive effects, none are commercially available.

Management Options to Overcome Ergotism

1. Graze intensely enough to prevent seed head development.
2. Avoid grazing or consuming ergotized seed heads.

Management Options to Overcome Perennial Ryegrass Toxicosis

1. Plant endophyte-infected lolitrem B free varieties

Management Options to *Phalaris* sp. Toxicosis

1. The long-term solution is to plant low alkaloid cultivars.
2. The most common option utilized is to avoid planting reed canarygrass and utilizing another cool-season perennial.

Management Options to Annual Ryegrass Toxicosis

1. First of all, it doesn't appear to be a major problem in the U.S.
2. In outbreak situations, dosing, sheep with cobalt sulfate appears to have some benefit.

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Practical measures for reducing risk of alfalfa bloat in cattle

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Abstract

Frothy bloat in cattle is a serious problem and is difficult to manage under field conditions as it progresses rapidly from early signs of distension to acute distress. Scientists at Agriculture and Agri-Food Canada centres in Western Canada are committed to the development of bloat-free alfalfa grazing systems, which may require feed additives or supplements. As well, a new cultivar of alfalfa (AC Grazeland), selected for a low initial rate of digestion, will soon be available. In grazing trials the cultivar reduced the incidence of bloat by an average of 56% compared with the control cultivar (Beaver). Commonly accepted mineral mixes for the prevention of bloat were tested and found ineffective but we have confirmed that poloxalene (Bloatguard®) is 100% effective if it is given intraruminally at the prescribed dose. However, under practical conditions, poloxalene can only be offered free choice and protection from bloat cannot be guaranteed. We have also shown that the water soluble polymer, Blocare® 4511, when used in the water supply is 100% effective in bloat prevention. This product is not yet registered in North America. Other strategies for bloat prevention will be discussed, including the selection of growth stages and grazing schedules, and the reduction of risk by wilting alfalfa or combining it with tannin-containing forages.

Key Words: pasture management, frothy bloat, legumes, feed additives

Resumen

El timpanismo espumoso es un problema serio en ganado y es difícil de manejar bajo las condiciones de campo conforme progresa rápidamente de los signos iniciales de distensión aguda. Científicos en los centros Agricultre and Agri-Food Canada del oeste de Canadá estan comprometidos al desarrollo de sistemas de apacentamiento de alfalfa libres de timpanismo, los cuales pueden requerir alimentos aditivos o suplementos. También un nuevo cultivar (AC Grazeland), seleccionado para una tasa inicial baja de digestión pronto estará disponible. En ensayos de apacentamiento el cultivar redujo la incidencia de timpanismo en promedio de 62% comparado con el cultivar control (Beaver). Se probaron mezclas minerales comúnmente aceptadas para evitar timpanismo y se encontró que fueron inefectivas, pero hemos confirmado que el Poloxeno (Bloatguard®) es 100% efectivo si es administrado intraruminalmente a la dosis recomendada. Sin embargo, bajo las condiciones practicas el poloxeno puede ser solo ofrecido a libre acceso y la protección contra timpanismo no puede ser garantizada. Tambiém hemos mostrado que cuando el polímero soluble en agua Blocare ® 4511 se utiliza en el suministro de agua es 100% efectivo para evitar el timpanismo. Este producto aun no es registrado en Norte América. Otras estrategias para evitar el timpanismo serán discutidas, incluyendo la selección de etapas de estados de crecimiento y calendarios de apacentamiento y la reducción del riesgo mediante el marchitamiento de la alfalfa o combinandola con forrajes que contienen taninos.

The incidence of frothy bloat in cattle increases worldwide as legume forages gain popularity in cultivated pastures and, more recently, in land reclamation. In North America, alfalfa (*Medicago sativa* L.) is the predominant legume forage and is favoured for its high yield, nutritional quality and winter hardiness. The economic benefits of alfalfa in grazing systems for cattle are not fully realized because of the risk of frothy bloat. This digestive disorder is difficult to manage under field conditions as it progresses rapidly and unpredictably from early signs of discomfort and distension to acute distress and pronounced swelling of the left flank. The inability to expel fermentation gases and the resultant formation of a stable foam in the rumen can have fatal consequences.

Bloat research with ruminally fistulated cattle at Kamloops, B.C. and more recently at Lethbridge, AB has been designed to better understand the plant, animal and microbial factors involved in the etiology of bloat. Feeding regimens in both pens and pastures have been developed to express bloat in cattle reliably and reproducibly thereby permitting evaluation of chemical, biological and climatic variables involved in bloat. Feed additives for the control and prevention of bloat have also been tested. This paper will summarize research results on bloat in Western Canada with a view of providing practical information on pasture management. It will also report on recent bloat trials with cattle that yielded further strategies for reducing the risk of alfalfa bloat.

Materials and Methods

Each trial was conducted with 2 to 4 groups of ruminally fistulated Jersey steers, 7 to 10 years old. There were 3 to 5 animals per group, with 4 animals per group used in most studies. Studies were conducted either in confinement, where animals were fed freshly harvested alfalfa cut daily at 0700 hours (58 kg head^{-1}, fresh weight), or in alfalfa pastures under grazing conditions. The alfalfa, which was irrigated, was cut with a flail-type harvester (New Holland, Crop-Chopper® Forage Harvester 38). Except for the stage of growth studies, the alfalfa was usually at the vegetative to early bud stage. The average crude protein and acid deter-

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gent fibre contents were 21.4 ± 0.49 and 29.1 ± 0.81% ($n=79$), respectively, on a dry matter basis. Studies were conducted during the summer growing season and in the fall at Kamloops, B.C. (lat. 50° 42' N, long. 120° 27' W). Animals were cared for under the guidelines of the Canadian Council on Animal Care. An animal was classified as bloated if it showed 1) visible distension of one or both flanks prior to removing the cannula plug and 2) release of internal pressure and ejection of a stream of frothy ruminal contents after plug removal. This event could occur within 1 hour of feeding in confinement or within 2 hours of grazing on the pasture.

Each trial was designed as a crossover experiment in which animal groups were switched after each test period to determine the effect of the treatment on all animals on test. In these trials, the length of each test period was not specified but was determined by the total number of cases of bloat observed. A single animal bloating on 1 day was counted as 1 case but the animal may have distended more than once on that day. A minimum of 24 cases of bloat per crossover period provided reasonable power for detecting treatment differences. All of the steers were susceptible to bloat as determined in previous trials but none were chronic bloaters. Statistical comparisons of the effects of treatments took into account the daily fluctuations in the bloat potential of the alfalfa, which affected the susceptibility of each animal on test (Majak et al. 1995). A significance level of 0.05 was used throughout to compare treatment effects.

Results and Discussion

Stage of Growth

It has long been accepted that the probability of legume bloat decreases with advancing stages of plant maturity. The decrease has been mainly attributed to a decrease in the soluble protein content of the legume (Majak et al. 1995). Alfalfa proteins can contribute to the frothiness of rumen contents (Howarth et al. 1986). The effect of plant maturity on the incidence of frothy bloat in cattle was examined in feeding trials. Alfalfa at the vegetative, bud and bloom stages of growth was simultaneously harvested and fed to 3 groups of cattle in a 3-way crossover experiment (Thompson et al. 2000). The vegetative stage yielded the highest incidence of bloat as compared with the bud or bloom stage. The bloom stage had no cases of bloat. These results indicate the potential for grazing management through selection of plant phenology as a method of bloat control. In practice, it would be essential to recognize the predominant stage of growth of the stand before turning out cattle to pasture. The leaf to stem ratio should also be recognized as a factor in bloat throughout all stages of growth (Thompson et al. 2000). An exceptional leafy bloom stage can also cause bloat (W. Majak, unpublished results).

AC Grazeland

The quest for a cultivar of alfalfa that was bloat-free began over 30 years ago when attempts were made to select an alfalfa strain with a low soluble protein content (Majak et al. 1995). Subsequently, extensive studies were conducted comparing legumes that do and those that do not cause bloat in order to elucidate the chemical and morphological features that distinguish the 2 types of species (Goplen et al. 1993). The net result of the investigation suggested that an alfalfa with a lower potential for bloat might be produced by reducing its initial rate of digestion (IRD). Selection for this trait was feasible using a modified nylon bag technique. The low IRD was mainly expressed at earlier stages of growth, when the potential for bloat was highest (Goplen et al. 1993, Berg et al. 1995). Low IRD selections were tested in grazing trials at Lethbridge and Kamloops. The resulting new alfalfa cultivar (AC Grazeland) reduced the incidence of bloat by an average of 56% compared with the control cultivar Beaver (Berg et al. 2000). As well, these initial studies suggested that the severity of bloat was reduced as indicated by the reduction in multiple distensions of the rumen with AC Grazeland (Majak et al. 1999).

The efficacy of AC Grazeland in the reduction of bloat could be further enhanced with the use of the ionophore monensin given intraruminally as a controlled release capsule (Rumensin CRC®). On average, a 50% reduction in bloat was obtained if the bolus was used in combination with AC Grazeland (Hall et al. 2001). The bolus reduced bloat by 50% in earlier trials with unspecified cultivars of alfalfa at unspecified stages of growth (Merrill and Stobbs 1993).

Feed Additives

In response to producers' inquiries and demands over the last decade, we have tested, under experimental conditions, a number of feed additives and supplements reputed to be effective in the prevention of pasture bloat. It should be noted that these tests were conducted under confinement conditions. Our experience suggests that unlike continuous grazing conditions, harvesting and feeding fresh herbage daily in confinement is a much more vigorous and reliable test of the efficacy of a treatment owing to the higher incidence of bloat that is generated (Majak et al. 1995). In a crossover experiment at Kamloops during 1999, more bloat ($P < 0.05$) occurred in confinement (30 cases) than during continuous grazing (21 cases).

As reviewed by Majak et al. (1995), numerous theories on the use of mineral supplements, household detergents and flocculants were tested for the prevention of alfalfa bloat and most were found to be ineffective. The surfactant poloxalene (Bloat Guard®) was 100% effective if given intraruminally at the prescribed dose even under severe bloat challenge. The major difficulty is that it is expensive and must be fed daily with a feed supplement, or with a salt or mineral mix. Protection from bloat cannot be guaranteed with poloxalene or other insoluble anti-bloat agents because they are given free choice and animal intake is highly variable. A more effective approach for administering anti-bloat agents to grazing cattle would be to administer them through the water supply. This would provide a uniform intake and rapid dispersal of the agent throughout the rumen. Such water-soluble products are available in New Zealand and Australia but they are not registered in North America. One such agent, Blocare® 4511, was recently tested at Kamloops under severe bloat challenge using 2 groups of 4 steers in a crossover design. The soluble agent was administered at 0.1% in the water supply. As shown in Table 1, Blocare® 4511 was 100% effective in the prevention of alfalfa bloat, even under conditions of severe bloat where many cases were designated at a rating of 4 on a scale of 1 to 5 (Majak et al. 1995).

Table 1. Effect of Blocare® 4511 treatment on the incidence of bloat in cattle fed alfalfa herbage during 1995.

	Treatment[1]	
Cross-over period	Control	Blocare® 4511
	- - (Number of bloat cases) - -	
29 June–23 July	24	0
27 July–5 August	24	0
Total[2]	48	0

[1] Two groups of 4 cattle were fed fresh alfalfa daily, with or without Blocare® 4511 in drinking water (100 ml Blocare® 100 litres^{-1} water).

[2] $P<0.01$.

It is generally accepted that high-molecular weight synthetic polymers such as poloxalene and Blocare® 4511 are non-toxic at the recommended formulations and that they are excreted intact from the ruminant digestive system. Recently the complete efficacy of Blocare® 4511 was substantiated in alfalfa grazing trials at 3 locations in Western Canada (Stanford et al. 2001). Clearly this product has the potential to protect livestock from alfalfa bloat and its registration in North America should be promoted.

Diet Manipulation

Non-bloating legumes such as sainfoin (*Onobrychis viciifolia* Scop.) have endogenous chemical and morphological features that render them digestible in the rumen without causing the rapid fermentation and excessive gas production conducive to foam formation. Sainfoin contains high levels of condensed tannins, polyphenolic polymers that can interact with feed, microbial and plant proteins. Unlike alfalfa, legumes that have high levels of condensed tannins are bloat-free due, in part to the protein binding capacity of the endogenous tannins. In recent studies, fresh alfalfa was fed alone or with sainfoin herbage (at 10 to 20% on a dry matter basis) to determine the impact of sainfoin tannins on the occurrence of alfalfa bloat. Sainfoin supplements were also given as hay or pellets. The crossover experiment utilized 2 groups of 4 steers during 1994 to 1997. Including sainfoin in the diet reduced ($P < 0.001$) the incidence of bloat by 45 to 93% in 3 of the 4 years irrespective of the form in which sainfoin was supplied (McMahon et al. 1999). The variation in the response to sainfoin supplements could be partly attributed to the chemistry of sainfoin tannin polymers, which show considerable variation with stage of leaf development (Koupai-Abyazani et al. 1993). Nevertheless, there is potential for reducing bloat by cultivation of pastures containing mixtures of alfalfa and sainfoin or other bloat-free legumes.

In contrast to condensed tannins, which can depress the incidence of alfalfa bloat, other feed supplements have the capacity to increase the risk of bloat. The escalation is usually caused by an excessive release and availability of nutrients in the rumen with a resultant burst of microbial fermentation and gas production. Where bloat problems are encountered and the diet contains rapidly fermentable feedstuffs, such as beet pulp or molasses, the removal of these components from the diet is often sufficient to control bloat. Molasses is composed of approximately 50% glucose and fructose (Harris et al. 1981) and these simple invert sugars are highly fermentable. A study was conducted in 1996 to compare the effects of 2 supplementary carbohydrate sources on the occurrence of alfalfa bloat in cattle (Table 2). More than twice as many cases of bloat occurred with molasses supplements ($P < 0.01$) than with barley, which was not significantly different from the control. The energy source in barley is starch, which ferments at a slower rate.

Table 2. Effect of barley or molasses top dressing on the incidence of bloat in cattle fed alfalfa herbage during 1996.

Cross-over period	Treatment[1]		
	Control	Barley	Molasses
	- - - - - - - - - - - - - - (Number of bloat cases)	- - - - - - - - - - - - -	
13–18 June	8	12	13
20–24 June	9	10	14
1–11 July	6	0	25
Total[2]	23	22	52

[1] Three groups of 4 cattle were fed fresh alfalfa daily, with or without a top dressing of barley (2.72 kg head^{-1}) or molasses (1.36 kg head^{-1}).

[2] $P < 0.01$ (molasses).

Swathing and Wilting

It is clear that alfalfa leaf proteins are intimately involved in the onset of bloat. A significant decrease in the frequency of bloat can occur if the alfalfa protein chemistry is modified through complex formation with tannins or during senescence. Alfalfa silage is virtually bloat-free owing in part, to protein degradation by proteolysis during ensilage. Wilting alfalfa for 24 hours also produced changes in protein configuration as evidenced by increases in the sulfhydryl and disulfide content of alfalfa proteins (Makoni et al. 1993). Studies were conducted recently to determine whether the changes in protein structure attributed to swathing and wilting could reduce the incidence of bloat in cattle. It should be emphasized that swathing differs from the regular harvesting of alfalfa for confinement studies. The latter yields chopped herbage using a flail-type harvester while the former is cut once usually for hay production using a swather. In our studies, a John Deere 1209 Mower-Conditioner was used for swathing.

Compared with feeding a fresh swath, wilting a swath for 24 or 48 hours significantly reduced ($P < 0.01$) the incidence of

Table 3. Effect of swathing and wilting alfalfa on the incidence of bloat in cattle fed alfalfa herbage during 1994, 1997, and 1999.

Cross-over period	Treatment[1]		
	Control	Wilted 24 hours	Wilted 48 hours
	- - - - - - - - - - - - - - (Number of bloat cases)	- - - - - - - - - - - - -	
1994:			
18–23 Aug	19	8	---
25 Aug–7 Sept	22	10	---
Total[2]	41	18	---
4–7 Sept	19	---	8
9–13 Sept	8	---	1
Total[3]	27	---	9
1997:			
5–16 Aug	19	8	0
17–29 Aug	14	14	0
30 Aug–3 Sept	14	13	0
Total[4]	47	35	0
1999:			
19–30 Aug	19 (81)[6]	---	0 (50)[7]
31 Aug– 5 Sept	17 (82)	---	6 (59)
Total[5]	36	---	6

[1] Two groups of 5 cattle in 1994, 3 groups of 4 in 1997, and 2 groups of 4 in 1999 were fed a fresh swath of alfalfa (WL 225) or a swath that was wilted 24 or 48 hours.

[2] $P < 0.01$.

[3] $P < 0.01$.

[4] $P < 0.05$ (24 hours), $P < 0.01$ (48 hours).

[5] $P < 0.01$.

[6,7] Average moisture content (%) in alfalfa herbage. [6]SE = 1.2, [7]SE = 8.2

alfalfa bloat in each year of the study (Table 3). The reduction was greater (P < 0.01) if the alfalfa was wilted for 48 hours and in 1997 bloat was eliminated after a 48 hour wilt. The difference between years in the response to the 48 hour treatment could be attributed to the swathing dates of the alfalfa. In 1994, the swaths were cut later in the season and the morning dew may have impeded wilting. A similar trend was observed in 1999. The moisture content of the wilted swath was lower in the first part of the crossover experiment when bloat was eliminated after a 48 hour wilt (Table 3). The results for 1999 suggest that a 30% reduction in moisture during wilting may be sufficient to eliminate the risk of bloat. Grazing alfalfa pastures that have been swathed and wilted provides yet another strategy for reducing the risk of bloat.

Climate

It is obvious that the growing conditions of the alfalfa can affect the protein content of the plant and the content of other plant constituents that may contribute to the onset of bloat. At Kamloops, alfalfa is grown under irrigation and the impact of seasonal rainfall patterns on the incidence of bloat cannot be assessed. Other climatic variables were screened at Kamloops but none were found to be useful indicators or predictors of the occurrence of bloat (Hall et al. 1984). The commonly held opinion that alfalfa is bloat-safe after a killing frost was also refuted (Hall and Majak 1991). More recently in Kamloops, an atypical cool, wet spring was associated with an extremely high incidence of bloat (Hall et al. 2001).

Feeding Regimens

Lastly, the feeding habits of the grazer need to be considered to further understand the etiology of alfalfa bloat. It is well established that feeding regimens that are continuous and uninterrupted are less likely to cause bloat (Majak et al. 1995). The key is to promote continuous and rapid turnover of the rumen and to prevent distortions of the natural processes of microbial fermentation that increase gas formation and reduce rumen bypass. When shifting from a pen to a pasture, it is essential to adapt cattle to a continuous grazing system where the intake is gradual and unimpeded. For example, a sudden change from a 6 hour grazing system to a continuous regimen resulted in a rash of bloat cases during the first few days of the new system (Majak, unpublished results). A 3 day adaptation to continuous grazing on grass pasture would be desirable before turning out cattle on alfalfa. As well, turning out onto alfalfa pasture in the afternoon is much less likely to cause bloat than turning out in the morning (Hall and Majak 1995). In summary, pasture management can be used to minimize the risk of bloat and the strategies involve an appreciation of the plant, animal, microbial and environmental factors that contribute to frothy bloat.

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Review of toxic glycosides in rangeland and pasture forages

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Abstract

Ruminants are a diverse group of mammals, both domestic and wild species, that exhibit microbial fermentation prior to gastrointestinal activity. During the digestive process, glycosides and other natural products are exposed to ruminal microorganisms and metabolised as substrates. Most compounds are converted into nutrients but some become toxic metabolites. At least 10 types of toxic glycosides occur in forage species. Glycosides are characterized by the presence of one or more sugars linked to the alcohol or thiol functions of the non-sugar portion of the molecule, which is called the aglycone. The biological activity of the glycoside is usually determined by the chemical nature of the aglycone. The aglycones are released by microbial enzymes and may undergo further enzymatic or non-enzymatic transformations to yield toxic metabolites that can be absorbed from the gastrointestinal tract. Microbial detoxification of the aglycone is also possible. Further biotransformation of the aglycone can occur in the liver. A review is presented on glycosides that are toxic to ruminants. The discussion covers aliphatic nitrocompounds, cyanogenic glycosides, cardiac glycosides, saponins, glucosinolates, diterpenoid glycosides, bracken glycosides, calcinogens, phenolic glycosides and ranunculin. Clinical signs of poisoning and treatment of livestock as well as management strategies for the prevention of poisoning are considered.

Key Words: poisonous plants, ruminants, cattle, rumen microbes

Resumen

Los rumiantes son un grupo diverso de mamíferos, que tanto especies domésticas como salvajes, que presentan fermentación microbiana antes de la actividad gastrointestinal. Durante el proceso digestivo los glicosidos y otros productos naturales son expuestos a los microorganismos ruminales y metabolizados como substratos. Muchos compuestos son convertidos en nutrientes pero algunos llegan a ser metabolitos tóxicos. Al menos 10 tipos de glicosidos tóxicos ocurren en las especies forrajeras. Los glicosidos son caracterizados por la presencia de uno o mas azúcares encadenados a las funciones alcohol o tiol de la porción no-azúcar de la molécula, la cual es llamada aglicone. La actividad biológica del glicosido usualmente es determinada por la naturaleza química del aglicone. Los aglicones son liberados por las enzimas microbianas y pueden llegar sufrir mas transformaciones enzimáticas o no-enzimáticas para producir metabolitos tóxicos que pueden ser absorbidos del tracto gastrointestinal. La detoxificación microbiana del aglicone también es posible. Mas biotransformaciones del aglicone pueden ocurrir en el hígado. Se presenta una revisión de los glicosidos que son tóxicos para los rumiantes. La discusión cubre compuestos nitrogenados alifático, glicosidos cianogénicos, glicosidos cardíacos, saponinas, glucosinolatos, glicosidos diterpenoides, calcinógenos, glicosidos fenólicos y ranuculina. Se consideran los signos clínicos de envenenamiento y tratamiento del ganado, así como las estrategias de manejo para la prevención del envenenamiento.

A diverse array of toxic glycosides occurs in higher plants, the most abundant of these being the glucosinolates (thioglycosides), the cyanogenic glycosides, the aliphatic nitrotoxins, and the cardiac glycosides. Glycosides are secondary plant products, many of which are recognized as active metabolites or allelochemicals that interact with other plants, microorganisms, insects, and animals. The roles of these compounds include the attraction of pollinators or seed dispersers and the repulsion or inhibition of herbivores and microorganisms (Rhoades 1979). Concentrations of toxic glycosides in plants can be affected significantly by physiological stress, such as water deficits or nutrient deficiencies. Other factors that may affect glycoside levels include stage of growth, accumulation in specific plant tissues, geographic or topographic location, and seasonal effects of soil and climate. This review will focus on the distribution of toxic glycosides in forage species and their mode of action in ruminants. Management strategies for the prevention and treatment of poisoning are also considered.

Glycosides are conjugated alcohols formed when the alcoholic function of the aglycone adds to a sugar such as D-glucose. The biological activity of the glycosides is usually determined by the chemical nature of the aglycone, which is the non-sugar portion of the molecule. Glycosides most commonly occur as *O*-ß-D-glucosides. The glycosidic bond renders the glycosides innocuous through stabilization of the reactive aglycone (Majak and Benn 2000). In ruminants, an important feature of the digestive system is the occurrence of microbial fermentation in the rumen prior to gastrointestinal activity. About 50% of rumen bacteria possess ß-glucosidase activity and the hydrolytic enzyme is also widely distributed among species of rumen ciliate protozoa and anaerobic fungi (Chesson and Forsberg 1988). Hydrolysis of the glycosidic bond is essential for the toxic expression of cyanogenic glycosides as well as aliphatic nitrotoxins such as miserotoxin. In monogastric animals the upper regions of the digestive tract are largely devoid of ß-glucosidase activity; ß-D-glucosides are not usually hydrolysed but are absorbed and excreted intact in the urine. Chemical inhibitors of ß-glucosidase are known. These inhibitory compounds, both naturally-occurrring and synthetic, are structural analogues of glucose that bind tightly to the active

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site of the enzyme; however, if absorbed from the rumen they can be toxic to livestock (Nash et al. 1998).

Glucosinolates are *S*-ß-D-glucosides and thus not substrates for *O*-ß-D-glucosidase. Both ovine and bovine rumen fluids are devoid of myrosinase, the hydrolytic enzyme that releases the thiol aglycone (Majak 1992); however, glucosinolate-containing plants all contain myrosinase. Thus the hydrolysis of glucosinolates in the rumen is contingent upon the activity of endogenous plant enzymes (Majak 1992, Majak et al. 1991). The thiol aglycone is unstable at physiologic pH and undergoes a non-enzymatic rearrangement to form isothiocyanates.

Hydrolysis of the glycosidic bond is not a prerequisite for the biological activity of polycyclic glycosides such as glycoalkaloids, saponins, and cardenolides. In fact, removal of the sugar units results in reduced activity with saponins and cardenolides, and loss of activity with glycoalkaloids (Majak and Benn 2000).

Nitrocompounds

Relatively few natural products contain the nitro group, but of those that do, 2 important sets correspond to sugar conjugates of 3-nitropropanol (NPOH) and 3-nitropropionic acid (NPA). Although the latter are not glycosides, they often resemble them structurally and their mammalian toxicities are similar; it is for these reasons that they receive attention here (Majak and Pass 1989). The toxin karakin [1,2,6-tris-*O*-(3-nitropropanoyl)-ß-D-glucopyranose] was the first nitrocompound to be isolated. The identification of miserotoxin (3-nitropropyl-ß-D-glucopyranoside) followed the observation that *Astragalus miser* var. *oblongifolius* (Rydb.) Cronq. was responsible for losses of stock on rangelands of the western United States. Glucose esters of NPA such as karakin are found in the Leguminosae (*Astragalus, Coronilla, Indigofera, and Lotus)* and miserotoxin occurs in numerous species of *Astragalus* (milkvetch). It has become well established that NPA is the lethal metabolite formed in the biotransformation of nitropropyl glycosides or nitropropanoyl glucose esters. The esters yield NPA directly upon hydrolysis, but the bioactivation of the glycosides requires a second metabolic step; after hydrolytic release of the aglycone, NPOH is oxidized to NPA, probably by liver alcohol dehydrogenase (Majak and Pass 1989). The NPA is a potent inhibitor of Krebs (tricarboxylic acid) cycle enzymes essential to respiration and, more recently it has been implicated as a causative agent of neuronal degeneration in mammals (Alexi et al. 1998).

The major clinical signs in the acute syndrome include incoordination, distress, labored breathing, cyanosis, muscular weakness, and collapse, with death occurring from a few hours to a day after ingestion of the toxin. In chronic poisoning, the animals lose weight and develop respiratory distress, a poor hair coat, hind limb paresis progressing to paralysis, and a nasal discharge. Early signs of poisoning in cattle under field conditions include frothy salivation, stupefaction, diarrhea and labored breathing (Majak and Pass 1989, Maricle et al. 1996). When forced to move as part of a group they exhibit signs of incoordination and will lag behind. Recent field observations do not support the concept of livestock addiction to NPOH-containing plants (Majak et al. 1996). No specific antidote is available for the treatment of livestock poisoned with aliphatic nitrotoxins but dietary protein supplements can enhance the activity of unique rumen bacteria capable of NPOH detoxification (Majak et al. 1996). These bacteria reduce the nitro group to the much less toxic amino group (Anderson et al. 1998).

Cyanogenic glycosides

In plants, cyanogenesis or the release of HCN is associated with the disruption of cells followed by autolysis as the glycosides are exposed to endogenous plant enzymes. The resulting aglycones are unstable cyanohydrins. At physiologic pH they undergo a rapid dissociation to yield HCN and either an aldehyde (e.g.benzaldehyde in the case of prunasin) or a ketone (e.g. acetone, in the case of linamarin). The dissociation is a pH-dependent reaction with higher rates of HCN formation occurring at a pH greater than 6 and much slower rates at pH 5-6. Cattle should be least susceptible to poisoning during feeding and digestion when the pH of rumen fluid is depressed and most susceptible after a 24 hour fast (Majak et al. 1990).

The HCN is extremely toxic because it blocks aerobic cellular respiration. The toxic effect is mainly attributed to inhibition of cytochrome oxidase but other metabolic processes may also be affected. Physiologically, HCN poisoning results in histotoxic anoxia with the initial manifestation of hyperpnea, followed by dyspnea, and then convulsive seizures. Clinical signs of poisoning with cyanogenic glycosides develop at a much slower rate than they do for sodium cyanide, which has been attributed to the slower release of HCN from the glycoside. The delayed release of HCN permits a greater degree of detoxification through thiocyanate formation. Clinical signs of subacute and acute poisoning in cattle resulting from administration of prunasin include tachycardia, hyperpnea, recumbency, increased pinkness of the mucous membranes, and tonic convulsive contractions (Majak et al. 1980). The classic nitrite-thiosulfate treatment is still the preferred therapeutic method, especially if it is supplemented with oxygen (Majak et al. 1980, Way 1984).

The distribution of cyanogenic glycosides in the plant kingdom has been extensively reviewed (Poulton 1983). The Leguminosae (*Trifolium* spp.), Rosaceae (*Prunus* spp. and *Amelanchier* spp.), and Juncaginaceae (*Triglochin* spp.) have been particularly rich sources where the glycosides occur in white clover, wild cherry, serviceberry and arrowgrass, respectively.

Cardiac glycosides

As a consequence of their powerful effect on the heart, preparations containing cardiac glycosides have a long history as medicinals and poisons. Probably most famous in the Western world is the introduction of digitalis, an extract of *Digitalis purpurea* L. (foxglove), for the treatment of heart disease, but similar usage of *Scilla maritima* L. (squill; sea onion) dates back to ancient civilizations. Cardiac glycosides are characterized by a steroidal aglycone which is 1 of 2 structural types: cardenolides, such as digitalin, or bufadienolides such as scilleroside. Both cardenolides and bufadienolides are plant products, common particularly in the Asclepiadaceae (milkweeds), Apocynaceae, and Liliaceae. Dogbane (*Apocynum cannabinum* L.) contains high concentrations of the cardenolide cymarin (0.1% on a dry wt basis, W. Majak unpublished results). Bufadienolides are also associated with the poison glands of toads (Joubert 1989, Majak and Benn 2000).

It is generally accepted that the Na^+-K^+-adenosinetriphosphatase in cardiac muscle is the major pharmacological receptor of cardiac glycosides. Inhibition by cardenolides such as ouabain and digitoxin affects intracellular electrolyte concentrations, resulting in more forceful contractions of the myocardium. Therapeutic at medicinal doses for the treatment of congestive heart failure in humans, they are toxic to domestic herbivores when consumed at the natural concentrations in plants. Sub-acute to acute signs of poisoning in cattle and sheep include restlessness, dyspnea, ruminal atony, frequent urination and defecation, tachycardia, arrhythmia, and ventricular fibrillation. The closely related bufadienolides produced similar signs of poisoning in cattle. All cardiac glycosides may be regarded as highly toxic (Joubert 1989, Majak and Benn 2000).

Various treatments for cardiac glycoside poisoning in humans and livestock have been reviewed (Joubert 1989); these include the use of activated charcoal, potassium chloride, atropine, digoxin-specific antibodies, ß-adrenergic blocking agents, procainamide and phenytoin.

Saponins

Saponins are glycosidic conjugates of triterpenes. The name derives from their soap like property of forming stable foams when shaken in dilute aqueous solutions. They are also noted for their ability to hemolyse red blood cells, even at high dilution. Historically, *Medicago sativa* L. (alfalfa) and *Dioscorea* species (yams) have been recognized as rich in saponins but they are widely distributed throughout the plant kingdom, to the point that they appear to be ubiquitous. In spite of their wide distribution, only a small number of species contain saponins that are toxic to mammals (Cheeke 1998). This has been attributed to their negligible degree of absorption from the gastrointestinal tract. There appears to be a growing list of saponin-containing forages that are implicated in hepatogenous photosensitization of livestock, with sapogenins being detected as crystals in obstructed bile ducts (Cheeke 1998).

The toxic saponin effect is usually initiated by interaction with mucosal membranes, causing permeability changes or loss of membrane-bound enzymes (Oakenfull and Sidhu 1989). Lysis of the mucosal cell membranes results in intestinal lesions and severe gastroenteritis. Under these conditions, saponins may be absorbed from the gastrointestinal tract and produce systemic effects such as liver damage, respiratory failure, violent convulsions, and coma. The ability of saponins to disrupt and lyse cell membranes enhances their activity when given intravenously. Saponins are also antinutritional factors in swine and poultry feeds such as alfalfa (Cheeke 1998). The adverse effects of saponins have been reversed by the inclusion of dietary cholesterol, presumably because saponins form insoluble complexes with cholesterol or they perturb cholesterol-containing micelles (Oakenfull and Sidhu 1989).

Glucosinolates

The glucosinolates, precursors of organic isothiocyanates (mustard oils) are mainly constituents of members of the Brassicaceae (Cruciferae), but they are also found in other smaller tropical families. Some glucosinolate breakdown products are goitrogenic agents that cause hyperplasia and hypertrophy of the thyroid gland. Two types of goitrogens are derived from glucosinolates, which act on the thyroid gland in different ways. The thiocyanate ion, the less potent of the 2, is derived from the breakdown of alkyl isothiocyanates or indole isothiocyanates. It inhibits uptake of inorganic iodide by the thyroid gland, apparently in a competitive way since the inhibition can be reversed with iodide supplements. The cyclic thiouracils, such as goitrin, are derived from the hydrolysis of glucosinolates containing a ß-hydroxyl substituent. Goitrin and other thiouracil analogues interfere with tyrosine iodination and the coupling reactions that sythesize thyroxine or triiodothyronine, and their effects cannot be reversed. Antithyroid drugs are available for the treatment of hyperthyroidism; these include methimazole, propylthiouracil, and such other antithyroid drugs as the sulfonamides, amphenone, and chlorpromazine (Fenwick et al. 1989).

Ingestion of mustard (*Brassica* spp.) seeds by cattle and the release of mustard oils can result in lesions in the gastrointestinal tract including profuse edema of the forestomachs and abomasum and mucosal necrosis and hemorrhage of the cecum and colon. In addition to the isothiocyanates, episulfides, thiocyanates and nitriles also are produced during autolysis of glucosinolates. Allylthiocyanate is formed during stinkweed (*Thlaspi arvense* L.) autolysis, and the irritant oil may cause severe gastric distress. Nitriles having pancreatotoxic and nephrotoxic effects can be generated during the autolysis of *Brassica* species and other crucifers (Majak 1992, Majak and Benn 2000).

Diterpenoid glycosides

The 1970-1980 decade saw the isolation and characterization of hypoglycemic agents from species of the Compositae such as *Atractylis*, *Xanthium* (cocklebur), and *Wedelia*. The toxic diterpenoid glycosides from these sources were respectively named atractyloside, carboxyatractyloside, and wedeloside. These glycosides can block the mitochondrial ADP/ATP energy-carrier system and the resultant cellular dysfunction is characterized by inhibited oxidative phosphorylation, accelerated anaerobic glycolysis, lactate production, and glycogenolysis. Clinical signs of poisoning in livestock include acute depression, weakness, and convulsions, and the accompanying pathologic changes include nephrosis, gastric irritation, hepatic necrosis, and marked hypoglycemia (Cole et al. 1989). A current and comprehensive review on the biochemistry and toxicology of atractylosides is available (Obatomi and Bach 1998).

Bracken glycosides

Poisoning of cattle by bracken (species of the fern *Pteridium*) had been suspected for many years, but the first report of lesions in experimental animals on a diet including bracken did not appear until 1965, when rats were found to develop cancers. Another 18 years passed before the carcinogenic agent was isolated and identified as the sesquiterpene glycoside ptaquiloside. Ptaquiloside and several analogues have since been isolated from other ferns. The prominent feature of "bracken poisoning" in cattle is depressed bone marrow activity that results in leukopenia, thrombocytopenia, and hemorrhages of the urinary bladder that give rise to hematuria. Ptaquiloside is apparently transferred to cows' milk, and could pose a human health hazard (Hirono 1986, 1989). Bracken also contains the enzyme thiaminase, which can induce polioencephalomalacia in monogastric animals and ruminants (Chick et al. 1989, Cheeke 1998).

Calcinogenic glycosides

Pathological calcinogenesis, *calcinosis*, refers to the deposition of calcium salts in soft tissues. A causative link between the ingestion of *Solanum glaucophyllum* Desf. *(S. malacoxylon* Sm.*)* and the incidence of a calcinotic disease of livestock in Argentina and Brazil was suspected for some time, as it was for *Cestrum diurnum* L. in Florida and *Trisetum flavescens* (L.) Beauv. in the European alps. An isolation of the biologically active fraction from *S. glaucophyllum*, treated with ß-glucosidase, released calcitriol (1α, 25-dihydroxy vitamin D_3). Subsequently, vitamin D_3 and its 25-hydroxy and 1α,24,25-trihydroxy derivatives were also found. The calcinogenic glycosides of *C. diurnum* and *T. flavescens* also proved to be derivatives of vitamin D_3 (Weissenberg 1989, Majak and Benn 2000).

Dietary or endogenous vitamin D_3 is hydroxylated at C_{25} and stored in the liver. It is activated further in the kidney by hydroxylation at C_1. This active form is required for the synthesis of calcium carrier proteins involved in the transport of the cation from the intestine under conditions of calcium deprivation. It is this dihydroxylated active form of vitamin D_3 that occurs in glycosidic forms in *Solanum glaucophyllum* and *Cestrum diurnum*. Consequently, consumption of this exogenous form of vitamin D_3 results in excess absorption of calcium and phosphate from the intestine leading to calcification of soft tissues. Symptoms of calcinogenesis in both livestock and laboratory animals have been reviewed comprehensively (Weissenberg 1989).

Phenolic glycosides

A very large number of phenolic glycosides have been isolated from plants, and their aglycones exhibit considerable structural diversity and biological activity. There is evidence to suggest that the phenolic glycosides of plants provide a defense against herbivorous insects but only a few are regarded as dangerously toxic to mammals. In most cases, the toxic agents have been identified as the phenolic aglycones. Classic examples include the isoflavonoid daidzein and formononetin, found in subterranean clover (*Trifolium subterraneum* L.*)*, and coumestrol, which occurs in alfalfa *(Medicago sativa* L.). Both of these phytoestrogens induce abortions in sheep. Reproductive problems were first encountered over 50 years ago with the establishment of subterranean clover on pastures in western Australia. A dramatic decrease in the fertility of sheep was noted. The failure to conceive was attributed to a change in the viscosity of the cervical mucus and the resultant impaired passage of spermatozoa. The condition was accompanied by cystic glandular hyperplasia of the cervix and uterus and lactation in nonpregnant ewes and wethers. Clinical signs of reproductive disorders diminished with the introduction of new cultivars of clover that were low in formononetin, but a temporary infertility still prevailed among ewes exposed to phytoestrogen-containing pastures. Reproductive disorders on alfalfa pastures usually are associated with increases in coumestrol concentrations resulting from fungal infections, often referred to as a phytoalexin response. Coumestrol and related coumestans decrease the ovulation rate in ewes. There is no satisfactory explanation for the reduced susceptibility of cattle as compared to sheep to the effects of phytoestrogen-containing pastures. Immunological approaches for the prevention of phytoestrogenic disorders have been partially successful under experimental and field conditions (Adams 1989).

Melilotoside, coumarinic acid ß-D-glucoside, is the bound form of coumarin that can be found in high concentrations in sweet clover (*Melilotus* spp.). Sweet clover poisoning is associated with moldy hay or silage where enzymes of fungal origin metabolize coumarin to dicoumarol, a potent anticoagulant. Dicoumarol interferes with the synthesis of thrombin, which is required for fibrin formation and blood clotting. Signs of poisoning in cattle include lethargy, anemia, and the development of subdermal swelling in reponse to internal hemorrhaging, which is the cause of death (Kingsbury 1964). The induced deficiency can be ameliorated with increased vitamin K, especially vitamin K_1 given intramuscularly (Alstad et al. 1985). “Low coumarin” cultivars of sweet clover are available but “high coumarin” *Melilotus* persists in pastures and as a weed.

Ranunculin

The recognition that chewing the fresh leaves or blossoms of buttercups released a vesicant substance must be prehistoric. The toxin has been identified as the unsaturated ϒ-lactone protoanemonin (5-methylene-2-oxodihydrofuran), but the storage form of this unstable compound remained in doubt until recently when the parent ß-D-glucoside was re-isolated by different extraction protocols and identified as ranunculin (Bai et al. 1996). Ingestion of the plant material can cause gastric distress, including irritation of the digestive tract, abdominal pain, and diarrhea. When *Ceratocephalus testiculatus* Crantz. (bur buttercup) was given to sheep, clinical signs of poisoning included weakness, depression, tachycardia, dyspnea, anorexia, diarrhea, and sometimes fever (Olsen et al. 1983). Ranunculin has been obtained from numerous species of the buttercup family (Ranunculaceae) (Bai et al. 1996). The purified glycoside is a substrate for ß-glucosidase which can release the aglycone; however, during the autolysis of ranunculin-containing forages, protoanemonin is released and not the aglycone. Two competing reactions occurred in rumen fluid when *Ranunculus cymbalaria* Pursh. was incubated in vitro: microbial hydrolases yielded the aglycone and the endogenous plant enzyme yielded protoanemonin (Majak et al., unpublished data). This is another example where the release of the toxic metabolite, protoanemonin, is contingent upon the specific activity of endogenous plant enzyme.

Cycasin

Two distinct field diseases have been recognized in livestock poisoning by cycads and zamias. One is a neurotoxic syndrome characterized by ataxia and permanent weakness of the hindquarters. A rare amino acid was implicated but others have excluded this agent (Charlton et al. 1992). The second syndrome is a hepatic and gastrointestinal disease attributed to cycasin, methylazoxymethanol-ß-D-glucoside (Hooper 1983). Acute cycasin toxicity in sheep and cattle is characterized by hepatitis, gastroenteritis, hemorrhages, and liver cirrhosis. In chronic poisoning, animals lose appetite and develop mild liver cirrhosis and nephrosis. The labile aglycone is the lethal metabolite.

In summary, 11 classes of toxic glycosides have been examined in this review. Bioactivation and toxicity of the glycosides mainly depend on 1) the rate of release of the aglycone by rumen microbes, 2) the rate of detoxification of the aglycone, and 3) the degree of absorption of the aglycone from the gastrointestinal tract. Plant enzymes may also be involved in the mode of action of toxic glycosides. Clearly, these results indicate that the rumen ecosystem is the first line of defense and it should be further exploited for pathways of detoxification.

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Book Review

The New Ranch Handbook: A Guide to Restoring Western Rangelands. By Nathan F. Sayre. Edited by Barbara H. Johnson. 2001. The Quivira Coalition, 551 Cordova Road, #423, Santa Fe, New Mexico 87501, USA. 102 + x p. US$10.00 (+ 3.00 S&H) paper. ISBN 0-9708264-0-0.

Western cattle producers are in chronic economic trouble and some extreme environmentalists are demanding total removal of livestock from arid and semiarid public rangelands. Yet there are many examples where ranchers, range managers, and conservationists are working together to produce livestock while simultaneously sustaining and restoring rangelands and rural communities.

The Quivira Coalition (http://www.quiviracoalition.org) is a New Mexico based organization of producers, agency range managers and environmentalists dedicated to promoting sustainable ranching and "sharing common-sense solutions to the rangeland conflict." They call this stance the "New Ranch." Their first major publication, *The New Ranch Handbook* by Nathan Sayre, is intended to describe the management practices that have improved economic and ecological sustainability in the Southwest, to place these in a scientific framework, and in so doing to offer a common vocabulary for, and increase awareness of the complexity of, sustainable grazing management.

The book is organized around 6 concise case studies of innovative cattle producers, each followed by chapters outlining the basic ecological processes which sustain the range livestock operation. Although Sayre states that half of the ranchers use short-duration grazing (SDG) and half use rest-rotation grazing, it is clear from the text that none uses rest-rotation as developed by Gus Hormay; all 6 use some form of intensive rotational grazing during the growing season, with longer grazing periods in the dormant season.

Sid Goodloe, the first holistic range manager in the U.S., has doubled the carrying capacity of his ranch near Capitan, N. M., through a combination of chaining junipers, prescribed burning, and SDG in the growing season. He stocks his ranch conservatively (slightly less than the official carrying capacity) with moderate size "Alpine Black" (3/4 Black Angus and 1/4 Brown Swiss) cattle. The breeding season is matched to peak forage conditions, and weaning is timed to occur before the first frost reduces the nutritional quality of the forage.

David Ogilvie (Silver City and Gila, N.M.) uses a combination of SDG and high intensity-low frequency grazing tactics during the growing season, such that each of his 18 pastures receives nearly yearlong rest and goes to seed every year. He has also implemented a small-scale burning program to control piñon-juniper encroachment into grasslands. The U Bar Ranch now boasts the largest concentration of endangered Southwestern willow flycatchers in the U.S. No information on stocking rates or cattle herd management is provided.

John and Mac Donaldson manage the Empire Ranch, most of which is on the BLM's Empire-Cienega National Conservation Area near Sonoita, Ariz. They practice flexible rotational grazing with long rest periods, and control distribution by manipulating access to water. They purchase all replacement heifers and run yearling stockers in years of high forage production to keep stocking rates conservative and very flexible (600–1,400 head). Recreation management is replacing grazing management as the most difficult planning issue.

Roger Bowe (San Jon, N.M.) switched from continuous grazing to SDG in response to poor distribution and slowly declining production. With an intensive, 62-pasture rotation, distribution has improved and stocking rate has more than doubled. Bowe reports that less labor is required, variable cost per lb of beef has decreased by > 50%, and net annual income per acre has tripled. Unfortunately the analysis does not include the sunk cost of the initial capital improvements. Bowe also employs a monitoring system tailored to his operation. No information on cattle herd management is provided.

Jim Winder also practices management-intensive SDG, on semiarid desert grassland near Nutt, N.M. With 66 pastures divided by electric fences, and moving his herd every one to three days during the growing season, Winder has doubled his stocking rate to well over the official carrying capacity. He is able to stock flexibly with a cow-calf-yearling operation; on average he maintains a herd of 60% mother cows and 40% stockers. Both the range (especially the riparian areas, which are grazed mostly in the winter and only for short periods) and the cattle are in substantially better condition than they were prior to implementing planned, controlled grazing. Winder plans for drought every year by making stocking decisions at the beginning of the dormant season and throughout the year, rather than at the beginning of the growing season.

Jim Williams (Quemado, N.M.) recently implemented planned rotational grazing and monitoring on his Cibola National Forest allotment, such that every pasture receives 90 days of rest during the growing season. Conditions have improved dramatically, especially along the Largo Creek riparian corridor. Relations with the Forest Service have also improved, and Williams is hopeful that a 1995 stocking rate reduction will be restored. No information on herd management is provided.

Chapter 1, "Ranching as Sustainable Agriculture," explains that grazing is a disturbance and that rangelands must be resilient to disturbance if grazing is to be sustainable. The discussion on disturbance stops just short of internalizing the idea in the larger concept of the ecosystem. Rangeland ecosystems are highly variable, and exhibit nonlinear dynamics and qualitative differences across scales; thus the linear tools of historic range management (estimates of carrying capacity, utilization, and range condition) are inadequate for large-scale management because they assume that the whole is simply the sum of the parts. Sayre suggests that a new view of grazing that focuses not simply on condition and trend but on the basic ecological processes underlying plant and animal production is necessary to avoid problems of scale.

Chapter 2 examines "Grazing as a Natural Process" to which forage plants and herbivores have adapted. In a short discussion of the debate over compensatory growth in response to grazing, Sayre concludes that compensation is more likely at larger scales (plant communities) and over longer (successional) timeframes– the scales most important to management. There is no distinct difference between “natural” and “unnatural” herbivory, except that the former is less likely to be characterized by sedentary, highly selective grazers. Grasses tolerate defoliation, but recover faster when more leaf area remains. The grazing disturbance needs to be understood and managed in terms of timing, frequency, and intensity.

Chapter 3, “The Spatial and Temporal Distribution of Water and Nutrients,” discusses how nutrient and especially water cycles affect plant community persistence. Total precipitation is not as important as the effectiveness of the precipitation. The more water retained in the soil, the more resilient is the system. Where soils are stable and watersheds are properly functioning, the potential for long-term sustainable livestock production is high.

Chapter 4, “Thresholds and Monitoring,” revisits the nonlinearity of ecological processes. Understanding state and transition models of vegetation change and patch dynamics is important for the appropriate use of the tools of timing, frequency, and intensity of grazing to maintain or enhance long term forage and livestock production. Because the crossing of thresholds leads to self-reinforcing changes, monitoring is critical to gauging the success of management strategies. Monitoring is a way of measuring ecological processes indirectly: litter cover as an indicator of nutrient cycling, and bare ground or total cover as an indicator of the water cycle. Body condition score is an important index of cattle herd nutrition and production, but not necessarily of vegetation trend because animals may continue to perform satisfactorily after ecological conditions begin to deteriorate. Monitoring must be consistent, practicable, and related to management goals; it is no longer optional but a cost of doing business. For technical assistance in designing a monitoring program, the reader is directed to the *Monitoring Manual for Grassland, Shrubland and Savanna Ecosystems* developed by scientists at the Jornada Experimental Range in 2000.

Chapter 5, “New Ranch Management,” discusses the application of the concepts developed previously to sustainable livestock production. The profiled ranchers have combined scientific knowledge with insights gained from living and working on the land—the integration that distinguishes sustainable range management as an art as well as a science. Sayre acknowledges that there is no scientific “proof” of the superiority of any one management program, including SDG, but points out that all 6 ranchers control timing, frequency, and intensity with frequent moves, high numbers of pastures, and rest periods sufficient for recovery. The ranchers with the highest management intensity (Bowe and Winder) also have the highest stocking rates. The ranchers manage their cattle in a single herd (or 2 herds to separate replacement heifers from mature cows). Distribution is controlled with fences, access to water, mineral blocks, and herding with low-stress livestock management methods. The ranchers all plan extensively, especially for drought. In years of high forage production they hold over some calves, run stockers, lease pastures, or engage in prescribed burning.

Chapter 6 discusses “Making the Leap” to New Ranch management. Sayre advises ranchers considering substantial changes to begin by examining their goals and then considering the resources of the current operation. Planning is the hard part. Grazing managers must find ways to work with natural processes, not against them; and most importantly, they must manage for the whole rather than just a few parts.

The Conclusion admonishes the reader to “Find and expand the radical center.” Both extremes in the rangeland conflict are wrong; reasonable people who set their differences aside and collaborate to develop shared visions can effect successful, on-the-ground management that benefits all involved. Stewardship is a bottom-up social process as well as an ecological one.

This book is by no means a complete treatise on sustainable livestock production in the arid and semiarid West. The articulation of grazing impacts in terms of timing, frequency, and intensity focuses on temporal aspects to the exclusion of the spatial dimension. It does not focus on matching cattle breeds to the harsh and variable conditions of rangeland environments, or timing the annual livestock production cycle of calving, breeding, weaning and sale to forage conditions, or nutritional management. Without discussion of livestock management *per se*, the book falls somewhat short of a truly holistic approach. That the author is an anthropologist and not a range or animal scientist shows, but it also frees the book of traditional professional worldviews. The book is a primer of modern range science, with a minimum of esoteric jargon, and as such is a valuable introduction to sustainable grazing land management for conservationists, range managers, and especially cattle ranchers. The synthesis and application of older and more recent ideas is indeed new and continually evolving. It is especially important that it comes from within the livestock community. The ranches profiled in *The New Ranch Handbook* demonstrate that livestock grazing can be ecologically and economically sustainable, compatible with native biodiversity, even on Western rangelands that receive less than 12 inches of rain per year. Perhaps the book’s greatest contribution is that it suggests a systems approach of planned yet adaptive management, responsive to opportunities and synergisms, that fosters productive and resilient rangelands and ranching operations.—*Matthew K. Barnes*, Utah State University, Logan, Utah.

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